



STRUCTURE AND CHANGE IN HERBACEOUS COMMUNITIES OF FOUR ECOSYSTEMS IN THE FRONT RANGE, COLORADO, U.S.A.*

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ABSTRACT

The structure of four herbaceous communities located in lower montane (2200 m), upper montane (2600 m), subalpine (3050 m), and alpine (3750 m) zones in the Front Range, Colorado, in 1981 was compared with that in 1953 when these same areas had been studied previously. Plant communities were compared primarily on the basis of number of species, species composition, species frequency, and community diversity. The herbaceous community at 2200 m had changed significantly since 1953 in frequencies and composition of species. The change is associated with a considerable disturbance of the tree canopy. The herbaceous community at 2600 m had remained relatively stable despite some moderate changes in the tree canopy. The herbaceous community at 3050 m was less diverse in 1981 than in 1953. The differences are associated with (1) successional changes in the overstory at this location and (2) the likelihood that somewhat different areas were studied in the 2 yr. The herbaceous community at 3750 m had shown remarkably little change in composition or relative abundances of species between 1953 and 1981.

The diversity of the herbaceous community at 2200 m in 1981 was significantly lower than the diversities of the communities at the other three elevations, possibly because this community is in an earlier successional stage due to recent disturbances. The herbaceous communities at 2200 and 2600 m had many species in common, but there were differences in frequencies of individual species. There was little overlap in species composition among the other communities.

At all elevations, the distribution of the species over frequency classes was quite similar for the herbaceous communities in 1953 and 1981, even when there were large differences in species composition between these dates. At the lower three elevations many species were present in low frequencies, and few species were common, while at 3750 m many species were common or abundant. Patterns of species abundance and estimates of species diversity did not coincide with each other across the four habitats.

INTRODUCTION

The steep elevational gradient of the Colorado Front Range, combined with great topographical diversity, accounts for well-defined plant communities in a variety of environmental conditions. Ramaley (1907) described

four different life zones above 1800 m in the Rocky Mountains of Colorado: the foothill zone, the montane zone, the subalpine zone, and the alpine zone. These zones reflect the changes in climate and, to a lesser extent, edaphic factors that accompany changes in elevation. Marr (1961) elaborated on this classification and named

*We dedicate this paper to John W. Marr.

the life zones climax regions. We will refer to these regions as "vegetation zones." Marr also established a series of environment measurement stations along an environmental gradient in Boulder County in 1951. In 1953, he described the communities near the stations, which are typical of the vegetation zones (Marr, 1961). Environmental data are still being collected at these stations by the University of Colorado, Institute of Arctic and Alpine Research.

Our primary objectives were to resurvey some of the communities studied in 1953 and to compare the herbaceous communities present at the two different times. In addition, we analyzed the structure of plant communities in the herb synusium (i.e., < 1 m) in detail. Sample plots were marked to allow future researchers to resample the same areas. In order to permit cross-reference with

Marr's (1961) work, some of his concepts, terms, and methods are used. The ecosystem containing the herbaceous community studied is called a stand. A vegetation zone, called climax region by Marr, is an area characterized by typical stand-types which may be either potential or realized.

This study was done on or near ridge-top sites, near the environment measurement stations at four elevations. At each site, one stand was surveyed. The structures of the vascular herbaceous communities of these stands in 1981 were compared to the 1953 data. They were also analyzed with respect to the number of species and species composition, the frequencies of the species and the distribution of the frequency classes, the diversity of the community, the distributional overlaps, and the associations of individual species.

STUDY AREAS

GEOGRAPHY

The four study areas (referred to as A-1, B-1, C-1, and D-1) and the approximate boundaries of the four vegetation zones (foothill, montane, subalpine, and alpine, respectively) are indicated on a map of the East Slope of the Front Range in Boulder County, Colorado (see Marr, 1961). The difference in elevation between the lower montane study area and the alpine study area is approximately 1550 m. The horizontal distance between these two locations is about 22 km.

ENVIRONMENT

The environmental conditions of the ridge-top stands are summarized in Figure 1 as a composite of five environmental parameters. There is a gradual decrease in air temperature and an increase in soil moisture along the elevational gradient. Annual rainfall is considerably higher in the subalpine and alpine zones than at lower elevations. Wind is also a major factor affecting the environment of the subalpine and alpine regions (Figure 1). The vegetation zones have distinct soil types (Marr, 1961).

STANDS

Ponderosa Pine Stand at 2200 m (A-1)

This stand is on a ridge south of Bummer's Gulch. In 1953 this stand consisted of many young trees and a very few mature trees over 100 yr old. Apparently the stand began to develop after a period of lumbering in the 1870s and was considered to be in an unstable successional stage in 1953 (Marr, 1961). Many ponderosa pine (*Pinus ponderosa*) trees died in 1955, probably from the effects of invasion of *Dendroctonus ponderosae*, the ponderosa pine bark beetle (Marr, pers. comm., 1980). Thus, major changes occurred shortly after the first survey. In addition, the ponderosa pine in this area have been severely infested with dwarf-mistletoe, *Arceuthobium vaginatum*. Subsequently, over 75% of the trees were killed by an epidemic of *D. ponderosae* from 1977 to 1980. The trees

which were not killed by pine beetles were vulnerable to wind throw, which has continued into the present time. Several mature trees were felled during heavy wind storms in January 1982. As a result of these disturbances, the tree canopy shades very little of the stand, and light is abundant.

Douglas-Fir/Ponderosa Pine Stand at 2600 m (B-1)

This stand is on the ridge of a hill just west of Sugarloaf Mountain and close to the Switzerland Trail. In 1953, large ponderosa pines and Douglas-firs (*Pseudotsuga menziesii*) were scattered individually or in small clumps throughout the stand. The Douglas-firs were over 350 yr old; the age of the oldest ponderosa pine tree was 122 yr. The two species had been present in about equal numbers before lumbering. The stand was considered to be successional in nature. It was expected that the stand would eventually return to approximately equal proportions of the two species. The vegetation was described as a mosaic of patches, with an abundance of herbs, and with *Arctostaphylos uva-ursi* on patches with deeper soil (Marr, 1961). From 1977 to 1980 deaths associated with the *D. ponderosae* invasion reduced the numbers of ponderosa pine by about 30%. In 1981, there was considerable evidence of damage to Douglas-fir by spruce budworm (*Choristoneura occidentalis*). The damage consisted of defoliation, but little or no tree mortality. Overall, some changes in the populations of ponderosa pine and Douglas-fir have taken place during most of the time interval between 1953 and 1981.

Aspen Stand at 3050 m (C-1)

The stand is on Hill's Mill Ridge, on a slope south of C-1 close to Four-Mile Creek. In 1953 this stand consisted of aspen (*Populus tremuloides*) trees ranging between 20 and 52 yr of age, and a large number of short ramets, probably of the same age as the trees but suppressed in growth. Seedlings and saplings of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and

limber pine (*Pinus flexilis*) were present at low frequencies. Before the aspen stand developed, the area was dominated by conifers as indicated from the stumps in the area. The aspen stand was considered to be transitional, and was expected to develop into a stable stand dominated by Engelmann spruce and subalpine fir (*Abies lasiocarpa*) in the absence of major disturbances (Marr, 1961). In 1981, we noted that, indeed, many of the large aspen trees had died, there were few new aspen ramets to take their place, and many young Engelmann spruce and subalpine fir were present in the stand.

