Gradient analysis of reversed treelines and grasslands of the Valles Caldera, New Mexico

Coop, Jonathan D.[1*] & Givnish, Thomas J.[1,2]

[1]*Department of Botany, University of Wisconsin Madison, Madison, WI 53706, USA;* [2]*E-mail givnish@wisc.edu;*
[*]*Corresponding author; Fax +1 5056721073; E-mail jonathancoop@hotmail.com*

Abstract

Objective: Treeless meadows and parks are widespread but poorly understood features of the montane vegetation of the western USA. These communities frequently form reversed treelines where grassy valleys occur below forested slopes above. Our purpose was to assess the environmental correlates of such treelines, as well as patterns in the composition and diversity of grasslands and forest margins in the Valles Caldera National Preserve.

Location: Valles Caldera National Preserve (35°50'-36°00' N, 106°24'-106°37' W, 2175-3150 m), Jemez Mountains, New Mexico, USA.

Methods: We conducted a gradient analysis based on 200 nested quadrats on transects crossing reversed treelines and spanning the compositional heterogeneity of grasslands. We used cluster analysis and non-metric multidimensional scaling to assess relationships between compositional variation and environmental variables.

Results: We found strong, highly significant relationships of the vegetation to gradients in slope inclination, soil texture, moisture, nutrient availability, and nighttime minimum temperatures. Reversed treelines are most strongly associated with shifts in the thermal regime, exhibit weaker relationships with soil texture and nutrient content, and show no relationship with gravimetric soil moisture. Gradients in aspect, soil moisture, and annual mean temperature are associated with compositional variation within grasslands and forest margins.

Conclusions: Lower nightly minimum temperatures and fewer consecutive frost-free days resulting from cold-air drainage may prevent tree seedling establishment in valley bottoms via photo-inhibition, tissue damage, or frost heaving. Fine-textured soils may also impede tree seedling establishment in valley bottoms. These findings lay the groundwork for experimental and physiological tests of these potential causes of these reversed treelines.

Keywords: Ecotone; Inverted timberline; Jemez Mountains; Meadow; Non-metric Multidimensional Scaling; Ordination; Park.

Nomenclature: Hartman & Nelson (2005); Anon. (2006)

Abbreviations: NMS = Non-metric Multidimensional Scaling; VCNP = Valles Caldera National Preserve.

Introduction

Montane and subalpine grasslands are important features of the southern Rocky Mountain region of the United States, though the causes of their occurrence in an otherwise forested landscape are not well known (Dick-Peddie 1993; Brown 1994; Peet 2000). These communities are commonly known as meadows or parks, or by the Spanish term *valles* in high-elevation valleys of northern New Mexico. They contribute to floristic diversity (Ramaley 1927; Peet 1981; Stohlgren et al. 1997), provide critical habitat for animals ranging from butterflies (Simonson et al. 2001) to elk (*Cervus elaphus*) (Boyce & Hayden-Wing 1979) and often benefit local economies through livestock grazing and recreation (Turner & Paulsen 1976). Grasslands in the southern Rockies have been the focus of few quantitative studies, except for early descriptions of Boulder Park, Colorado (Rydberg 1913; Reed 1917; Robbins 1918; Ramaley 1927) and more recent work by Moir (1967) and Allen (1984) on high-elevation, grassy balds in the Sierra Blanca and Jemez Mountains of New Mexico. Moreover, the causes of the treeline ecotones that define these grasslands – and the existence of these grasslands in an otherwise forested landscape – are unknown, although they have been the subject of considerable discussion.

Throughout the southern Rocky Mountain region, grasslands often occur on level or shallowly-sloping topography in valley bottoms (Ramaley 1927; Turner & Paulsen 1976; Brown 1994; Peet 2000), and form abrupt, reversed treelines with forested mountain slopes above. Hypotheses proposed to account for this pattern include the effects of *edaphic factors*, *moisture limitations* or *excesses*, and *thermal conditions* on tree establishment or growth. Meadows and parks are frequently associated with fine-textured soils in the southern Rocky Mountains (Ramaley 1910, 1927; Daubenmire 1943; Peet 1981, 2000; Veblen & Lorenz 1986). Heavy soils have been proposed to directly impede root penetrance by tree seedlings in parks (Daubenmire 1943). The increased moisture-holding capacity and nutrient availability of fine-textured soils has been hypothesized to promote such

a dense growth of grasses that tree seedling establishment is prevented by competition (Ramaley 1910, 1927; Peet 1981, 2000). Other researchers have proposed that soil drought (Doering & Reider 1992; Koterba & Habeck 1971) or, conversely, waterlogging (Ives 1942; Rydberg 1913) maintains high-elevation grasslands in valleys in the Rockies. Finally, cold-air drainage has been the favored explanation for analogous grasslands in concave basins in the mountains of Australia and New Zealand (Wardle 1971; Moore & Williams 1976; Paton 1988), where the term 'inverted treeline' or 'inverted timberline' is widely used to describe the shift from grassy basins to forested slopes. However, grass competition (Fensham & Kirkpatrick 1992) and waterlogged soils (Gilfedder 1988) have also been proposed as causes of treelines in these systems. Grassy openings in the Rockies also occur on steep, south-facing slopes and mountain tops, where fire (Langenheim 1962; Allen 1984) or reduced soil depth and moisture availability (Rydberg 1913; Moir 1967; Daubenmire 1968) are thought to be responsible.

Our objectives are to (1) characterize the previously undescribed grasslands and forest-grassland ecotones in the Valles Caldera National Preserve; (2) relate variation in grassland and forest edge composition to environmental factors; and (3) determine whether the position of the reversed treelines can best be predicted from soil texture, soil moisture, temperature, or other variables. We focus especially on the abiotic factors that may determine treeline position, but also examine ecological correlates of diversity, dominance, and compositional variation within both forests and grasslands.

Study area and Methods

Study area

All measurements were made within the Valles Caldera National Preserve (VCNP, 35°50'-36°00' N, 106°24'-106°37' W) in the Jemez Mountains of northern New Mexico (Fig. 1). The caldera itself is a 24 km-wide basin formed by volcanic eruptions and the subsequent collapse of the underlying magma chamber ca. 1.22 Ma. The VCNP contains ca. 10 000 ha of montane grasslands, primarily in the valley bottoms of the caldera floor 2575-2700 m elevation (Fig. 1). Grasslands also occur in minor valleys and drainages across a wider range of elevations, and on some upper mountain slopes above ca. 3000 m.

Rock types of mountain slopes are ignimbrite and rhyolite; the caldera floor is underlain by a combination of alluvial and lacustrine sediments (Smith et al. 1970). The climate is semi-arid and continental. No long-term climatological data exist for the VCNP, but mean annual precipitation is probably slightly higher than the 57.6 cm recorded at the nearest climate station at Wolf Canyon, NM (35°57' N, 106°45' W; 2506 m elevation, 50-year mean 1954-2004). May and June are the driest months (3.4 and 3.0 cm precipitation) and July and August are the wettest (8.6 cm for both). At Wolf Canyon, mean monthly high and low temperatures for January are 3.4 °C and -13.5 °C; for July, they are 24.9 °C and 5.7 °C. During the two years of this investigation, 2001 and 2002, precipitation at Wolf Canyon was 16% and 18% below the 50-year mean.
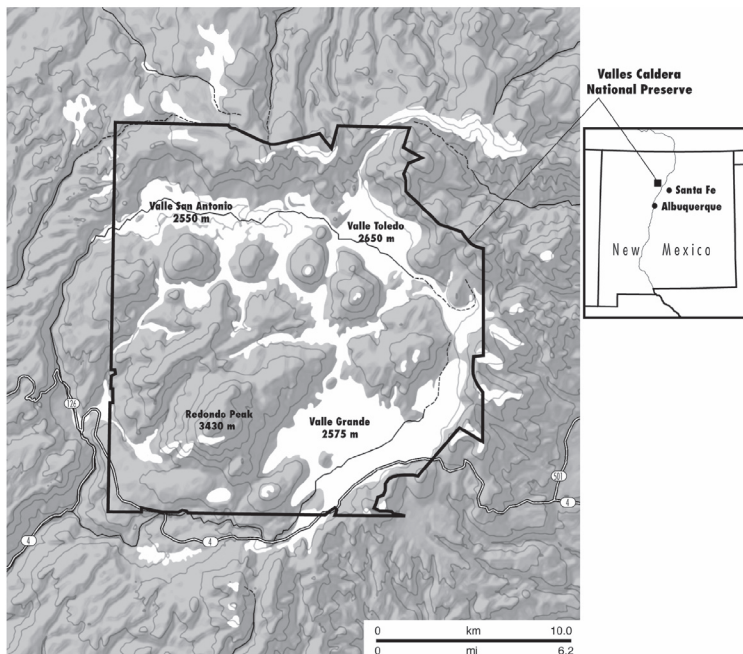
Fig. 1. The Valles Caldera National Preserve (VCNP) in the Jemez Mountains, New Mexico. White indicates grassland vegetation, grey indicates forest.

The area occupied by the VCNP was a privately-owned ranch from 1860 until 2000, and subjected to periods of intensive grazing and logging operations throughout that period (Martin 2003 and sources cited therein). Elk, which were extirpated from the Jemez Mountains toward the end of the 19th century, were re-introduced in 1947; the population is currently estimated between 4000 and 8000. These factors, as well as fire suppression both direct and indirect – e.g. the cessation of frequent surface fires ca. 1890 due to removal of grassy fuels by heavy livestock grazing (Touchan et al. 1996) – have undoubtedly resulted in some changes in composition, structure, and functioning of ecological communities, but the extent of these changes is uncertain. Historic photos (Hogan & Allen 1999) indicate recent encroachment of forests into grasslands at some locations in the Valles Caldera. In 2000, most of the Valles Caldera was transferred to public ownership in the 36000-ha VCNP.