Kobresia Meadow Stand at 3750 m (D-1)

The stand is on the crest of Niwot Ridge. The 1953 sur-

vey was conducted on the part of the stand surrounding the D-1 measurement station. Because of considerable traffic in this area, a permanent sampling strip was staked out west of the station and also west of a U.S. Geological Survey marker. The kobresia meadow stand was described in 1953 as a true climatic climax of the alpine tundra region of the Colorado Front Range, implying that the plant community would be mainly determined by the extremes of the physical environment (Marr, 1961). *Kobresia myosuroides* occupied the centers of large polygons, which measured 3 to 5 m across. *Acomastylis rossii*, *Trifolium dasyphyllum*, and *Selaginella densa* were abundant on coarser soil surrounding *Kobresia myosuroides*.

METHODS

FIELD

Details of field methods are provided in Kooiman Halford (1983). As indicated below in relevant places, whenever possible, our methods duplicated those of Marr (1961) in order to facilitate comparisons between the two

studies. The number of quadrats used by Marr varied with elevation. The numbers used are indicated in the relevant tables. At each study area we selected a sampling strip which appeared to be representative for the plant community as a whole. The phrase "study area" refers to the

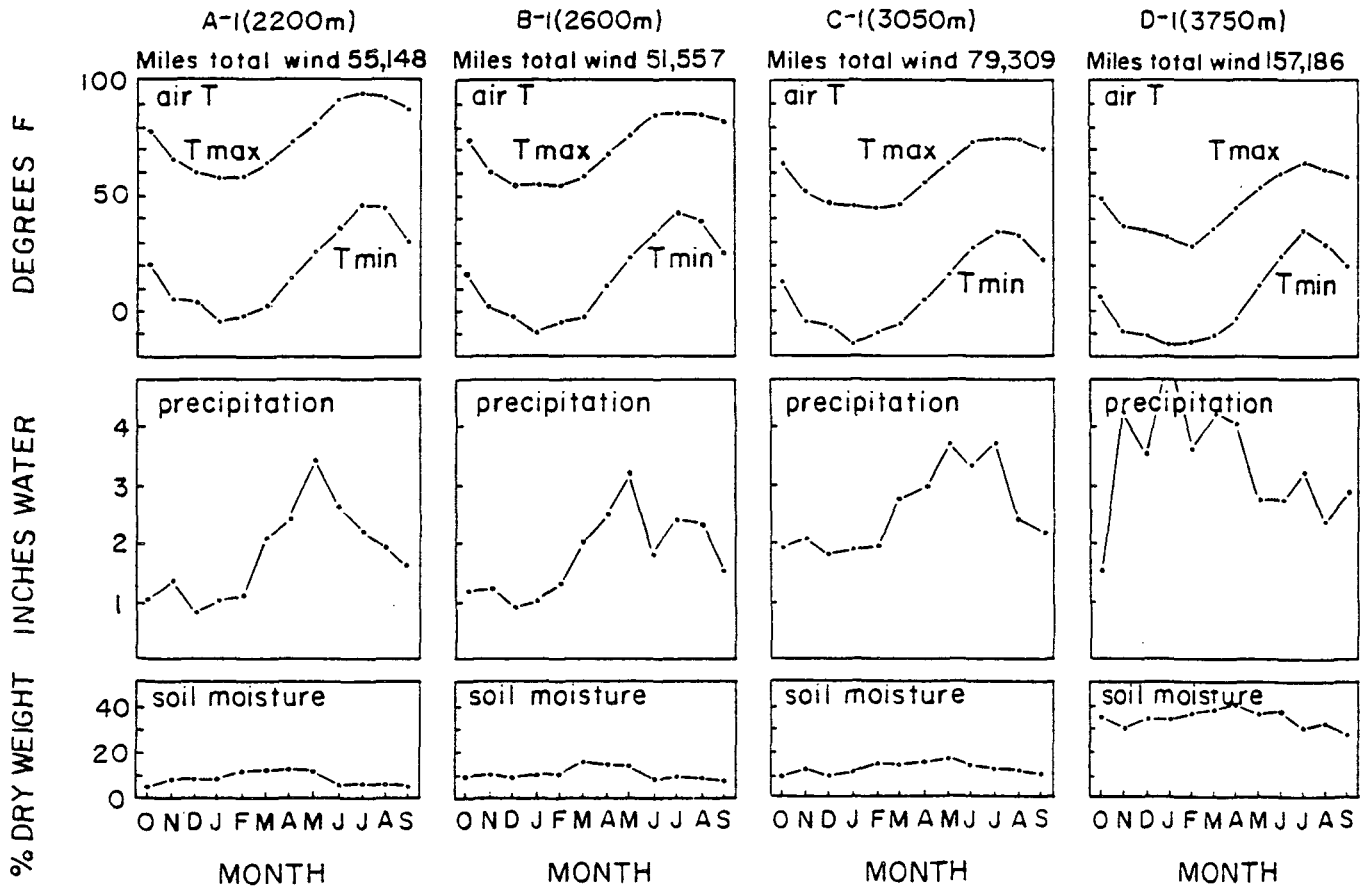


FIGURE 1. Climatological conditions at the four elevations. Shown are the mean monthly values over a period of 12 yr (1952-1964) for four parameters (run of wind, temperature, precipitation, soil moisture) collected by Marr (1961); original units of measurement are retained. The precipitation data for 3050 and 3750 m are mean values over a period of 5 yr (Barry, 1972).

location of the particular stand being studied. We were able to re-sample three of the study areas which were surveyed in 1953 by Marr (1961; and field visits). Iron stakes were driven into the ground at intervals of 10 m along a surveying line 100 m long. Every 2 m a plot was sampled along the line, alternately to the left and to the right of the line; this is an adaptation of Whittaker's 0.1-ha strip quadrat (Whittaker, 1973). The wooden frame used to delineate the plots was subdivided into 10 cells of equal size. It measured 85 by 100 cm and had approximately the same area as that used in 1953, which was 3 × 3 ft. The corners of the plots were marked with large nails to allow repeated sampling of the same plots during the growing season. The 50 plots are distributed over a sampling strip of 200 m².

Species present in the strip but not within the plots were also recorded. These additional species were not used for the statistical analyses but provided information against which the results of the analysis could be interpreted. For the sake of comparison, an effort was made to locate species present in 1953 which were not found in the sampling strips in 1981. Each strip was surveyed several times during the summer to insure that species emerging at different periods were included. At the lower elevations, data were collected during June, July, and August 1981. Only on Niwot Ridge (D-1) were all data collected during a single period of a few weeks in August, because flowering occurs primarily at that time.

COMMUNITY ATTRIBUTES

Plant community structure can be described by a number of parameters including number and abundance of species, species composition, species frequency, distribution of frequency classes, diversity, distributional overlaps, and associations between species.

Species Number

The number of species present is an indication of richness of a plant community. The jackknife procedure was used to estimate the number of species in a community; the estimate is a function of the number of unique species, i.e., species which occur in only one plot (Heltshe and Forrester, 1983). In the 1953 survey the shrubs were counted in plots of a different size than the herbaceous species. For this reason, we did not include the shrubs in the comparative study of the 2 yr. The following species were considered to be shrubs in the 1953 survey: *Aemilanchier alnifolia*, *Arctostaphylos uva-ursi*, *Ceanothus fendleri*, *Juniperus communis*, *Lonicera involucrata*, *Pentaphylloides floribunda*, *Ribes cereum*, *Rubus idaeus*, and *Vaccinium myrtilus*. At that time *Rosa acicularis* was treated as an herbaceous species and was therefore included with the herbaceous species of the aspen stand at 3050 m (C-1). Woody species with a height of less than 1 m were not used in the comparisons between 1953 and 1981. However, they were present in the herb synusium and therefore were included in the detailed analysis of the 1981 data. Mosses, lichens, trees, and tree-seedlings were excluded from the study.

Species Composition

All species found are listed in Appendix A. Botanical nomenclature follows Weber (1976) and Weber and Wittman (1982). Both current names and names used in 1953 are provided by Kooiman Halford (1983).

Species Abundance

We determined a measure of the abundance of a species in a given plot by noting its presence or absence in each of the 10 cells within a plot. Abundance values within an individual frame range from 0 to 10. This method of estimating abundance (which was not used in 1953) provides consistency and eliminates bias in sampling of all species regardless of variability in morphology and growth patterns (Kooiman Halford, 1983). It also allows resampling without a large personal bias. The abundances of all vascular plant species in the 50 plots were recorded in this fashion.

Species Frequency

The frequency of a species can be defined as the probability of finding the species within a plot in the sampling area. The measure is influenced by plot size and shape, and species distribution patterns. If plot sizes are equal and the number of plots is sufficiently large, comparisons of species frequencies may be made. The measure gives information about the uniformity of distribution of a species but not necessarily about the abundance of that species (Daubenmire, 1968). A plant is counted as present only if it is rooted within the sampling plot.

Distribution of Frequency Classes

The distribution of species over the different frequency classes shows the distribution patterns of the species within a community. Like the measure for frequency itself, the distribution over frequency classes depends upon the size and shape of the plot.

Measure of Diversity

The diversity of a community can be expressed in terms of the number of species present in a sampling unit placed within that community. This is the most fundamental measure of diversity (Whittaker, 1973; Poole, 1974). A measure of diversity which has its basis in information theory is the Shannon-Wiener diversity index (Shannon and Weaver, 1963). This index is based on the assumption that the number of species is known from the sampling. In reality, there are almost always species with a low frequency that may well go undetected. This introduces a particular kind of bias to this index, which is separate from the usual statistical bias. The degree of bias depends upon the accuracy of the estimate of the number of species. Jackknife estimates of diversity give generally a more accurate estimate of the diversity index than does Shannon's index directly, as a substantial amount of bias is reduced by the procedure (Sokal and Rohlf, 1981a; Zahl, 1977).

Distributional Overlap

Distributional overlap measures the degree to which two species use the same resources in a community. Its interpretation should not go beyond its use as an index of common use of resources by two species. Though it has been used frequently as an estimate of the degree of competition between two species, it may as well be interpreted as evidence against the existence of competition (Colwell and Futuyma, 1971; Ricklefs, 1979; Christensen and Peet, 1984). Methods of analysis are presented in the next section. A summary of the results is presented here. Detailed results are available in Kooiman Halford (1983).

Associations between Species

It is of interest to identify species which show a positive or a negative association with each other, since the concept of a community is based in part on the idea that there is interaction between species. Fisher's exact test for 2×2 frequency data was used to provide information on possible relationships between species (Rohlf, 1982). Detailed results are available in Kooiman Halford (1983).

DATA ANALYSES

There are several limitations to our data. Frequencies of the plant species were determined by noting the presence or absence of the species in a number of plots. The number of plots chosen strongly affects the precision of the estimate of the true frequency. Compromises had to be made between available time and precision of estimates based on data gathered in the field. The level of precision of an estimate based on 10, 20, or even 50 plots is quite low, and only large differences between communities can be detected (Greig-Smith, 1983). A plot size which is optimal for the type of plant community present at one location is not necessarily optimal for another type of plant community. In this study, the plot size was predetermined by the size of the sampling plots in the 1953 survey. An evaluation of the 1981 sampling techniques is provided in Kooiman Halford (1983).

COMPARISON BETWEEN THE PLANT COMMUNITIES IN 1953 AND IN 1981

A summary of the comparison between conditions and results in 1953 and 1981 is provided in Table 1. The vascular herbaceous and woody species recorded in 1981 are listed in Appendix A. A similar list of all species present in 1953 was compiled by Marr (1961). Detailed results of the data analyses comparing the plant communities which were present in the two different years are given in Figure 2, in Tables 1 and 2, and in Appendix B.

Ponderosa Pine Stand at 2200 m (A-1)

Table 1 shows that the number of herbaceous species found in 1953 is almost identical to the number of species

Comparisons between Results of 1953 and 1981

(1) The numbers of species which were present in the two years were tabulated.

(2) An estimate of the frequencies of the species was made based on their presence or absence within the quadrats. The 95% confidence intervals for the estimates were obtained from tables with confidence intervals for percentages based on the binomial distribution (Owen, 1962; Sokal and Rohlf, 1981b). A graphical representation was made of a species-by-species comparison between the plant communities of 1953 and 1981 for each of four elevations (Figure 2).

(3) The nonparametric rank coefficients (Kendall's tau and Spearman's r_s) were calculated for the plant communities in the different years, using the common species, i.e., with a frequency of at least 20% in either 1953 or 1981. The 20% frequency was used by Marr (1961) as a cut-off when tabulating his results. Species below that frequency were not ranked by frequency but simply listed if present in a community. Any ambiguous data were omitted, including species which were likely missed in 1981 because of the advanced season and species of questionable identity. The Spearman coefficients are given here. Results with Kendall's tau were very similar and are given in Kooiman Halford (1983).

Detailed Analysis of the 1981 Data

Diversity indices were calculated using the abundances of the plant species within the plots. As before, estimates of the diversity and the 95% confidence intervals were obtained using the jackknife procedure.

The calculations of distributional overlaps were done with use of a FORTRAN program by Colwell (1977). We calculated relative values of overlap by the so-called circular method: the same set of weighting factors was used for calculating the distributional overlap of all pairs of species. In addition, Fisher's exact test was used to identify positive and negative associations between species. The test is provided by Rohlf (1982). Only species with a frequency of at least 20% were included for these calculations.

RESULTS

present in an equal number in plots in 1981. Based on the rank correlation coefficients for the communities in the 2 yr, there is no significant relationship between the species rankings (Table 1) and little similarity in their relative frequencies (Figure 2). The changes in tree canopy in the ponderosa pine stand are associated with a significant turnover of herbaceous species in the interval between 1953 and 1981.

Douglas-Fir/Ponderosa Pine Stand at 2600 m (B-1)

In terms of the number of species present in 1953 and in 1981, the general pattern is very similar to that of the ponderosa pine stand at 2200 m (Tables 1 and 2). The number of species found in 1953 was very similar to the

number of species found in an equal number of plots in 1981. The total number of herbaceous species in the plots in 1981 was much higher than in 1953 because more plots were sampled. There is a significant rank correlation between the common species of the plant communities in this stand in the two years (Table 1), and their frequencies are also similar (Figure 2). The null hypothesis of independence is rejected.

Changes in the tree populations must have created continuing environmental changes for the herbaceous species in this Douglas-fir/ponderosa pine stand, but the reduction in canopy cover was much less severe at B-1 than at A-1. The stability of the herbaceous community in both composition and structure suggests that, at B-1, canopy changes had little impact on the herbaceous community, which contrasts with the situation at A-1.

Aspen Stand at 3050 m (C-1)

The total number of species in the 2 yr is notably similar. Even though only 12 plots were surveyed in 1953, the total number of herbs and shrubs equals the number of species tabulated for the whole strip in 1981. Rank correlation between the herbaceous communities of the aspen

stand in 1953 and 1981 is not significant. The high number of species tabulated in 1953 can probably be explained by the fact that the creek bed was included that year, while it was explicitly excluded from the 1981 survey which focused on a homogeneous stand to be consistent with methods at other elevations. The precise location of the 1953 survey could not be identified; consequently, the two surveys were probably conducted in slightly different areas. Successional changes also occurred in the overstory during the 1953 to 1981 time period (see "stand description"). Thus, the differences between the herbaceous communities in the two years can be explained by a combination of different sampling method, differences in locations, and successional changes in the tree populations.