Sampling methodology

Data on plant community composition, community structure, and environmental factors were collected in 2001 and 2002 in 200 quadrats dispersed in a spatially stratified, hierarchical design. Each quadrat was 5 m × 20 m. Because our main objective was to characterize vegetation-environment relationships across treelines, most quadrats were placed along transects crossing forest-grassland ecotones, stratified spatially as follows. First, boundaries between forest and grassland were identified on the 7.5' USGS topographic quadrangles that cover the VCNP. Second, treeline boundaries were divided into 20 sections of roughly equal length, and one transect was randomly located in each section; 18 of these transects were ultimately sampled. Third, on each side of the treeline (defined by a generally abrupt shift from open communities to those with > 50% cover by trees), equal numbers of quadrats were placed at exponentially increasing distances from the ecotone, with the long axis of each quadrat perpendicular to the transect. On 12 transects, eight quadrats were placed at 5, 20, 50, and 110 m on either side of the ecotone; on six transects, four quadrats were sampled at 20 and 110 m from the ecotone. Finally, to sample the compositional heterogeneity of grasslands more completely, we extended sampling further into the valleys. We added 40 quadrats by lengthening several transects, sampling at increments of 60 m. Another 40 quadrats were subjectively placed in infrequently encountered plant assemblages.

In each 100-m^2 quadrat, the total basal area, density, and mean and maximum height of each tree (≥ 2.5 cm DBH) species were tallied. Percent cover of tree seedlings (< 2.5 cm DBH) and shrubs was visually estimated in five 9-m^2 (3 m × 3 m) subquadrats spaced at regular intervals inside each quadrat. Herbaceous species cover was visually estimated in five 1-m^2 plots nested in the center of each 9-m^2 subquadrat, using the following classes: 0% (absent), 1%, 2-3%, 3-6%, 6-10%, 10-15%, 15-20%, and at increments of 10% up to 100%. Mean cover of each tree-seedling, shrub and herbaceous species was calculated across the sub-samples within each quadrat. Shrub and herb species present within the 100-m^2 quadrat but outside of the sampled subquadrats and plots was scored as 0.2% for the quadrat. Herb cover was censused in August when most species reached their maximum coverage. Tree canopy cover was estimated above the center of each subquadrat using a densiometer. To estimate the percent cover by each tree species for a given quadrat, we multiplied the mean percent canopy cover by the proportions of the total basal area accounted for by each tree species present. Vouchers specimens for all herb and shrub species were deposited in the Wisconsin State Herbarium.

Environmental data sampled in the center of each quadrat included slope inclination and aspect (using a compass and a clinometer), and spatial position (UTM *x*, UTM *y*, and elevation, using a hand-held GPS unit with 15-m resolution [Garmin, Olathe, KS]). Limitations of time, funding, and access made it impossible to measure all remaining environmental variables in every quadrat. These variables were sampled in partially overlapping subsets of the 200 quadrats (Table 1). Three soil cores (2.5 cm diameter, 0-15 cm depth) collected from the center and ends of each quadrat were pooled for texture analysis using a modified hydrometer method (Day 1965) for 150 quadrats. Soil samples were sieved to remove the coarse fraction, heated with H_2O_2 to remove organic matter, and soaked for 12 hours in an NaHMP (sodium hexametaphosphate) solution to increase particle dispersion before testing.

For 32 of these soil cores, a series of macronutrient concentrations (available P; exchangeable K, Ca, and Mg; total N), pH, and % organic matter were measured by the University of Wisconsin Soils and Plant Tissue Analysis Laboratory, using techniques summarized in Table 1. Soil temperatures at 50 cm depth were sampled at the center of 60 quadrats during August 2001. Soil moisture was measured at three-week intervals during the 2002 growing season, between 1 June and 1 September, using gravimetric analysis of soil cores collected to a depth of 15 cm. Soil moisture was sampled at 64 sites corresponding to quadrats at 20 and 110 m from the ecotone on 13 transects (52 sites); at five other locations in valley bottom meadows chosen to include a broader range of grassland compositional variation; and seven additional mountain slope locations where timber-harvest units and large canopy gaps facilitated an examina-

Table 1. Environmental variables measured.

Variable	Code	N	Sampling methodology	Transformation
Spatial location (x,y)	Space	200	UTM x,y GPS reading (meters)	None
Elevation	Elev	200	GPS reading (meters)	None
Slope	Slope	200	Clinometer reading across steepest reach of quadrat (proportion)	ln
Aspect	Aspect	200	Compass bearing (degrees)	$-\cos(\text{degrees}-45°)$
Coarse fraction	Coarse	150	Oven-dry mass coarse fraction/ oven dry mass sand + silt + clay (proportion)	ln
Sand	Sand	150	Modified hydrometer method (proportion dry mass)	$2/\pi * \arcsin(\text{squareroot})$
Silt	Silt	150	Modified hydrometer method (proportion dry mass)	$2/\pi * \arcsin(\text{squareroot})$
Clay	Clay	150	Modified hydrometer method (proportion dry mass)	$2/\pi * \arcsin(\text{squareroot})$
pH	pH	32	pH meter; soil pH in water using a 1:1.3 soil:solution ratio $(-\log[H^+])$	None
Organic matter	OM	32	Loss-on-ignition (360°C for 2 hours) (proportion dry mass)	ln
Available P	P	32	Acid extraction (0.002 $\underline{M}$ sulfuric acid) (ppm)	ln
Exchangeable K	K	32	Extracted in 1 $\underline{M}$ NH$_4$OAc at pH 7.0 (ppm)	ln
Exchangeable Ca	Ca	32	Extracted in 1 $\underline{M}$ NH$_4$OAc at pH 7.0 (ppm)	None
Exchangeable Mg	Mg	32	Extracted in 1 $\underline{M}$ NH$_4$OAc at pH 7.0 (ppm)	None
Total N	N	32	(Org N + NH$_4$-N + NO$_3$-N, NO$_2$-N) digested with sulfuric acid, metal catalyst, salicylic acid (ppm)	ln
Soil moisture	SoilH$_2$0	64	Mean value of gravimetric moisture content; sampled every 3 weeks June-August 2002 (proportion dry mass)	ln
Soil moisture Standard deviation	SDH$_2$0	64	Standard deviation of gravimetric moisture content, 3 soil cores 15 cm depth pooled for each quadrat; sampled every 3 weeks June-August 2002 (proportion dry mass)	ln
Soil temperature	Soiltemp	60	50 cm depth at center of quadrat, August 2001 (degrees C)	None
Weekly minimum air temperature (June-Aug)	JJA lowtemp	28	Mean of minimum air temperatures recorded each week June-August 2002, 15 cm above ground surface, using a combination of max/min thermometers (16) and dataloggers (12) (degrees C)	None
Mean air temperature (June-Aug)	JJA meantemp	12	Mean air temperature, 15 cm height, June-August 2002, using dataloggers (degrees C)	None
Annual mean air temperature	Yrmean temp	12	Mean air temperature, 15 cm height, June 2001-June 2002, using dataloggers (degrees C)	None
Days between 0°C	Days btwn 0°C	12	Longest period between air temperatures of 0°C, June 2001-June 2002 (days)	None
Days between –5°C	Days btwn -5°C	12	Longest period between air temperatures of -5°C, June 2001-June 2002 (days)	None

tion of the effect of landform position on soil moisture independent of the potentially confounding effect of the forest canopy. Growing-season air temperatures in 2002 were measured from 1 June to 1 September, using a combination of max/min thermometers (reset weekly) and thermistor readings (weekly maximum and minimum resampled from temperatures measured at 0.5-hour intervals) using 12 single channel dataloggers (Hobo Pro Temp, Microdaq.com, Ltd., Warner, NH) at 15 cm above the ground surface at 28 sites. Thermometers and dataloggers were protected from direct sunlight using white plastic radiation shields. Twenty-one of these were quadrats at 20 or 110 m on either side of the ecotone; the remaining seven sites were in adjacent canopy openings, as described above. Data logging of air temperatures continued through 1 July 2003. Environmental measurements were transformed as needed to approximate normal distributions for the purposes of standard parametric tests of significance (Table 1).

Statistical analysis

We characterized the pattern of variation in plant community composition in grasslands and adjacent forest borders using cluster analysis and NMS ordination with overlays of environmental variables. We first conducted a hierarchical, agglomerative cluster analysis using the flexible beta linkage method with $\beta = -0.25$ implemented by PC-Ord 3.0 (McCune & Mefford 1997). We generated the compositional dissimilarity matrix using Sørensen pairwise distances between all 200 quadrats, based on the square-root of coverages by all 206 species. Square-root transformation decreased skewness and kurtosis for each species and increased the effect of sub-dominant species on the dissimilarity matrix. To determine the most ecologically meaningful number of groups for cluster analysis, we used the indicator species analysis method outlined by McCune & Grace (2002). Using this method, the ideal number of groups minimizes indicator species p-values and maximizes the number of significant ($\alpha = 0.05$) indicators.

Using the compositional dissimilarity matrix described above, we ordinated plot data in species space using global non-metric multi-dimensional scaling (NMS) as implemented by PC-ORD 3.0 (McCune & Mefford 1997). To ensure appropriate dimensionality of the final ordination, we assessed declines in the reduction in stress with increasing dimensionality. To find the best solution, we ran the ordination 100 times using random starting coordinates, with a stability criterion of 0.0001. The best (least-stress) solution emerging from this analysis was then used to provide starting coordinates for an additional 100 runs. The best solution resulting from these runs was rotated to maximize the variance explained by the first axis. To explore relationships between ordination axes and measured environmental variables, we used joint plots (PC-Ord method, see McCune & Grace 2002). Vectors representing the strength and direction of correlations were drawn from the centroid of the ordination, with the components of each vector corresponding to the correlation coefficients between each environmental variable and the quadrat scores on each ordination axis. Only environmental variables with a total $r^2 > 0.15$ were plotted.