Kobresia Meadow Stand at 3750 m (D-1)

The total number of species found within comparable numbers of plots in 1981 is similar to the number of species tabulated in 1953 (Table 1). The Shannon-Wiener diversity index is not significantly different for the two years (Table 2). Most species present in 1953 were also represented in 1981. Moreover, there is a good one-to-one correspondence between the frequencies of the indi-

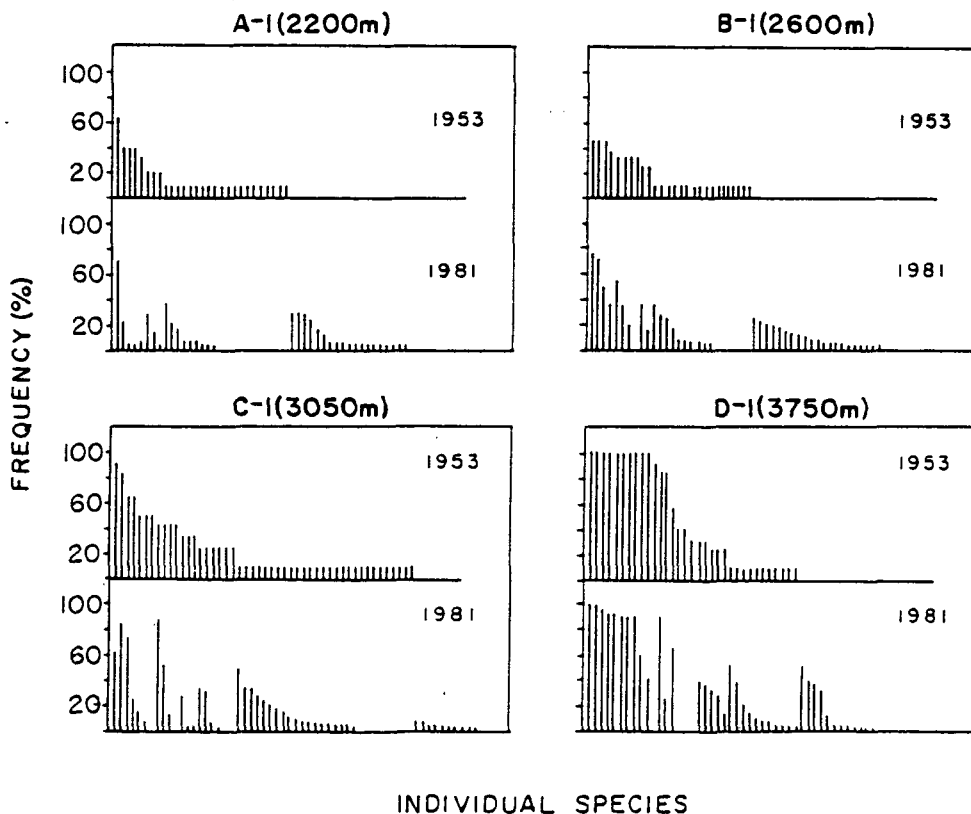


FIGURE 2. A species-by-species comparison between the plant communities in 1953 and 1981. Each species is represented for each elevation by its position on the abscissa. The percentage of plots in which the species was found (i.e., a measure of its frequency) is given along the ordinate. Presence of a species in the strip in 1981 but not within the plots is indicated by a dot on the abscissa. Species found only in 1953 or 1981 have blank spots in the corresponding location at the other time. Note that this produces an apparent bimodality in the 1981 distributions which is due to the fact that, at all elevations, some species were recorded in 1981, but not in 1953.

vidual species (Figure 2). The first five species show the same order in the 2 yr, and the two lists are remarkably similar (Appendix B). There is a highly significant rank correlation between the herbaceous communities in the 2 yr (Table 1). The results indicate that remarkably little change occurred in the kobresia meadow stand during the period between 1953 and 1981.

COMPARISON AMONG THE PLANT COMMUNITIES AT FOUR ELEVATIONS IN 1981

The great majority of the herbaceous species at all four elevations are perennial dicots. Strictly annual species are very rare (two to four species at the three lower elevations and none at 3750 m). The proportions of grasses and sedges (15 to 22%) are similar at all elevations. The large and consistent number of plots sampled, and the fact that data were collected with respect to the abundances of the species within the plots, make it possible to compare the plant communities at the different elevations in some detail (Tables 1 and 2).

The jackknife estimate of the diversity (based on abun-

dance) of the herbaceous community at 2200 m is significantly lower ($p < 0.05$) than the estimates for the three other communities (Table 2). As noted above, only about 80% of all species in the sampling strip were present within the plots at sites A-1 and B-1, which might be due to the fact that many species were represented in low frequency classes at this elevation. Even though much of the sampling bias will have been removed by the jackknife procedure, the low value of the estimated diversity may be due to the incomplete representation of species. The same argument would apply to the community at B-1. However, the jackknife estimate of diversity of the community at site B-1 is 3.15, which is significantly higher ($p < 0.05$) than the jackknife estimates of the diversities of the communities at C-1 (2.98) and D-1 (2.90). The diversity indices of the communities at C-1 and D-1 do not differ significantly from one another.

Table 1 shows the percentage of all species present in the plots, which are in the lower 10% and the upper 20% frequency classes. The species tend to become more equally distributed over all frequency classes at the higher

TABLE 1
Summary of major characteristics of herbaceous plant communities and general conditions in 1953 and 1981 at four elevations in the Colorado Front Range^a

Stand designation Location Features	Ponderosa Pine 2200 m (A-1) Drastic changes in forest canopy		Ponderosa/Doug.-fir 2600 m (B-1) Changes in tree canopy		Aspen 3050 m (C-1) Gradual successional changes in tree composition		Kobresia Meadow 3750 m (D-1) No drastic changes					
	1953	1981	1953	1981	1953	1981	1953	1981				
Year	1953	1981	1953	1981	1953	1981	1953	1981				
No. plots surveyed	15	15	50	16	16	50	12	12	50			
No. species in plots	28	29	36	27	31	40	50	25	45	33	27	41
No. species in strip			44			48			48			42
S (jackknife estimates)			48			48			52			47
(95% C.I.)			(40-55)			(41-54)			(46-57)			(42-52)
No. genera in strip			40			45			46			35
% species restricted to this stand			39			40			68			91
Diversity Index H												
Presence/absence	3.07		3.05	3.13		3.24	3.61		3.25	3.22		3.29
Abundance (jackknife estimate)			2.68			3.15			2.98			2.90
Rank correlation												
Coefficient between 1953 and 1981												
Spearman's <i>r</i>			-0.33			0.58			0.12			0.68
Significance of test			0.252			0.02			0.582			0.002
Percentage of species												
0-10% frequency (rare)			66.7			47.5			55.6			31.0
81-100% frequency (very frequent)			0			0			4.4			21.4
Percentage of significant associations												
Positive			26.6			6.7			13.3			7.2
Negative			4.4			7.6			7.6			1.4

^aS is jackknife estimate of number of species. 95% C.I. are confidence intervals. The 1953 to 1981 comparisons involved herbaceous species only. The 1981 analyses involve herbaceous species and shrubs <1 m tall. See text for details.

elevations; this is particularly marked in the kobresia meadow. The same pattern of increasing evenness of frequency distributions is shown in Figure 2.