To evaluate the validity of hypotheses regarding the determinants of treeline position – involving soil texture, grass competition, soil moisture, and air or soil temperature – we also used multiple linear regression to test for significant relationships between predictor variables (soil texture, soil moisture, thermal data, distance from ecotone, and slope aspect) and measures of tree vigor and abundance not represented in our community composition data (mean and maximum height and basal area of each species, total basal area, stand density, and seedling abundance). All regressions were conducted using S-Plus (Insightful Corp, 2001 release).

Results

Vegetation composition

We encountered 206 vascular plant species in 200 quadrats (total sample area = 2 ha) in grasslands and adjacent forests in the Valles Caldera National Preserve (see App. 1).

Plant species richness per 100-m^2 quadrat ranged from 2 to 45, with a mean of 22.2 ± 6.7 (SD) species for grasslands, 18.0 ± 7.3 for forests, and 20.9 ± 7.2 across all quadrats. Grassland quadrats had significantly more species per 100 m^2 ($P < 0.0005$, 2-tailed t-test, $df = 198$). Richness in 1-m^2 subquadrats ranged from 0 to 23 species, with a mean value of 10.4 ± 5.0 for all quadrats. The difference between grasslands and forests was even more pronounced at this level, with 12.3 ± 4.2 species in grasslands and 6.5 ± 4.3 in forests ($P << 0.0001$, 2-tailed t-test with $df = 998$).

Only 14 of the 206 taxa encountered were exotic to the region; however, two of these, *Poa pratensis* and *Taraxacum officinale* were highly abundant, with total coverages across the gradient of 8.8% and 2.5%, respectively. Forest edges were generally dominated by *Pinus ponderosa* (mean cover of 11.0%), or by *Picea pungens* (4.6%). After *Poa pratensis,* the most abundant grassland species were *Danthonia parryi* (6.3%) and *Festuca arizonica* (4.4%). The five most frequent species were *Achillea millefolium* var. *occidentalis* (occurring in 78% of quadrats), *Poa pratensis* (75%), *Taraxacum officinale* (74%), *Potentilla hippiana* (71%), and *Erigeron formosissimus* (58%).

Community classification

Cluster analysis and indicator-species analysis identified nine groups of quadrats that resulted in both the lowest average indicator-species *p*-value and the greatest number of significant indicators. For convenience, we use names for these vegetation-types based on the dominant species (e.g. *Ponderosa Pine*) or, where no species exhibited consistent dominance, we label groups based on general composition or position in the landscape (e.g. *Mixed Conifer*, *Wet Meadows*). Three groups (*Ponderosa Pine, Blue Spruce,* and *Mixed Conifer*) reflect forested communities of mountain slopes. One group (*Aspen Groves and Subalpine Balds*) combines forested and grassy communities generally found at higher elevations on mountain slopes. Five groups (*Arizona Fescue*, *Parry's Oatgrass, Mesic Grasslands*, *Wet Meadows*, and *Sedge Meadows*) represent graminoid-dominated communities of valley bottoms. The three most abundant species, as well as measures of species diversity and richness for each group, are listed in Table 2. Table 3 presents the mean values of several environmental variables for each group.

Ordination and gradient analysis

Non-metric multidimensional scaling produced a 3-dimensional solution (Fig. 2) with a stress value of 14.27 ($p < 0.01$ based on 100 runs with randomized data) and a final instability of 6×10^{-5}. The ordination explained 83% of the variance in the original dissimilarity matrix, with axes 1 and 2 accounting for 38% and 25% of the total, respectively. Groupings identified by cluster analysis segregate well along both axes 1 and 2 (Fig. 2). Axis 1 clearly separates forest from grassland types, and correlates strongly with measures relating to *cold-air drainage* (consecutive days between minimum temperatures below 0 °C [$r = 0.92$] or –5 °C [$r = 0.97$],

Table 2. Groups identified by cluster analysis, with the three most abundant species in each group and mean ± s.d. values for species richness and diversity. Subplot richness is measured in 1-m^2 subquadrats and does not include the tree layer; total plot richness includes all plant species occurring in each 100-m^2 sampling unit.

Group	Dominant species(mean percent cover)	Subplot richness	Total plot richness	Simpson diversity index
Communities of Mountain Slopes				
Subalpine Balds and Aspen Groves	*Festuca thurberi* (36) *Populus tremuloides* (19) *Danthonia parryi* (19)	8.3 ± 3.2	17.7 ± 5.7	0.58 ± 0.19
Mixed Conifer	*Pseudotsuga menziesii* (63) *Abies concolor* (23) *Picea engelmannii* (4)	5.3 ± 5.6	18.8 ±10.8	0.54 ± 0.20
Blue Spruce	*Picea pungens* (63) *Populus tremuloides* (5) *Carex siccata* (3)	5.9 ± 4.6	18.3 ± 8.3	0.60 ± 0.20
Ponderosa	*Pinus ponderosa* (57) *Poa pratensis* (9) *Danthonia parryi* (6)	6.1 ± 3.7	17.1 ± 5.7	0.55 ± 0.19
Communities of Valley Bottoms				
Arizona Fescue	*Festuca arizonica* (20) *Muhlenbergia montana* (9) *Blepharoneuron tricholepis* (7)	13.1 ± 2.8	22.4 ± 3.6	0.88 ± 0.03
Parry's Oatgrass	*Danthonia parryi* (22) *Poa pratensis* (19) *Taraxacum officinale* (5)	13.2 ± 3.4	26.5 ± 5.8	0.77 ± 0.17
Mesic Grasslands	*Blepharoneuron tricholepis* (11) *Festuca idahoensis* (10) *Poa pratensis* (8)	12.9 ± 3.5	22.2 ± 4.4	0.86 ± 0.09
Wet Meadows	*Poa pratensis* (12) *Deschampsia caespitosa* (11) *Carex pellita* (10)	11.6 ± 4.5	20.7 ± 6.4	0.82 ± 0.06
Sedge Meadows	*Carex aquatilis* (20) *Deschampsia caespitosa* (12) *Carex pellita* (9)	8.0 ± 5.0	17.3 ± 9.8	0.69 ± 0.25

mean minimum growing-season temperature [$r = 0.85$]). Mean minimum temperatures were 3.8 to 6.8 °C higher in forested communities of mountain slopes than in grassland communities of the valley bottoms (Table 3). Axis 1 is associated less strongly with shifts in *soil texture* and *cation availability* (% sand [$r = 0.46$]), % clay [$r = -0.59$], soil [Ca^{++}] [$r = -0.70$], and soil Mg^{++} [$r = -0.57$]), as well as *% slope* ($r = 0.66$), which correlates with both cold-air drainage and soil texture. Several groupings within forests and grasslands also segregate along axis 2, which correlates well with *aspect* ($r = 0.40$), *soil moisture* ($r = 0.51$), and *annual mean temperature* ($r = 0.43$), as
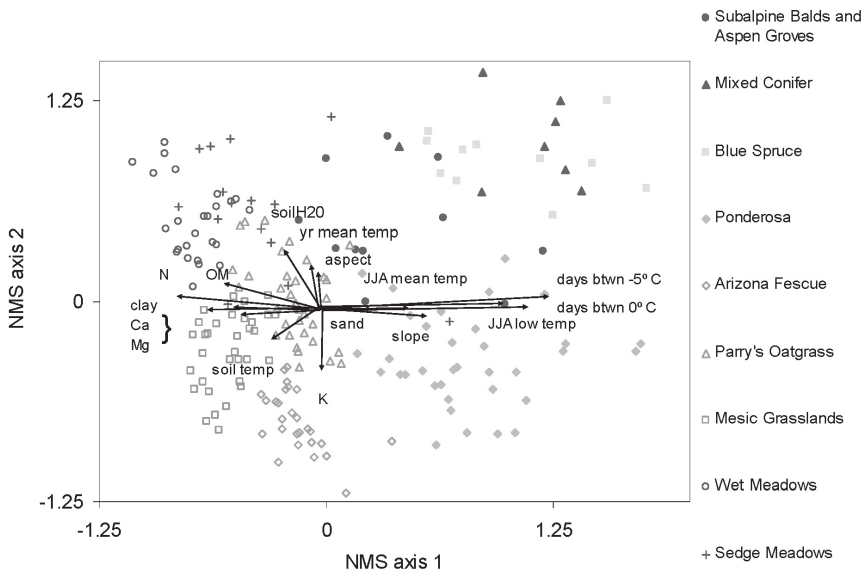
Fig. 2. Ordination joint plot, showing the position of sites on the first and second NMS axes and vectors representing the correlation between ordination axes and measured environmental variables. Sites are highlighted by symbols corresponding to the nine vegetation types identified by cluster and indicator-species analyses: filled symbols identify forest types; hollow symbols signify grassland types.

Table 3. Mean (± s.d.) elevation, slope, soil texture, summer soil moisture, and summer minimum temperatures in each of the nine vegetation groups.

Group	N	Mean elevation(m)	Mean % slope	Soil textural classes	Mean June-August % soil moisture (mass basis)	Mean June-August weekly min. temp. (°C)
Communities of Mountain Slopes						
Subalpine Balds and Aspen Groves	12	2943 ± 233	28.2 ± 47.4	Sandy loam, loam, sandy clay loam	9.6 ± 3.3	N/A
Mixed Conifer	9	2874 ± 222	25.8 ± 12.3	Loam	17.1 ± 2.6	4.6 ± 2.2
Blue Spruce	12	2657 ± 41	27.0 ± 8.9	Sandy loam, loam	13.6 ± 4.6	4.9 ± 0.9
Ponderosa	36	2660 ± 84	26.2 ± 11.7	Sandy loam, loam	10.5 ± 2.6	4.1 ± 1.5
Communities of Valley Bottoms						
Arizona Fescue	29	2625 ± 46	15.7 ± 8.6	Loam	10.7 ± 2.4	0.3 ± 0.5
Parry's Oatgrass	36	2651 ± 37	12.0 ± 6.1	Loam	16.0 ± 5.0	–1.0 ± 1.9
Mesic Grasslands	34	2624 ± 38	5.2 ± 4.1	Clay loam	14.2 ± 2.1	–1.4 ± 1.6
Wet Meadows	26	2658 ± 49	3.7 ± 3.4	Clay loam, clay	21.9 ± 8.8	–1.9 ± 1.8
Sedge Meadows	16	2615 ± 62	1.8 ± 1.4	Clay loam	65.5 ± 56.9	–0.2 ± 0.3

well as soil [K] ($r = –0.53$). Axis 3 accounts for 19.8% of the variance but shows only weak relationships to most environmental variables and ecological communities, except for *Sedge Meadows*, which segregate well on axis 3 but poorly on axes 1 and 2.

While forest types are generally found on mountain slopes above grassland communities of the valley bottoms, grassy balds dominated by *Festuca thurberi* also occur at the highest elevations sampled. Our cluster analysis did not separate these sites from groves of *Populus tremuloides*, which often occur adjacent to or interspersed within these grassy balds. Subalpine forests on cooler, north-facing slopes at higher elevations are dominated by *Picea engelmannii*, occasionally with *Abies arizonica*. Cluster analysis included these stands with those from slopes at somewhat lower elevations, and across a range of aspects, which included a mixture of *Picea engelmannii*, *Abies concolor*, and *Pseudotsuga menziesii*. At the lowest elevations, and on shallow slopes adjacent to the vast grassy basins of the VCNP, *Picea pungens* dominates stands on north and east aspects and *Pinus ponderosa* dominates those of south and west aspects (Tables 2 and 3).

Grassland assemblages appear to sort primarily along catenas of soil moisture, texture, and nutrient availability. *Festuca arizonica* dominates the driest, loamy soils on gentle slopes with a southwest aspect; *Danthonia parryi* dominates similar landforms with cooler, moister, northeastern aspects. Increasingly mesic, clay-rich, and organic soils on level sites are dominated by *Blepharoneuron tricholepis* and *Festuca idahoensis* in mesic grasslands; then by *Poa pratensis*, *Deschampsia caespitosa* and *Carex pellita* in wet meadows. The wettest, lowest, flattest sites show dominance by *Carex aquatilis* or *Carex utriculata* (Tables 2 and 3).

*Treeline stand structure and seedling abundance*

Treeline ecotones in the Valles Caldera are generally marked by a sharp transition from completely open herbaceous communities to fairly dense forests. Across the narrowest sampling interval of 10 m, average tree density increased abruptly from <1 to 8.5 stems per 100 m² quadrat (850 stems/ha) where *Pinus ponderosa* formed the forest boundary, and from <1 to 12 stems per quadrat (1200 stems/ha) for *Picea pungens*. The abruptness of the shift from grassland to forest is further highlighted by the lack of a significant positive relationship of stand density or total basal area to distance from the ecotone. Based on regression analysis, mean tree height, girth, and basal area showed no increase with distance into the forest from the ecotone, for individual species or all species in a stand combined. Mean tree height and girth 5 m from the ecotone were not significantly different from those 110 m into the forest. At 5 m from the treeline, mean tree height was 12.4 m (11.3 m for *Pinus ponderosa*, and 14.5 m for *Picea pungens*) vs. 12.3 m for stands 20-110 m into the forest. Mean basal area per individual at 5 m from the ecotone was 5.6 dm², vs. 6.3 dm² for 20-110 m, a small and non-significant increase. However, maximum tree height within stands did show a significant increase with distance from the ecotone (regression $r^2 = 0.12$, $P = 0.017$, $df = 48$).

Tree seedling density was very low, with most sampled quadrats having no seedlings present. Across the entire gradient, there was a striking sigmoid shift in tree seedling density based on distance from treeline, increasing from nearly zero in or immediately adjacent to grasslands to over 200 seedlings/ha at more than 100 m upslope from the ecotone (Fig. 3, regression $r^2 = 0.13$, $P < 0.0001$, $df = 198$). Multiple regression models that included distance from treeline as a predictor of tree

seedling density retained no other significant predictor variables. Mean seedling density in forested quadrats was 7.2 seedlings in each 45-m^2 sampling unit (159 seedlings/ha), but only 1.1 seedlings in grassland quadrats (25 seedlings/ha, two-tailed t-test $P < 0.0001$).

To account for the potential effects of forest canopy cover and proximity of seed sources on establishment, we separated grassland quadrats and forest quadrats in testing for relationships between seedling abundance, herbaceous cover, and environmental variables. The abundance of tree seedlings on forested sites showed no relationship to canopy cover, thermal variables, soil texture, or distance from the treeline ecotone, but did show a strong positive relationship to soil moisture ($r^2 = 0.30$, $p < 0.005$, $df = 23$). In grasslands, tree seedling abundance was positively related to % sand (regression $r^2 = 0.11$, $p < 0.001$, $df = 95$) and negatively related to % clay ($r^2 = 0.09$, $p < 0.005$, $df = 95$). Too few grassland quadrats contained tree seedlings to test for relationships with either thermal conditions or soil moisture. Seedling abundance in grasslands was not related to above-ground cover by grasses, or to total herbaceous cover, as might be expected if grass or herb competition were limiting tree establishment in the grasslands. Additionally, neither grass cover nor total herbaceous cover exhibited a significant relationship with percent sand or clay *within* the grasslands. In fact, grass cover was slightly positively correlated with percent sand ($r^2 = 0.05$, $p < 0.02$, $df = 96$). Total herbaceous cover in grasslands was positively related to soil moisture ($r^2 = 0.18$, $p = 0.015$, $df = 30$).

We also examined the potentially confounding effect of forest canopy cover on the apparent relationships between topography and both soil moisture and air temperature by sampling these factors in logged openings on mountain slopes adjacent to sampled forested quadrats. Mean soil moisture beneath closed forest canopies was only 0.6 % greater than that beneath adjacent openings (11.4% vs. 10.8%). Closed canopies and adjacent openings did exhibit a 1.4 °C difference in minimum temperature (4.6 vs. 3.2 °C; two-tailed paired *t*-test *P* = 0.03, *df* = 6). This 1.4 °C difference due to tree cover was dwarfed by differences due to topography; mean minimum temperature in the valley bottoms (–1.3 °C) was 5.9 °C cooler than forested slopes (two-tailed *P* << 0.0001) and 4.5 °C cooler than openings on slopes above (two-tailed *P* << 0.0001).
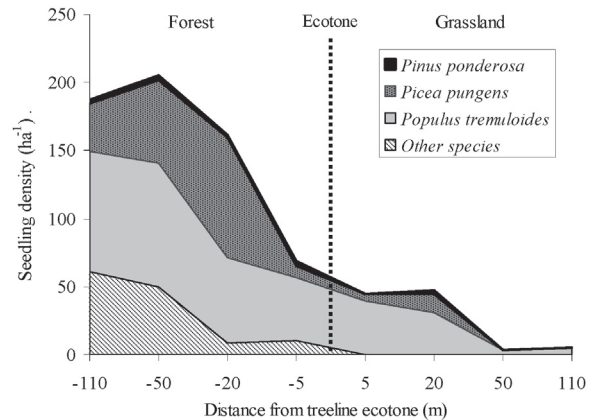
Fig. 3. Tree seedling density (all species) and distance from reversed treeline ecotones in sampled quadrats.

Discussion

Forests and grasslands of the Valles Caldera

Cluster analysis and NMS ordination concur in the vegetation patterns they identify (Fig. 2; Tables 2 and 3). Cluster analysis identified three forest types (*Ponderosa Pine, Colorado Blue Spruce,* and *Mixed Conifers*), five grassland types (*Arizona Fescue, Parry's Oatgrass, Mesic Grasslands, Wet Meadows,* and *Sedge Meadows*), and one heterogeneous type containing a mix of both forests and meadows (*Aspen Groves -Subalpine Balds*). The three forest types we found support groupings previously reported in the American Southwest (Alexander & Ronco 1987; DeVelice et al. 1986; Dick-Peddie 1993; Brown 1994) and correspond with associations within the *Pinus ponderosa* and *Picea pungens* forest alliances, and to a lesser extent the *Abies concolor* forest alliance identified within the U.S. National Vegetation Classification System (Anderson et al. 1998). The grassland communities we identified show little resemblance to groupings proposed by Dick-Peddie (1993) and Brown (1994), but offer some support for National Vegetation System associations. The *Arizona Fescue* and *Parry's Oatgrass* groups we identified in our analysis match alliances (*Festuca arizonica* and *Danthonia parryi* alliances) which are described for Colorado and Wyoming (Anderson et al. 1998). Our *Mesic Grassland*, *Wet Meadow,* and *Sedge Meadow* types do not clearly correspond with any National Vegetation Classification groupings; this may be due to more floristically heterogeneous nature of these communities, which show much weaker patterns of dominance (Table 2). Lastly, our mixed meadow- and forest- community *Subalpine Balds - Aspen Groves* partially matches both the *Festuca thurberi Subalpine Grassland* and the *Populus tremuloides/Festuca thurberi Associations* included

in the National Vegetation Classification (Anderson et al. 1998).