The communities at 2200 and 2600 m have five species with a frequency of at least 20% in common (Appendix B). All common species at B-1 were at least present in the sampling strip at A-1, if not within the plots (Appendix A). Including all herbaceous and woody species found within the sampling strips, the plant communities at A-1 and B-1 have 27 species in common. A shift in frequencies of many species appears to be the major difference between the two herbaceous communities. The

proportion of species restricted to one stand increases greatly from 2600 m upwards (Table 1).

The values of distributional overlaps tend to be considerably higher at 3750 m than at the lower elevations due to the fact that many species are present at very high frequencies in this area. We considered the overlaps at the lower and higher end of the ranges as indices of a low or high similarity of resource utilization. Fisher's exact test shows a large number of significant positive and negative associations. In most cases, those associations agree with results obtained in analyses of overlaps (Kooiman Halford, 1981).

DISCUSSION

Ecological analyses of plant communities along elevational gradients have been very useful in revealing patterns of community structure and factors affecting such structure (Whittaker, 1967, 1975). The results of our study contribute further insights into these patterns. Other analyses of communities in the same geographical region provide an opportunity to study changes in community structure over time and space. Marr's data, which were collected in 1953 at the same or similar locations we chose for our work, can be used to look at changes over time. This temporal comparison is especially instructive because it involves plant communities growing near ongoing environment measurement stations. Therefore,

the physical environment within which vegetation changes have occurred has been monitored. In addition, Peet (1978, 1981) studied the forest vegetation of the Colorado Front Range, mainly in Rocky Mountain National Park, and Whittaker and Niering (1965) analyzed the vegetation of an elevational gradient in the Santa Catalina Mountains of Arizona. Results of these studies are compared to ours (see below).

In many studies of community structure, results based on calculations of species numbers (or "richness") and diversity appear to be quite similar (Poole, 1974; Ricklefs, 1979). In contrast, our results indicate that numbers and diversity do not follow a parallel course at the four sites

TABLE 2
Comparison of Shannon-Wiener diversity indices based either on presence/absence or on abundance of the herbaceous species in the plots^a

	Location (m)	Year	Q	H'	Jackknife H' 95% C.I. (S.E.)	H' _{min}	H' _{max}
Presence/absence	2200 (A-1)	1953	28	3.07		1.80	3.33
		1981	36	3.05	3.15 2.98-3.32 (0.084)	2.14	3.58
	2600 (B-1)	1953	27	3.13		1.76	3.30
		1981	40	3.24	3.30 3.21-3.39 (0.046)	2.29	3.69
	3050 (C-1)	1953	48	3.61		2.56	3.87
		1981	45	3.25	3.31 3.18-3.43 (0.062)	2.46	3.81
	3750 (D-1)	1953	33	3.22		2.39	3.50
		1981	41	3.29	3.31 3.25-3.37 (0.031)	2.30	3.71
Abundance	2200 (A-1)	1981	36	2.60	2.68 2.53-2.82 (0.072)	0.47	3.58
	2600 (B-1)	1981	40	3.08	3.15 3.05-3.25 (0.049)	0.53	3.69
	3050 (C-1)	1981	45	2.93	2.98 2.85-3.10 (0.062)	0.59	3.81
	3750 (D-1)	1981	41	2.89	2.90 2.84-2.96 (0.029)	0.54	3.71

^aQ: number of species; H': estimated diversity index; jackknife H': jackknife estimate of diversity index; C.I.: confidence interval; S.E.: standard error; H'_{min} and H'_{max}: minimum and maximum values of H' given Q species.

which we studied (Tables 1 and 2). The four communities have similar species numbers. However, these species are organized very differently as communities at the four elevations (Tables 1 and 2, Figure 2). In addition, species diversities show somewhat different trends depending upon the method of calculation (Table 2). Perhaps the lack of congruence is due to the fact that the range of variation in species numbers and diversities is small. It does suggest that no one measure provides an adequate summary of community characteristics. Only at 2200 m (A-1) was there a correlation between the smallest numbers of species recorded in the plots and the lowest estimates of diversity. The communities at 2200 m (A-1) and 2600 m (B-1) strongly resemble one another climatically (Figure 1) and biotically (they share over 60% of their species). Both are characterized by a great deal of spatial heterogeneity, with many species found in 10% or less of the plots and no species at high (>80% plots) frequency. At 2200 m, most species are rare (i.e., represented by few individuals), and species diversity is lowest, yet the proportion of positive associations between pairs of species is highest. At 2600 m fewer species are rare and the percentage of positive associations is much lower (Kooiman Halford, 1983). Both communities showed changes in the tree canopy, but the change at 2200 m was much more drastic. Exact measures of change in canopy cover are not possible since such cover was not recorded in 1953. However, based on the reduction in numbers of live trees, it can be estimated that the reduction amounted to approximately 70 to 80% at A-1 and 20 to 30% at B-1. The more drastic change at A-1 is associated with a significant alteration in species composition since 1953.

The aspen community at 3050 m (C-1) is subjected to a somewhat different climatic regime (Figure 1). This is reflected in the high proportion of species (68%) and genera (41%) unique to that location. Because of the presence of trees, it has a degree of spatial heterogeneity comparable to the communities at lower elevations, with many species found in 10% or less of the plots. Other species are distributed more uniformly and a few species were present at a frequency >80%. Differences between 1953 and 1981 are probably due to a combination of successional changes in the overstory, sampling differences, and the likelihood that somewhat different areas were studied in the 2 yr.

The kobresia meadow community at 3750 m (D-1) differs from lower communities in many respects. Environmental conditions are very different with much higher winds, higher total precipitation, and shorter growing season (Figure 1). As a result, few species from lower elevations can survive at this location, and more than 90% of the species and 57% of the genera in this community are unique to this elevation. Species are distributed much more uniformly over the plots than at other elevations. This is probably associated with a reduced environmental heterogeneity due to the absence of a tree canopy. The proportions of significant positive and negative associations are low in this community. A smaller plot size would presumably have allowed us to detect greater numbers

of these. This community has remained remarkably stable both in composition and relative abundance of species since 1953 (Tables 1 and 2).

Whittaker and Niering (1965) found an increase in richness (number of species per 0.1 ha) with decrease of elevation and moisture, from forests through woodlands to grasslands. They thought that a thinner tree canopy on the drier sites allowed more light to the herbaceous vegetation and thus allowed a greater richness on these sites. At a higher elevation the richness increased slightly in the transition from pine forests to fir forests. Whittaker (1975) pointed out that broadleaf deciduous forests on the average maintain a considerably higher number of species than do conifer forests in a similar environment as a result of a different character of leaf litter and a different chemical constitution of the top soil. In our study, the aspen stand at 3050 m supports a far richer undergrowth than an adjacent lodgepole pine stand.

For several reasons it is difficult to make comparisons between Peet's (1978) results and ours except in very general terms. He used a frame of 1 m², while our frame was 0.85 m². This difference in plot size affects all measures of frequency and diversity. Peet calculated diversity indices for his communities with values which reflected estimates of both frequency and cover of the species (Peet, pers. comm., 1984). The assignment of our stands to his community types can only be approximate. In his studies, Peet (1978) also found a general trend toward an increase in species richness with decrease in elevation. Within the intermediate elevations, the lowest numbers of species were found at sites with an intermediate moisture level. A relatively high species richness was found at the transitions from forest to grass or shrub communities, at the limits of his study region. He did not extend his work above treeline. He reported the presence of many rare species at lower elevations, which agrees with our observations.

Taking all species of herbs and shrubs in the 200-m² strips into consideration, we found the species richness to be very similar at the three lower sites and somewhat lower at the kobresia meadow site.

The relatively high number of species at 3050 m may be explained by the fact that the aspen stand is in a transitional stage. It is made up of aspen ramets and young conifers. As yet it is still a fairly open stand with more light available to the herbaceous species than there is in conifer forests, which may account for a high number of species in the plots.