The separation of forest communities from each other corresponds primarily to aspect and elevation and correlated shifts in soil moisture and soil cations (Fig. 2; Table 3). *Ponderosa Pine* and *Colorado Blue Spruce* communities occur on southwest vs. northeast exposures near 2650 m elevation, with dominance shifting to other conifer species in stands of *Mixed Conifers* over a wide range of aspects at elevations about 200 m higher. The five grassland community types appear to be distributed along soil catenas of increasing % silt, % clay, and % organic matter below where they abut forests, usually at a topographic break from slopes at least twice as steep (Fig. 2; Table 3). The *Arizona Fescue* community dominates on southwest aspects of gentle slopes immediately below treeline stands of ponderosa pine, while *Parry's Oatgrass* occurs on more mesic, northeast facing slopes, generally below blue spruce treelines. *Mesic Grasslands* and *Wet Meadows* occur further downslope with the more clay-rich soils and greater cold-air drainage. The transition into these floristically heterogeneous communities is often marked by the replacement of several species by others in the same genera. The most striking cases involve *Festuca arizonica* being replaced by *Festuca idahoensis* (Table 2) and *Danthonia parryi* being replaced by *Danthonia intermedia*. A similar pattern is shown by *Agoseris, Allium, Campanula*, and *Muhlenbergia*. *Sedge Meadows* are usually dominated by *Carex aquatilis* or *Carex utriculata* in areas that are perennially wet, or by *Eleocharis palustris* in areas that are seasonally dry.

Only one community type identified by cluster analysis, *Aspen Groves and Subalpine Balds*, contains a mix of grass- and tree-dominated stands. These quadrats all come from higher-elevations where meadows and grassy openings occur not only in flat areas and concave depressions, but also on south-facing slopes. Unlike the sharply defined treelines bordering valley bottoms, treelines on south-facing slopes tended to be more diffuse and savanna-like. The placement of such a heterogeneous collection of grasslands and open woodlands in a single community type reflects the presence of *Festuca thurberi* at open sites as well as sites with a substantial aspen cover, and the occurrence of several species of forbs and other graminoids in both aspen forests and high-elevation meadows. A similar association between *Populus tremuloides* and *Festuca thurberi* has been reported from the mountains of northern Colorado (Hess 1981), and may reflect aspen invasion into grasslands and the persistence of long-lived bunchgrasses beneath the aspen canopy.

Causes of reversed treelines

In the Valles Caldera, topographic shifts from steep mountain slopes to gently inclined valley bottoms are consistently associated with reversed treeline ecotones. NMS ordination indicates that the shift from forests to grasslands is most strongly related to lower nighttime temperatures (mean minimum temperature and number of consecutive days between temperatures reaching 0 or –5 °C), but not to mean annual temperature (Fig. 2). Minimum weekly temperatures in valley bottoms averaged –1.3 °C between June and August. These results strongly support minimum nighttime temperatures as at least one cause of the position of reversed treelines in the Valles Caldera. Tree seedlings may be damaged or killed by freezing, frost-heaving, or cold-temperature photo-inhibition. For *Pinus ponderosa*, growing-season temperatures that dip below –3 °C are detrimental to seedling growth and survival (Schubert & Adams 1971), and frosts have been demonstrated to be a large source of seedling mortality via frost heaving (Larson 1960, 1961). Ball et al. (1991), Germino & Smith (1999), and Germino et al. (2002) have demonstrated that tree seedling growth and survival near alpine treelines are adversely affected by photo-inhibition in areas of cold-air drainage or locally severe re-radiative cooling.

Our results also indicate correlations between the shift from forests to grasslands with transitions to finer-textured soils with greater total N, % organic matter (to which [N] is often correlated), and the concentrations of several major cations (Fig. 2). Fine-textured soils may impede seedling root growth (Daubenmire 1943), or decrease tree growth by reducing the availability of deep moisture to trees (Walter 1971). The fact that soil texture and minimum nighttime temperature are both correlated with the transition from forests to grasslands suggests that both factors may be important in setting the position of reversed treelines. These factors may interact through frost heaving, which has been shown to be much greater, and be more lethal to pine seedlings, on fine-textured and/or moister soils (Heidmann & Thorud 1976). The absence within grasslands of a significant negative relation of seedling density to grass cover, or of a significant positive relation of grass cover to increased nutrient concentrations, offers no support for the hypothesis that reversed treelines in the VCNP are caused by increased grass competition with tree seedlings on finer-grained, richer soils on flats below mountain slopes. Likewise, our data provide no evidence that excessively dry or excessively wet soils control the position of these treelines (Fig. 2; Table 3).

In the Valles Caldera, the low density of tree seedlings in forest margins and their extremely low abundance on grassland sites (Fig. 3), as expected if constraints

on tree establishment (and not decreased tree growth or increased mortality) cause the reversed treelines. Similar results were reported by Shauer et al. (1998), who experimentally tested tree seedling establishment in a subalpine park in Colorado. In this study we found no tendency for mean or maximum tree basal area to decrease with increasing proximity to subalpine treelines in the VCNP. Maximum tree height did show a systematic decrease from forest interiors toward the treeline ecotone, as would be expected if treeline formation is driven by limitations on woody plant growth imposed by a gradient of increasing environmental severity (e.g. see Givnish 1995). However these results are likely to have been impacted both by historic logging along forest-grassland edges and encroachment of treelines into grasslands, and may not reflect natural patterns of stand structure near treelines.

Photographs taken by members of Vernon Bailey's 1907 U.S. Bureau of Biological Survey expedition (Hogan & Allen 1999) indicate that reversed treelines in the Valles Caldera were located slightly further upslope in many areas nearly a century ago, suggesting that location-specific constraints on tree establishment have been relaxed over that period. Elsewhere in the southern Rockies, shifts in the position of montane and subalpine treelines have been attributed to climatic changes (Dyer & Moffett 1999) and to changing human land use, especially livestock grazing and fire suppression (Allen 1984; Mast et al. 1997). If reversed treelines in the Valles Caldera are maintained solely by the adverse effects of cold-air drainage in valley bottoms on tree seedling establishment or growth, then climatic warming could clearly shift treelines downslope. However, prior to ca. 1890, such a constraint on tree seedling establishment or growth would have operated in conjunction with frequent, low-intensity fire, which would have increased the interval of time required for seedlings to reach sufficient size to survive low-intensity fire. As such, the required fire-free interval in valley bottoms may have greatly exceeded the short mean fire-return intervals (< 5-25 years) that characterized the ponderosa pine and mixed-conifer forests of the Jemez Mountains (Touchan et al. 1996; Allen 2002) and the southwestern U.S. as a whole (Swetnam & Baisan 1996) prior to the initiation of regionally extensive livestock grazing in the late 19th century. Continued fire suppression may allow a gradual encroachment by trees into sites even where tree establishment is infrequent and/or growth is slow.

References

Anon. 2005. *The PLANTS Database, Version 3.5.* URL: http://plants.usda.gov. Data compiled from various sources by Mark W. Skinner. USDA, NRCS, Natl. Plant Data Center, Baton Rouge, LA, US.

Alexander, R.R. & Ronco, F., Jr. 1987. *Classification of the Forest Vegetation on the National Forests of Arizona and New Mexico.* USDA For. Serv. Rocky Mount. For. and Range Exp. Stn. Res. Note RM-469. Fort Collins, CO, US.

Allen, C.D. 1984. *Montane grasslands in the landscape of the Jemez Mountains, New Mexico.* M. Sc. Thesis, University of Wisconsin, Madison, WI, US.

Allen, C.D. 2002. Lots of lightning and plenty of people: An ecological history of fire in the upland Southwest. In: Vale, T.R. (ed.) *Fire, native peoples, and the natural landscape*, pp. 143-193. Island Press, Covelo, CA, US.

Anderson, M., Bourgeron,, P., Bryer, M.T., Crawford, R., Engelking, L., Faber-Langendoen, D., Gallyoun, M., Goodin, K., Grossman, D.H., Landaal, S., Metzler, K., Patterson, K.D., Pyne, M., Reid, M., Sneddon, L. & Weakley, A.S. 1998. *International classification of ecological communities: Terrestrial vegetation of the United States. Vol. II. The National Vegetation System: List of Types.* The Nature Conservancy, Arlington, VA, US.

Ball, M.C., Hodges, V.S. & Laughlin, G.P. 1991. Cold-induced photoinhibition limits regeneration of snow gum at treeline. *Funct. Ecol.* 5: 663-668.

Boyce, M.S. & Hayden-Wing, L. 1979. *North American Elk.* Univ. Wyoming Press, Laramie, WY, US.

Brown, D.E. (ed.) 1994. *Biotic communities: Southwestern United States and Northwestern Mexico.* University of Utah Press, Salt Lake City, UT, US.

Daubenmire, R. 1943. Vegetational zonation in the Rocky Mountains. *Bot. Rev.* 9: 325-393.

Daubenmire, R. 1968. Soil moisture in relation to vegetation distribution in the mountains of Northern Idaho. *Ecology* 49: 431-438.

Day, P.R. 1965. Particle fractionation and particle-size analysis. In: Black, C.A. (ed.) *Methods of soil analysis, part I. Physical and mineralogical properties, including statistics of measurement and sampling,* pp. 545-567 American Society of Agronomy, Madison, WI, US.

DeVelice, R.L., Moir, W.H. & Ronco, F., Jr. 1986. *A classification of forest habitat types of northern New Mexico and southern Colorado.* USDA Forest Service Rocky

Mountains Forest and Range Exp. Stn. Gen. Tech. Rep. RM-131. Fort Collins, CO, US.

Dick-Peddie, W.A. 1993. *New Mexico Vegetation: past, present, and future*. University of New Mexico Press, Albuquerque, NM, US.

Doering, W.R. & Reider, R.G. 1992. Soils of Cinnabar Park, Medicine Bow Mountains, Wyoming, U.S.A.: indicators of park origin and persistence. *Arct. Alp. Res.* 24: 27-39.

Dyer, J.M. & Moffett, K.E. 1999. Meadow invasion from high-elevation spruce-fir forest in south-central New Mexico. *Southw. Nat.* 44: 444-456.