With respect to species diversity, Peet (1978) stated that this measure appeared to be affected by the following three parameters: elevation, site moisture conditions, and the successional status of the stand. He found no single pattern. In general, the forests which were intermediate with respect to the three parameters had the lowest diversities. Relatively high diversities were found at sites with harsh environments. Whittaker and Niering (1965) found that in drier areas diversity frequently peaks at intermediate elevations. This agrees with our result of a maximum diversity of the community at 2600 m.

The relatively low level of abundance-based species diversity we found at the 3750-m elevation may be explained on the basis of the high stability of the stand. Kobresia meadows have been described as exceptionally stable communities (Osburn, 1958; Willard, 1963). Willard (1963) believed that some of these kobresia stands may have taken up to 1000 yr to develop. The shallow, dense root system is competing so effectively for water that species with long taproots may eventually be excluded (Osburn, 1958). Kiener (1967) reported that with increase in stand age, *Kobresia myosuroides* becomes increasingly common. The result is a decrease in the species diversity of the community.

Studies in some ecosystems have demonstrated that species diversity is associated with habitat heterogeneity and with periodic and patchy disturbance (e.g., Connell, 1978; Spurr and Barnes, 1980). This relationship does not hold in the herbaceous communities studied here. The most homogeneous and least disturbed community by far is the kobresia meadow and it has intermediate species richness and diversity. Conversely, the heterogeneous and disturbed ponderosa pine community has the lowest richness and diversity.

The difference in constitution between the kobresia meadow and the other communities brings to mind the difference in viewpoints between the Clements (1916) and Ramensky (1924)-Gleason (1926) perspectives. Environmental conditions at the tundra site are so different from

those at lower elevations that the species community is quite different. The kobresia meadow has identifiable boundaries and is an illustration of a closed community. At lower elevations environmental conditions form more of a continuum, distributions overlap to a greater degree, the communities are much more open systems, and noticeable continuum of distributions.

In two of the three communities (2600 m and 3050 m) where the vegetation was sampled in the same areas in 1953 and 1981 the structure of the herbaceous communities showed remarkable stability over the 28 yr. The similarities of structure involve both the relative abundance of the species present and the hierarchy of abundances, with some species being very common and others rare, and stable for long periods.

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APPENDIX A SPECIES LIST

List of vascular herbaceous and woody species and their abundances tabulated in the 1981 survey of four study areas. Abundances were determined from presence in 10 individual cells within 50 quadrats per location; thus, maximum abundance per location is 500. Trees (marked with *) were not used in the analyses. This list includes 145 herbaceous species in 102 genera.

Name of species	2200 m (A-1)	2600 m (B-1)	3050 m (C-1)	3750 m (D-1)	Name of species	2200 m (A-1)	2600 m (B-1)	3050 m (C-1)	3750 m (D-1)
<i>Abies lasiocarpa</i>	—	—	*	—	<i>Artemisia ludoviciana</i>	37	90	0	0
<i>Acetosella vulgaris</i>	0	0	0	1	<i>Artemisia scopulorum</i>	0	0	0	15
<i>Achillea lanulosa</i>	7	33	157	0	<i>Aster campestris</i>	†	0	0	0
<i>Acomastylis rossii</i>					<i>Aster foliaceus</i>	0	0	33	0
<i>ssp. turbinata</i>	0	0	0	409	<i>Aster porteri</i>	1	1	0	0
<i>Aletes acaulis</i>	†	39	2	0	<i>Astragalus adsurgens</i> var.				
<i>Allium cernuum</i>	†	1	0	0	<i>robustior</i>	0	7	0	0
<i>Amelanchier alnifolia</i>	4	†	0	0	<i>Astragalus shortianus</i>	0	4	0	0
<i>Androsace septentrionalis</i>	0	†	2	0	<i>Astragalus tenellus</i>	0	16	0	0
<i>Anisantha tectorum</i>	11	0	0	0	<i>Bahia dissecta</i>	0	1	0	0
<i>Antennaria parviflora</i>	4	†	34	0	<i>Besseyia alpina</i>	0	0	0	1
<i>Antennaria rosea</i>	0	0	15	0	<i>Bistorta bistortoides</i>	0	0	0	181
<i>Anticlea elegans</i>	0	0	8	1	<i>Bistorta douglasii</i>	0	0	10	0
<i>Arabis fendleri</i>	†	25	0	0	<i>Bistorta vivipara</i>	0	0	0	34
<i>Arctostaphylos uva-ursi</i>	76	75	0	0	<i>Boechera drummondii</i>	0	0	6	0
<i>Arenaria fendleri</i>	0	0	0	36	<i>Calamagrostis canadensis</i>	0	0	7	0
<i>Artemisia campestris</i> ssp.					<i>purpurascens</i>	0	0	0	2
<i>caudata</i>	0	†	0	0	<i>Caltha leptosepala</i>	0	0	6	0
<i>Artemisia frigida</i>	0	†	0	0	<i>Campanula rotundifolia</i>	3	0	24	0

APPENDIX A (cont.)

Name of species	2200 m (A-1)	2600 m (B-1)	3050 m (C-1)	3750 m (D-1)	Name of species	2200 m (A-1)	2600 m (B-1)	3050 m (C-1)	3750 m (D-1)
<i>Campanula uniflora</i>	0	0	0	198	<i>Lonicera involucrata</i>	0	0	4	0
<i>Carex albonigra</i>	0	0	0	13	<i>Lupinus argenteus</i>	0	1	81	0
<i>Carex arapahoensis</i>	0	0	0	5	<i>Mertensia ciliata</i>	0	0	2	0
<i>Carex heliophila</i>	237	136	0	0	<i>Mertensia lanceolata</i>	20	5	0	0
<i>Carex norvegica</i>	0	0	0	6	<i>Mertensia viridis</i>	0	0	0	57
<i>Carex norvegica</i> ssp. <i>norvegica</i>	0	0	0	2	<i>Minuartia obtusiloba</i>	0	0	0	87
<i>Carex occidentalis</i>	0	0	28	0	<i>Muhlenbergia montana</i>	1	8	0	0
<i>Carex rupestris</i>	0	0	0	3	<i>Oreoxis alpina</i>	0	0	0	424
<i>Castilleja occidentalis</i>	0	0	0	†	<i>Orthilia secunda</i>	0	0	46	0
<i>Ceanothus fendleri</i>	†	0	0	0	<i>Oxytropis fendleri</i>	0	0	9	0
<i>Cerastium beeringianum</i>					<i>Oxytropis multiceps</i>	0	†	0	0
ssp. <i>earlei</i>	0	0	0	1	<i>Penstemon virens</i>	6	111	†	0
<i>Chamerion angustifolium</i>	0	0	230	0	<i>Penstemon whippleanus</i>	0	0	4	0
<i>Chenopodium atrovirens</i>	5	0	0	0	<i>Pentaphylloides floribunda</i>	0	0	34	†
<i>Chenopodium fremontii</i>	0	11	0	0	<i>Phacelia heterophylla</i>	28	16	0	0
<i>Chenopodium</i> sp.	0	0	4	0	<i>Phleum commutatum</i>	0	0	†	0
<i>Cirsium centaureae</i>	0	0	†	0	<i>Phlox sibirica</i> ssp. <i>pulvinata</i>	0	0	0	214
<i>Clematis rhodantha</i>	0	0	1	0	<i>Picea engelmannii</i>	—	—	*	—
<i>Collinsia parviflora</i>	48	3	0	0	<i>Pinus contorta</i> var. <i>latifolia</i>	—	—	*	—
<i>Cryptantha</i> sp.	0	†	0	0	<i>Pinus ponderosa</i> var. <i>scopulorum</i>	*	*	—	—
<i>Cystopteris fragilis</i>	0	0	2	2	<i>Poa agassizensis</i>	1	0	0	0
<i>Danthonia intermedia</i>	0	0	0	2	<i>Poa fendleriana</i>	6	2	0	0
<i>Danthonia parryi</i>	0	0	8	0	<i>Poa glauca</i>	0	0	0	73
<i>Delphinium nelsonii</i>	6	0	0	0	<i>Poa nemoralis</i> ssp. <i>interior</i>	0	0	3	0
<i>Delphinium</i> sp.	0	7	0	0	<i>Polemonium viscosum</i>	0	0	0	67
<i>Decathea pulchellum</i>	0	0	29	0	<i>Populus tremuloides</i>	—	—	*	—
<i>Draba streptocarpa</i>	0	0	1	0	<i>Potentilla gracilis</i> var. <i>pulcherrima</i>	0	0	92	0
<i>Drymocallis fissa</i>	65	45	0	0	<i>Potentilla hippiana</i>	0	†	0	0
<i>Elymus canadensis</i>	†	0	0	0	<i>Potentilla nivea</i>	0	0	0	54
<i>Elymus longifolius</i>	3	0	0	0	<i>Potentilla rubricaulis</i>	0	0	0	39
<i>Elymus</i> sp.	0	0	2	0	<i>Pseudocymopterus</i> <i>montanus</i>	0	0	26	0
<i>Eriogonum compositus</i>	0	9	0	0	<i>Pseudotsuga menziesii</i>	*	*	—	—
<i>Eriogonum umbellatum</i>	14	7	0	0	<i>Pulsatilla patens</i> ssp. <i>multifida</i>	0	1	0	0
<i>Eritrichium aretioides</i>	0	0	0	38	<i>Pyrola minor</i>	0	0	1	0
<i>Erysimum asperum</i>	0	2	0	0	<i>Ribes cereum</i>	2	3	0	0
<i>Erysimum capitatum</i>	0	0	0	25	<i>Rosa acicularis</i>	0	0	58	0
<i>Euphorbia robusta</i>	1	0	0	0	<i>Rubus deliciosus</i>	0	†	0	0
<i>Festuca saximontana</i>	0	†	0	0	<i>Rubus idaeus</i> ssp. <i>melanolasius</i>	0	†	0	0
<i>Fragaria ovalis</i>	0	0	252	0	<i>Salix</i> sp.	0	0	†	0
<i>Gaillardia aristata</i>	3	25	0	0	<i>Saxifraga rhomboidea</i>	0	0	0	14
<i>Gayophytum nuttallii</i>	46	43	5	0	<i>Schizachyrium scoparium</i>	†	0	0	0
<i>Geranium caespitosum</i>	9	9	0	0	<i>Scutellaria brittonii</i>	67	29	0	0
<i>Gilia pinnatifida</i>	0	14	0	0	<i>Sedum lanceolatum</i>	0	58	10	0
<i>Harbouria trachypleura</i>	6	36	3	0	<i>Senegalinella densa</i>	0	11	51	177
<i>Helictotrichon mortonianum</i>	0	0	0	38	<i>Senecio fendleri</i>	2	43	0	0
<i>Heterotheca fulcrata</i>	0	12	0	0	<i>Senecio integerrimus</i>	69	0	0	0
<i>Heterotheca villosa</i>	7	0	0	0	<i>Senecio triangularis</i>	0	0	2	0
<i>Hymenoxys grandiflora</i>	0	0	0	5	<i>Silene acaulis</i> ssp. <i>subcaulescens</i>	0	0	0	20
<i>Juncus arcticus</i> ssp. <i>ater</i>	0	0	48	0	<i>Silene scouleri</i> ssp. <i>hallii</i>	0	0	6	0
<i>Juniperus communis</i> ssp. <i>alpina</i>	45	0	4	0	<i>Smilacina</i> sp.	†	0	3	0
<i>Kobresia myosuroides</i>	0	0	0	353	<i>Solidago missouriensis</i>	110	0	0	0
<i>Koeleria macrantha</i>	0	16	0	0					
<i>Lesquerella montana</i>	1	2	0	0					
<i>Leucocrinum montanum</i>	2	0	0	0					
<i>Leucopoa kingii</i>	28	75	0	0					
<i>Lewisia pygmaea</i>	0	0	0	1					
<i>Liatris punctata</i>	1	0	0	0					
<i>Lloydia serotina</i>	0	0	0	320					

APPENDIX A (cont.)

Name of species	2200 m 2600 m 3050 m 3750 m				Name of species	2200 m 2600 m 3050 m 3750 m			
	(A-1)	(B-1)	(C-1)	(D-1)		(A-1)	(B-1)	(C-1)	(D-1)
<i>Solidago multiradiata</i>	0	58	34	0	<i>Tragopogon dubius</i>	2	0	0	0
<i>Sporobolus cryptandrus</i>	†	0	0	0	<i>Trifolium dasyphyllum</i>	0	0	0	254
<i>Stipa comata</i>	1	0	0	0	<i>Trifolium nanum</i>	0	0	0	55
<i>Stipa lettermanii</i>	0	5	0	0	<i>Trisetum spicatum</i>	0	0	8	0
<i>Taraxacum ceratophorum</i>	0	0	0	79	<i>Vaccinium myrtillus</i> ssp.				
<i>Taraxacum officinale</i>	0	0	87	0	<i>oreophilum</i>	0	0	25	0
<i>Thermopsis divaricarpa</i>	0	0	51	0	<i>Verbascum thapsus</i>	5	0	0	0
<i>Thlaspi montanum</i>	0	0	0	11	<i>Veronica wormskjoldii</i>	0	0	4	0
<i>Tonestus pygmaeus</i>	0	0	0	16					

†Not present in the plots, but found along the transect.

APPENDIX B

Herbaceous species, which were present at a frequency of at least 20% in either 1953 or 1981, are presented in order of decreasing frequency. The 95% confidence limits (C.I.) for a binomial distribution are given in parentheses. The arbitrary frequency 10% was assigned for ranking purposes to the species which were present in 1953 in fewer than 20% of the plots.

PONDEROSA PINE STAND
(A-1)

1953 (15 plots)		1981 (50 plots)	
<i>Carex heliophila</i>	67(38-88)	<i>Carex heliophila</i>	72(58-84)
<i>Geranium caespitosum</i>	40(16-68)	<i>Scutellaria brittonii</i>	38(25-53)
<i>Harbouria trachypleura</i>	40(16-68)	<i>Collinsia parviflora</i>	30(18-45)
<i>Drymocallis fissa</i>	40(16-68)	<i>Gayophytum nuttallii</i>	30(18-45)
<i>Heterotheca villosa</i>	33(12-62)	<i>Solidago missouriensis</i>	30(18-45)
<i>Gayophytum nuttallii</i>	20(4-48)	<i>Senecio integerrimus</i>	28(16-42)
<i>Antennaria parviflora</i>	20(4-48)	<i>Phacelia heterophylla</i>	24(13-38)
<i>Eriogonum umbellatum</i>	20(4-48)	<i>Leucopoa kingii</i>	22(12-36)
<i>Leucopoa kingii</i>	10	<i>Drymocallis fissa</i>	22(12-36)
<i>Scutellaria brittonii</i>	10	<i>Eriogonum umbellatum</i>	14(6-27)
		<i>Heterotheca villosa</i>	8(1-23)
		<i>Geranium caespitosum</i>	6(1-17)
		<i>Harbouria trachypleura</i>	4(0-14)
		<i>Antennaria parviflora</i>	2(0-11)