Fensham, R.J. & Kirkpatrick, J.B. 1992. The eucalypt forest-grassland/grassy woodland boundary in central Tasmania. *Aust. J. Bot.* 40: 123-138.

Germino, M.J. & Smith, W.K. 1999. Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant Cell Environ.* 2:407-415.

Germino, M.J., Smith, W.K. & Resor, A.C. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecol.* 162: 157-168.

Gilfedder, L. 1988. Factors influencing the maintenance of an inverted *Eucalyptus coccifera* tree-line on the Mt. Wellington Plateau, Tasmania. *Aust. J. Ecol.* 13: 495-503.

Givnish, T.J. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. In: Gartner, B.L. (ed.) *Plant stems: physiology and functional morphology,* pp. 3-49 Chapman and Hall, New York, NY, US.

Hartman, R.L. & Nelson, B.E. 2005. *Checklist of the vascular plants of the Valles Caldera National Preserve, New Mexico: summers 2001, 2002, 2003, 2004.* Unpubl. report on file with the Valles Caldera Trust, Los Alamos, NM, US.

Heidmann, L.J. & Thorud, D.B. 1976. *Controlling frost heaving of ponderosa pine seedlings in Arizona*. USDA Forest Service Rocky Mountains Forest and Range Exp. Stn. Res. Pap. RM-172. Fort Collins, CO, US.

Hess, K. 1981. *Phyto-edaphic study of the Arapaho and Roosevelt National Forests*. PhD. Thesis, Colorado State University, Fort Collins, CO, US.

Hogan, J.T. & Allen, C.D. 1999. *Use of repeat photography for historical ecology research on the Baca Ranch in the Jemez Mountains, New Mexico*. Unpubl. report on file with the USGS, Jemez Mountains Field Station, Los Alamos, NM, US.

Ives, R.L. 1942. Atypical subalpine environments. *Ecology* 23: 89-96.

Koterba, W.D. & Habeck, J.R. 1971. Grasslands of the North Fork Valley, Glacier National Park, Montana. *Can. J. Bot.* 49:1627-1636.

Langenheim, J.H. 1962. Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. *Ecol. Monogr.* 32: 249-285.

Larson, M.M. 1960. *Frost heaving influences drought-hardiness of ponderosa pine seedlings*. USDA Forest Service Rocky Mountains Forest and Range Exp. Stn. Res. Note RM-45. Fort Collins, CO, US.

Larson, M.M. 1961. *Seed size, germination dates, and survival relationships of ponderosa pine in the Southwest*. USDA

Forest Service Rocky Mountains Forest and Range Exp. Stn.. Res. Note RM-66. Fort Collins, CO, US.

Martin, C. 2003. *Valle Grande: History of the Baca Location Number 1*. All Seasons Publishing, Los Alamos, NM, US.

Mast, J.N., Veblen, T.T. & Hodgson, M.E. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. *For. Ecol. Manage.* 93: 181-194.

McCune, B. & Grace, J.B. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR, US.

McCune, B. & Mefford, M.J. 1997. *PC-ORD: multivariate analysis of ecological data. Version 3.0.* MjM Software Design, Gleneden Beach, OR, US.

Moir, W.H. 1967. The subalpine tall grass, *Festuca thurberi* community of Sierra Blanca, New Mexico. *Southw. Nat.* 12: 321-328.

Moore, R.M. & Williams, J.D. 1976. A study of a subalpine woodland-grassland boundary. *Aust. J. Ecol.* 1: 145-153.

Paton, D.M. 1988. Genesis of an inverted treeline associated with a frost hollow in southeastern Australia. *Aust. J. Bot.* 36: 655-663.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. *Vegetatio* 45: 3-75.

Peet, R.K. 2000. Forests and meadows of the Rocky Mountains. In: Barbour, M.G. & Billings, W.D. (eds.) *North American terrestrial vegetation,* pp. 75-122 Cambridge University Press, Cambridge, UK.

Ramaley, F. 1927. *Colorado plant life*. University of Colorado. Boulder, CO, US.

Reed, E.L. 1917. Meadow vegetation in the montane region of Northern Colorado. *Bull. Torrey Bot. Club* 44: 97-109.

Robbins, W.W. 1918. Successions of vegetation in Boulder Park, Colorado. *Bot. Gaz.* 65: 493-525.

Rydberg, P.A. 1913. Phytogeographical notes on the Rocky Mountain region V. Grasslands of the Subalpine and Montane Zones. *Bull. Torrey Bot. Club* 42: 629-642.

Schubert, G.H. & Adams, R.S. 1971. *Reforestation practices for conifers in California*. Cal. Div. For., Sacramento, CA, US.

Shauer, A.J., Wade, B.K. & Sowell, J.B. 1998. Persistence of subalpine forest meadow ecotones in the Gunnison Basin, Colorado. *Great Basin Nat.* 58: 273-281.

Simonson, S.E., Opler, P.A., Stohlgren, T.J. & Chong, G.W. 2001. Rapid assessment of butterfly diversity in a montane landscape. *Biodiv. Conserv.* 10: 1369-1386.

Smith, R.L., Bailey, R.A. & Ross, C.S. 1970. *Geologic Map of the Jemez Mountains, New Mexico*. Misc. Geol. Inv. Map I-571. USGS, Reston, VA, US.

Stohlgren, T.J., Chong, G.W., Kalkhan, M.A. & Schnell, L.D. 1997. Multi-scale sampling of plant diversity: effects of minimum mapping unit size. *Ecol. Appl.* 7: 1064-1074.

Swetnam, T.W. & Baisan, C.H. 1996. Historical fire regime patterns in the southwestern United States since AD 1700. In: Allen, C.D. (ed.) *Fire effects in southwestern forests: Proceedings of the Second La Mesa Fire Symposium*, pp. 11-32. USDA Forest Service Rocky Mountains Forest and Range Exp. Stn. Gen. Tech. Rep. RM – 286. Fort Collins, CO, US.

Touchan, R., Allen, C.D. & Swetnam, T.W. 1996. Fire history and climatic patterns in ponderosa pine and mixed-conifer forests of the Jemez Mountains, northern New Mexico. In: Allen, C.D. (ed.) *Fire effects in southwestern forests: Proceedings of the Second La Mesa Fire Symposium*, pp. 33-46. USDA Forest Service Rocky Mountains Forest and Range Exp. Stn. Gen. Tech. Rep. RM – 286. Fort Collins, CO, US.

Turner, G.T. & Paulsen, H.A., Jr. 1976. *Management of mountain grasslands in the central Rockies: the status of our knowledge*. USDA Forest Service Rocky Mountains Forest and Range Exp. Stn. Res. Pap. RM – 161. Fort Collins, CO, US.

Veblen, T.T. & Lorenz, DC. 1986. Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. *Phys. Geog*. 7: 1-24.

Walter, H. 1971. *Ecology of tropical and subtropical vegetation*. Oliver and Boyd, Edinburgh, UK.

Wardle, P. 1971. An explanation for alpine timberline. *N.Z. J. Bot*. 9: 371-402.

App. 1. List of 206 vascular plant taxa sampled in 200 (5 × 20 m²) quadrats in mountain grasslands and forest edges in the Valles Caldera National Preserve. Nomenclature follows USDA (2005) and Hartman & Nelson (2005). Species pairs that could not be consistently distinguished in the field were included together (e.g. *Antennaria parvifolia* and *A. marginata*); for several taxa, no determination beyond genus was possible (e.g. *Stellaria* spp.). Taxa are listed in order of abundance (percent cover on all quadrats); percent frequency is also given. Group occurrences are also noted as follows: 1, Aspen Groves and Subalpine Balds; 2, Mixed Conifer; 3, Blue Spruce; 4, Ponderosa Pine; 5, Arizona Fescue; 6, Parry's Oatgrass; 7, Mesic Grasslands; 8, Wet Meadows; 9, Sedge Meadows. Exotic species are denoted with an asterisk *.

Binomial	Common name	Percent cover	Percent frequency	Groups
Pinus ponderosa Douglas ex P. & C. Lawson var. *scopulorum* Engelm.	ponderosa pine	11.049	19.5	1,3,4,5
* *Poa pratensis* L	Kentucky bluegrass	8.829	75.0	1,2,3,4,5,6,7,8,9
*Danthonia parryin*Scribn.	Parry's oatgrass	6.25	35.5	1,2,3,4,5,6,7,8
Picea pungens Engelm.	Colorado blue spruce	4.578	10.5	1,2,3,4,6
Festuca arizonica Vasey	Arizona fescue	4.38	47.5	1,3,4,5,6,7
Blepharoneuron tricholepis (Torr.) Nash	pine dropseed	3.177	44.5	1,2,4,5,6,7,8,9
Potentilla hippiana Lehm.	wooly cinquefoil	2.97	71.0	1,2,3,4,5,6,7,8,9
Festuca thurberi Vasey	Thurber's fescue	2.899	17.0	1,2,3,4,6,7,8
* *Taraxacum officinale* G.H. Weber ex Wiggers	common dandelion	2.492	73.5	1,2,3,4,5,6,7,8,9
Festuca idahoensis Romer	Idaho fescue	2.467	27.5	4,5,6,7,8,9
Muhlenbergia montana (Nutt.) Hitchc.	mountain muhly	2.379	39.0	4,5,6,7,9
Deschampsia caespitosa (L.) Beauv.	tufted hairgrass	2.262	18.0	6,7,8,9
Carex pellita Willd.	wooly sedge	2.055	21.5	4,5,6,7,8,9
Achillea millefolium L. var. *occidentalis* DC.	western yarrow	1.934	78.0	1,2,3,4,5,6,7,8,9
Koeleria macrantha (Lebed.) Schult.	Junegrass	1.795	50.5	1,4,5,6,7,8,9
Pseudotsuga menziesii (Mirb.) Franco var *glauca* (Beiss.) Franco	Douglas fir	1.758	5.5	2,3,4
Juncus balticus Willd. var. *montanus* Engelm.	Baltic rush	1.621	56.5	4,5,6,7,8,9
Antennaria parvifolia Nutt./*A. marginata* Greene	small-leaf pussytoes, white margin pussytoes	1.584	39.5	1,2,3,4,5,6,7
Carex aquatilis Wahlenb.	water sedge	1.511	7.0	8,9
Muhlenbergia wrightii Vasey ex Coult.	spike muhly	1.37	16.5	5,6,7,8,9
Abies concolor (Gord. & Glend.) Hildebr.	white fir	1.35	6.5	1,2,3,4
* *Trifolium repens* L.	white clover	1.347	31.5	2,3,4,5,6,7,8,9
Populus tremuloides Michx.	quaking aspen	1.309	4.5	1,2,3
Danthonia intermedia Vasey	timber oatgrass	1.09	9.5	6,7,8
Erigeron formosissimus Greene	beautiful fleabane	1.082	57.5	1,2,3,4,5,6,7,8,9
Symphyotrichum adscendens (Lindl.) Nesom.	western aster	1.053	27.0	1,4,5,6,7,8,9
Carex praegracilis W. Boott	clustered field sedge	0.984	36.5	2,4,5,6,7,8,9
Arenaria fendleri Gray	Fendler's sandwort	0.871	29.5	1,4,5,6,7
*Bouteloua gracilis (*Kunth) Lag.	blue grama	0.858	13.0	4,5,6
Erigeron flagellaris A. Gray	trailing fleabane	0.84	41.0	2,3,4,5,6,7,8
Carex utriculata Boott.	Northwest territory sedge	0.729	8.0	8,9
Iris missouriensis Nutt.	Rocky Mountain iris	0.718	23.5	1,2,4,6,7,8,9
Carex microptera Mack.	smallwing sedge	0.697	19.5	3,6,7,8,9
Eleocharis palustris (L.) Roemer & J.A. Schultes	common spikerush	0.667	5.0	7,8,9
Carex inops Bailey ssp. *heliophila* (Mackenzie) Crins	sun sedge	0.663	29.5	1,2,4,5,6,7,8
Argentina answerina (L.) Rydb.	silverweed cinquefoil	0.636	10.5	6,7,8,9
Carex rossii Boott.	Ross' sedge	0.625	18.0	1,2,3,4
Ranunculus cardiophyllus Hook	heart-leaf buttercup	0.574	36.5	4,5,6,7,8,9
Agrostis scabra Willd.	rough bentgrass	0.546	24.5	2,3,4,5,6,7,8,9
Muhlenbergia richardsonis (Trin.) Rydb.	mat muhly	0.472	26.0	5,6,7,8,9
Elymus pseudorepens (Scribn. & J.G. Sm.) Barkworth & D.R. Dewey	hybrid wheatgrass	0.462	35.5	1,3,4,5,6,7,8,9
Poa fendleriana (Steud.) Vasey	muttongrass	0.459	27.0	1,3,4,5,6,7
Carex siccata Dewey (*C. foenea* Willd. var. *foenea*)	dryspike sedge	0.441	16.0	1,2,3,4,6
Penstemon rydbergii A. Nelson	Rydberg's penstemon	0.437	9.5	5,6,7,8
Carex obtusata Lilj.	obtuse sedge	0.429	28.0	1,3,4,5,6,7,8
Antennaria rosulata Rydb.	Kaibab pussytoes	0.417	8.0	4,5,6,7
Heterotheca villosa (Pursh) Shinners	hairy false goldenaster	0.401	11.0	4,5,6
Elymus elymoides (Raf.) Swezey ssp. *brevifolius* (J.G. Sm.) Barkworth	squirreltail	0.385	31.0	1,3,4,5,6,7
Carex simulata Mack.	analogue sedge	0.334	4.0	7,9
Campanula rotundifolia L.	Parry's bellflower	0.299	34.0	1,3,4,5,6,7,8
Carex petasata Dewey	Liddon sedge	0.296	33.5	1,5,6,7,8
Juniperus communis L.	common juniper	0.267	9.0	2,3,4,6
Dodecatheon pulchellum (Raff.) Merr.	darkthroat shootingstar	0.265	4.5	6,8,9
Bromus porteri (Coult.) Nash	Porter brome	0.261	26.0	1,4,5,6,7
Dasiphora floribunda (Pursch) Kartesz	shrubby cinquefoil	0.216	11.5	6,7,8,9
Fragaria virginiana Duchesne ssp. *glauca* (S. Wats.) Staudt	Virginia strawberry	0.214	13.0	1,2,3,4,6
Vicia americana Muhl. ex Willd.	American vetch	0.209	31.0	1,3,4,5,6,7,8,9

→

App. 1, cont.

Binomial	Common name	Percent cover	Percent frequency	Groups
* *Phleum pratense* L.	timothy	0.203	11.5	4,5,6,7,8,9
Cerastium arvense L.	field chickweed	0.201	20.0	1,2,3,4,5,6,7,8,9
Artemisia carruthii Wood ex Carruth.	Caruth's sagewort	0.2	15.0	4,5,7
Picea engelmannii Parry ex. Englm.	Engelmann spruce	0.198	1.5	2,3
Fragaria vesca L. *ssp. americana* (Porter) Staudt	woodland strawberry	0.197	9.0	1,2,3,4,6
Hordeum brachyantherum Nevski	meadow barley	0.195	5.5	7,8,9
Symphiotrichum Nees spec.	aster	0.178	7.0	7,8,9
Elymus L. spec.	wheatgrass	0.175	5.0	1,3,4,6
Abies arizonica Merriam	corkbark fir	0.172	1.0	2
Lathyrus lanszwertii Kellogg	Nevada pea	0.16	20.0	1,2,3,4,5,6,7
Potentilla pulcherrima Lehm.	beautiful cinquefoil	0.154	15.0	1,2,3,4,6,7,8,9
Phleum alpinum L.	alpine timothy	0.154	8.5	6,8,9
Geranium richardsonii Fisch. & Trautv.	Richardson's geranium	0.153	8.0	1,2,3,4,6
Trifolium longipes Nutt.	longstalk clover	0.147	10.0	6,7,8,9
Viola adunca Sm.	hookspur violet	0.144	15.0	1,3,4,5,6,8,9
Allium geyeri S. Wats.	Geyer's onion	0.143	20.5	6,7,8,9
Erigeron eximius Greene	sprucefir fleabane	0.129	4.5	2,3
Bromus ciliatus L. var. *richardsonii* (Link) Boivin	fringed brome	0.128	9.0	1,2,3,4
Pascopyrum smithii (Rydb.) A. Löve	western wheatgrass	0.116	5.0	4,5,6,7,8
Poa palustris L.	fowl bluegrass	0.112	4.0	8,9
* *Prunella vulgaris* L.	self-heal	0.112	4.5	5,6,8
Trisetum montanum Vasey	spike trisetum	0.093	7.0	1,2,3,4
Calamagrostis canadensis (Michx.) P. Beauv. var. *canadensis*	bluejoint	0.091	3.5	6,8,9
Agoseris glauca (Pursh) Raf.	pale agoseris	0.086	13.0	5,6,7,8,9
Carex douglasii Boott.	Douglas' sedge	0.079	6.0	4,5,6,7,8
Pseudocymopterus montanus (Gray) Coult. & Rose	alpine false springparsley	0.076	19.5	1,2,3,4,6,7
Vaccinium myrtillus L.	whortleberry	0.076	1.0	2,3
Hypericum scouleri Hook.	Scouler's St. Johnswort	0.074	3.0	6,8,9
Mertensia oblongifolia (Nutt.)G.Don	oblongleaf bluebells	0.069	8.5	1,3,4,5,6
Geranium caespitosum James	James geranium	0.069	6.5	1,4,5
Orthocarpus luteus Nutt.	yellow owl's clover	0.068	9.0	1,4,5,6,8
Solidago missouriensis Nutt.	Missouri goldenrod	0.066	3.0	5,6,7
Hymenoxys hoopesii (Gray) Bierner	sneezeweed	0.063	3.0	1,6,8
Veratrum viride Ait.	false hellebore	0.062	0.5	8
Viola canadensis L.	Canadian white violet	0.062	3.5	2,3,4
Geum triflorum Pursh	prairiesmoke	0.061	9.0	1,4,5,6,7
Crepis runcinata (James) Torr.&Gray	fiddleleaf hawksbeard	0.056	4.0	1,6,8,9
Campanula parryi A. Gray	bluebell bellflower	0.052	10.5	1,4,5,6,7,8,9
Hierochloë odorata (L.) P. Beauv.	sweetgrass	0.052	3.0	8,9
* *Rumex acetosella* L.	sheep sorrel	0.05	4.0	3,6,8,9
Galium aparine L.	bedstraw	0.046	5.0	1,2,3,4,6
Gentiana affinis Griseb.	pleated gentian	0.045	10.0	5,6,7
Agoseris aurantica (Hook.) Greene	orange agoseris	0.044	10.0	1,5,6,7,8
Artemisia ludoviciana Nutt.	white sagebrush	0.044	13.0	2,4,5,6,7
Galium boreale L.	northern bedstraw	0.044	6.0	4,3,6,8
Krigia biflora (Walt.) Blake	twoflower dwarfdandelion	0.043	1.5	8,9
Schizachyrium scoparium (Michx.) Nash	little bluestem	0.043	0.5	5
Thermopsis divaricarpa A. Nels.	spreadfruit goldenbanner	0.043	1.0	1,6
Carex duriuscula C.A. Mey	needleleaf sedge	0.042	3.5	5,6,8
Erigeron subtrinervis Rydb. ex Porter and Britton	threenerve fleabane	0.041	1.5	8
Osmorhiza depauperata Phil.	sweet cicely	0.039	3.0	2,3
Besseya plantaginea (James) Rydb.	White River coraldrops	0.034	4.5	3,5,6
* *Tragopogon dubius* Scop.	yellow salsify	0.033	2.0	1,2,5,6
Erigeron speciosus (Lindl.) DC.	aspen fleabane	0.032	5.5	2,3,4
Festuca saximontana Rydb.	Rocky Mountain fescue	0.031	1.0	6
Packera neomexicana (Gray) W.A. Weber & A. Löve	New Mexico groundsel	0.03	6.0	5,6,7
Caltha leptosepala DC.	white marsh marigold	0.028	2.5	8,9
Oxalis violacea L.	violet woodsorrel	0.026	3.5	2,3,4
Cicuta maculata L.	spotted water hemlock	0.025	1.0	8,9
Carex occidentalis Bailey	western sedge	0.024	3.5	2,4,6
Allium cernuum Roth	nodding onion	0.023	7.5	2,4,5,6,7,8
Pyrrochoma Hook spec.	goldenweed	0.023	3.0	6,8
Polygonum douglasii Greene ssp. *johnstonii* (Munz) Hickman	Johnston's knotweed	0.022	5.5	4,5,6
Eleocharis quinqueflora (F.X. Hartmann) Schwarz	fewflower spikerush	0.021	1.0	8,9
Acer glabrum Torr.	mountain maple	0.019	0.5	2
Lupinus argenteus Pursh	silvery lupine	0.018	2.0	5
Paxistima myrsinites (Pursh) Raf.	mountain-lover	0.018	2.5	2,3