DOUGLAS-FIR/PONDEROSA PINE STAND
(B-1)

1953 (16 plots)		1981 (50 plots)	
<i>Carex heliophila</i>	45(20-69)	<i>Carex heliophila</i>	76(62-87)
<i>Penstemon virens</i>	45(20-69)	<i>Penstemon virens</i>	72(58-84)
<i>Leucopoa kingii</i>	45(20-69)	<i>Artemisia ludoviciana</i>	54(39-68)
<i>Drymocallis fissa</i>	38(15-64)	<i>Leucopoa kingii</i>	50(36-64)
<i>Artemisia ludoviciana</i>	31(11-58)	<i>Aletes acaulis</i>	36(23-51)
<i>Harbouria trachypleura</i>	31(11-58)	<i>Drymocallis fissa</i>	36(23-51)
<i>Achillea lanulosa</i>	31(11-58)	<i>Harbouria trachypleura</i>	34(21-49)
<i>Lithospermum incisum</i>	31(11-58)	<i>Sedum lanceolatum</i>	34(21-49)
<i>Sedum lanceolatum</i>	25(7-52)	<i>Senecio fendleri</i>	28(16-42)
<i>Geranium caespitosum</i>	25(7-52)	<i>Gayophytum nuttallii</i>	24(13-38)
<i>Aletes acaulis</i>	10	<i>Phacelia heterophylla</i>	24(13-38)

APPENDIX B (cont.)

DOUGLAS-FIR/PONDEROSA PINE STAND

1953 (12 plots)		1981 (50 plots)	
<i>Gayophytum nuttallii</i>	10	<i>Arabis fendleri</i>	22(12-36)
<i>Senecio fendleri</i>	10	<i>Achillea lanulosa</i>	20(10-34)
		<i>Solidago multiradiata</i>	20(10-34)

ASPEN STAND
(C-1)

1953 (12 plots)		1981 (50 plots)	
<i>Taraxacum officinale</i>	92(62-100)	<i>Chamerion angustifolium</i>	90(78-97)
<i>Fragaria ovalis</i>	83(52-100)	<i>Fragaria ovalis</i>	86(73-94)
<i>Achillea lanulosa</i>	66(35-90)	<i>Achillea lanulosa</i>	74(60-85)
<i>Antennaria parviflora</i>	66(35-90)	<i>Taraxacum officinale</i>	64(49-77)
<i>Carex bella</i> and <i>C. foenea</i>	50(21-79)	<i>Lupinus argenteus</i>	52(37-66)
<i>Trifolium repens</i>	50(21-79)	<i>Potentilla gracilis</i>	50(36-64)
<i>Caltha leptosepala</i>	50(21-79)	<i>Juncus arcticus</i>	34(21-49)
<i>Chamerion angustifolium</i>	42(15-72)	<i>Pseudocymopterus montanus</i>	34(21-49)
<i>Lupinus argenteus</i>	42(15-72)	<i>Selaginella densa</i>	34(21-49)
<i>Sedum lanceolatum</i>	42(15-72)	<i>Solidago multiradiata</i>	32(20-47)
<i>Ligusticum porteri</i>	42(15-72)	<i>Campanula rotundifolia</i>	28(16-42)
<i>Poa pratensis</i> and <i>P. palustris</i>	33(10-65)	<i>Rosa acicularis</i> ^a	28(16-42)
<i>Rosa acicularis</i> ^a	33(10-65)	<i>Thermopsis divaricarpa</i>	26(15-40)
<i>Clematis rhodantha</i>	33(10-65)	<i>Antennaria parviflora</i>	24(13-38)
<i>Draba streptocarpa</i>	25(5-57)	<i>Aster foliaceus</i>	20(10-34)
<i>Pseudocymopterus montanus</i>	25(5-57)	<i>Sedum lanceolatum</i>	12(5-24)
<i>Arnica cordifolia</i>	25(5-57)	<i>Bistorta</i> spp.	8(1-23)
<i>Bistorta vivipara</i>	25(5-57)	<i>Caltha leptosepala</i>	8(1-23)
<i>Solidago multiradiata</i>	25(5-57)	<i>Clematis rhodantha</i>	2(0-11)
<i>Viola adunca</i>	25(5-57)	<i>Draba streptocarpa</i>	2(0-11)
<i>Aster foliaceus</i>	10	<i>Poa nemoralis</i>	2(0-11)
<i>Campanula rotundifolia</i>	10		
<i>Juncus arcticus</i>	10		
<i>Potentilla gracilis</i>	10		
<i>Selaginella densa</i>	10		
<i>Thermopsis divaricarpa</i>	10		

^aThis woody species was tabulated with the herbaceous species in 1953.

KOBRESIA MEADOW STAND
(D-1)

1953 (12 plots)		1981 (50 plots)	
<i>Acomastylis rossii</i>	100(74-100)	<i>Acomastylis rossii</i>	98(89-100)
<i>Oreoxis alpina</i>	100(74-100)	<i>Oreoxis alpina</i>	98(89-100)
<i>Campanula uniflora</i>	100(74-100)	<i>Campanula uniflora</i>	94(84-99)
<i>Kobresia myosuroides</i>	100(74-100)	<i>Kobresia myosuroides</i>	92(81-99)
<i>Lloydia serotina</i>	100(74-100)	<i>Lloydia serotina</i>	92(81-99)
<i>Phlox sibirica</i>	100(74-100)	<i>Bistorta bistortoides</i>	90(78-9)
<i>Selaginella densa</i>	100(74-100)	<i>Phlox sibirica</i>	90(78-9)
<i>Trifolium dasyphyllum</i>	100(74-100)	<i>Selaginella densa</i>	88(76-)
<i>Minuartia obtusiloba</i>	100(74-100)	<i>Trifolium dasyphyllum</i>	88(76-)
<i>Eritrichium aretioides</i>	100(74-100)	<i>Poa glauca</i>	66(51-)
<i>Carex scopulorum</i>	92(62-100)	<i>Minuartia obtusiloba</i>	58(43-)
<i>Bistorta bistortoides</i>	83(52-100)	<i>Helicotrichon mortonianum</i>	52(37-)
<i>Bistorta vivipara</i>	83(52-100)	<i>Taraxacum ceratophorum</i>	52(37-)
<i>Poa arctica</i>	58(28-85)	<i>Eritrichium aretioides</i>	42(2-)
<i>Draba albertina</i>	42(15-72)	<i>Mertensia viridis</i>	40(2-)
<i>Draba fladnizensis</i>	42(15-72)	<i>Potentilla nivea</i>	40(2-)
<i>Comastoma tenellum</i>	33(10-65)	<i>Trifolium nanum</i>	40(2-)

APPENDIX B (cont.)

1953 (16 plots)		KOBRESIA MEADOW STAND		1981 (50 plots)	
<i>Potentilla rubricaulis</i>		33(10- 65)	<i>Erysimum capitatum</i>		
<i>Trifolium nanum</i>		33(10- 65)	<i>Potentilla rubricaulis</i>		
<i>Arenaria fendleri</i>		25(5- 57)	<i>Arenaria fendleri</i>		
<i>Saxifraga rhomboidea</i>		25(5- 57)	<i>Polemonium viscosum</i>		
<i>Silene acaulis</i>		25(5- 57)	<i>Bistorta vivipara</i>		
<i>Mertensia viridis</i>		10	<i>Silene acaulis</i>		
<i>Taraxacum ceratophorum</i>		10	<i>Thlaspi montanum</i>		
<i>Thlaspi montanum</i>		10	<i>Saxifraga rhomboidea</i>		

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