→

Binomial	Common name	Percent cover	Percent frequency	Groups
Rorippa sphaerocarpa (Gray) Britt.	roundfruit yellowcress	0.018	3.5	7,8,9
Silene drummondii Hook./*S. scouleri* Hooker	Drummond's campion/ simple campion	0.017	8.0	1,2,3,5,6,7,8
Sisyrinchium montanum Greene	blue-eyed grass	0.017	5.0	6,7,8
Heuchera parvifolia Nutt. ex Torr. & A. Gray	littleleaf alumroot	0.016	4.0	1,3,4,6
Thalictrum fendleri Engelm. ex A. Gray	Fendler's meadowrue	0.016	1.0	1,2
Juncus saximontanus A. Nels.	Rocky Mountain rush	0.015	1.5	8,9
Cyperus fendlerianus Boeckl.	Fendler's flatsedge	0.014	1.5	4
Mirabilis comata (Small) Standl.	hairy-tuft four o'clock	0.014	2.0	4,5
Saxifraga rhomboidea Greene	diamondleaf saxifrage	0.013	4.5	4,6,7,8
* *Descurainia sophia* (L.) Webb ex. Prantl.	sophia tansymustard	0.013	2.0	3,5
Erigeron lonchophyllus Hook.	shortray fleabane	0.013	2.0	8,9
Androsace septentrionalis L.	rockjasmine	0.012	5.0	2,4,6,7,9
* *Chamaesyce serpyllifolia* (Pers.) Small	thymeleaf sandwort	0.012	1.0	7
Cystopteris fragilis (L.) Bernh.	brittle bladderfern	0.011	1.0	2
Hymenopappus newberryi (Gray) I.M. Johnston	Newberry's hymenopappus	0.01	2.0	4,5
Ribes inerme Rydb.	whitestem gooseberry	0.01	2.5	2,4
Artemisia franserioides Greene	ragweed sagebrush	0.01	1.0	2
* *Carex conoidea* Schkuhr ex Willd.	openfield sedge	0.01	0.5	8
* *Madia glomerata* Hook	mountain tarweed	0.01	0.5	9
Mahonia repens (Lindl.) G. Don	creeping barberry	0.01	1.0	4
Veronica peregrina L.	neckweed	0.01	3.0	7,8,9
Oenothera flava (A. Nels.) Garrett	yellow evening primrose	0.01	1.0	7
Arabis drummondii Gray	Drumond's rockcress	0.009	3.0	5,6,7
Gentianella amarella (L.) Boerner	autumn dwarf gentian	0.009	4.0	1,6,7,8
Plantago major L.	common plantain	0.009	2.5	6,7,8
Mentha arvensis L.	wild mint	0.008	2.0	8,9
Rubus ideas L.	American red rasberry	0.008	2.0	2,3
Solidago simplex Kunth ssp. *simplex*	Mt. Albert goldenrod	0.008	1.0	1
Elymus trachycaulus (Link) Gould ex Shinners ssp. *trachycaulus*	slender wheatgrass	0.007	1.0	7,8
Hieracium fendleri Schultz-Bip.	Fendler's hawkweed	0.007	2.5	4,3
Ranunculus aquatilis L.	whitewater crowfoot	0.007	0.5	9
Torreyochloa pallida (Torr.) Church var. *pauciflora* (J. Presl) J.I. Davis	pale false mannagrass	0.007	1.0	8,9
Calochortus gunnisonii S. Wats.	Gunnison's mariposa lily	0.006	3.0	6,8
Castilleja. Mutis ex. L.f. spec	sulfur Indian paintbrush	0.006	2.0	5
Clematis columbiana (Nutt.) Torr. & A. Gray	rock clematis	0.006	0.5	2
Juncus longistylis Torr.	longstyle rush	0.006	1.5	8,9
Linum lewisii Pursh	prairie flax	0.006	1.0	1
Packera fendleri (Gray) W.A. Weber & A. Löve	Fendler's ragwort	0.006	0.5	4
Penstemon barbatus (Cav.) Roth	beardlip penstemon	0.006	2.0	5
Quercus gambelii Nutt.	Gambel's oak	0.006	2.0	4,6,8
Stellaria L. spec.	starwort	0.006	2.0	2,3,4,8
Carex deweyana Schwein.	Dewey sedge	0.005	1.5	2,3
Epilobium leptophyllum Raf.	bog willowherb	0.005	2.5	9
Pinus strobiformis Englm.	southwestern white pine	0.005	1.0	2,4
Galium trifidum L.	threepetal bedstraw	0.005	1.5	7,8,9
Gentianopsis detonosa (Rottb.) Ma	windmill fringed gentian	0.005	0.5	9
Lappula occidentalis (S.Wats.) Greene	flatspine stickseed	0.005	1.0	5
* *Lepidium virginicum* L. var. *pubescens* (Greene) Thellung	hairy pepperweed	0.005	1.0	5
Ranunculus inamoenus Greene	graceful buttercup	0.005	2.0	2,3
Cerastium brachypodum (Engelm. Ex Gray) B.L. Robins.	shortstalk chickweed	0.004	0.5	9
Oreochrysum parryi (Gray) Rydb.	Parry's goldenrod	0.004	1.0	1
Ranunculus macounii Britt.	Macoun's buttercup	0.004	1.0	8
Rosa nutkana C. Presl.	Nootka rose	0.004	1.0	4,3
Triglochin palustre L.	marsh arrowgrass	0.004	1.0	8,9
Veronica americana Schwein. ex Benth. in DC.	American speedwell	0.004	1.0	9
Artemisia frigida Willd.	fringed sage	0.003	1.5	5
Chenopodium fremontii S. Wats.	Fremont's goosefoot	0.003	1.5	4,3,6
Conioselinum scopulorum (A.Gray) J.M. Coult. & Rose	Rocky Mountain hemlockparsley	0.003	0.5	2
Festuca sororia Piper	ravine fescue	0.003	1.5	1,3,4
Polygonum aviculare L.	prostrate knotweed	0.003	0.5	9
Rudbeckia hirta L.	blackeyed Susan	0.003	0.5	1
Aquilegia elegantula Greene	western red columbine	0.002	0.5	2
Cirsium parryi (Gray) Petrak	Parry's thistle	0.002	1.0	6,9
Draba aurea Vahl. ex Hornem.	golden draba	0.002	1.0	5,6

→

App. 1, cont.

Binomial	Common name	Percent cover	Percent frequency	Groups
Linnaea borealis L.	twinflower	0.002	1.0	2,3
Maianthemum racemosum (L.) Link. var. *amplexicaule* (nutt.) Dorn	false lily-of-the-valley	0.002	1.0	2
* *Poa compressa* L.	Canada bluegrass	0.002	1.0	2,7
Sambucus racemosa L.	red elderberry	0.002	0.5	3
Spiranthes romanzoffiana	ladies tresses	0.002	1.0	8
Urtica dioica L. var. *procera* (Muhl. ex. Willd.) Wedd.	stinging nettle	0.002	1.0	2,3
Zigadenus elegans Pursch	mountain deathcamus	0.002	1.0	6
Juniperus scopulorum Sarg.	Rocky Mountain juniper	0.001	0.5	4
Bromus carinatus Hook. & Arn.	California brome	0.001	0.5	9
Corydalis aurea Willd.	golden smoke	0.001	0.5	2
Draba rectifructa C.L. Hitchc.	mountain draba	0.001	0.5	6
Erysimum capitatum (Douglas ex. Hook.) Greene	sanddune wallflower	0.001	0.5	5
Gentiana fremontii Torr.	moss gentian	0.001	0.5	9
Hymenoxys richardsonii (Hook.) Cockerell var. *floribunda* (A.Gray) Bierner	pingue rubberweed	0.001	0.5	4
Mimulus guttatus DC.	seep monkeyflower	0.001	0.5	9
Senecio eremophilus Richardson	desert ragwort	0.001	0.5	2
Senecio wootonii Greene	Wooton's ragwort	0.001	0.5	4
Shepherdia canadensis (L.) Nutt.	buffaloberry	0.001	0.5	3

OPULUSPRESS