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Changes in stand composition and structure between 1981 and 1996 in four Front Range plant communities in Colorado

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Abstract

We conducted a study analyzing the vegetation dynamics in four communities along an elevational gradient in the Front Range of the Colorado Rocky Mountains and compared our results with previous research conducted in 1981. The objective of this study was to determine whether the successional plant community trajectories hypothesized by the original investigator (Marr) in 1953 were consistent with plant community parameters measured in subsequent years. The ponderosa pine and Douglas-fir/ponderosa pine communities' herbaceous composition remained relatively constant between 1981 and 1996; however, a few individual species in both communities experienced significant changes in frequency over time. These individual species changes, along with dominant shifts in the forest canopy, were inconsistent with Marr's original successional hypotheses for these stands that stated the ponderosa pine stand would remain dominated by ponderosa pine and grassy openings and the Douglas-fir/ponderosa pine stand would eventually have equal dominance between the two tree species. The aspen herbaceous community experienced the most significant change between 1981 and 1996. Significant decreases in species richness and diversity were recorded along with large changes in species composition and frequencies of individual species. These changes were associated with successional changes in the forest canopy, which was congruent with Marr's successional hypothesis for this stand. The kobresia meadow herbaceous community showed the least change between 1981 and 1996 among the four communities; however, there was variation in frequency percentages for a few individual species over time and a small turnover in species composition. Marr's hypothesis that this stand represented a climax community is consistent with our results.

Introduction

Long-term ecological studies are essential for understanding the dynamics of natural systems. They provide a framework for distinguishing isolated events from successional changes and allow researchers to better interpret the mechanisms behind change by penetrating the 'invisible present' created in short-time studies (Magnuson et al. 1991). Short-term studies do not reveal slow changes that occur over many years, leading to possible misinterpretations of unusual events (Weatherhead 1986).

Our research continued and expanded upon the only long-term study along an elevational gradient in the Colorado Front Range, started by Marr (1961) and continued by Kooiman and Linhart (1986). Specifically, our primary objective was to determine if successional plant community trajectories hypothesized by Marr in 1953 were congruent with stand dynamics in 1981 and 1996. This study is useful in developing a record of the vegetation dynamics for plant communities in this region and improving our understanding of the ecological processes along this elevational gradient.

Historical methods of classifying Rocky Mountain vegetation by elevation have divided the landscape into regions of similar environmental conditions and vegetation. Ramaley (1907) conducted the first general classification of vegetation in the Colorado Rocky Mountains, dividing it into four life zones above

1800 m: the foothills zone, the montane zone, the subalpine zone, and the alpine zone. Marr (1961) refined these life zones into four climax regions with distinct patterns of stand types based primarily on elevation. Marr (1961) defined a stand as a 'concrete unit' of vegetation that could be researched in detail. In 1953, Marr (1961) established environmental measurement stations and conducted a quantitative analysis of the plant communities for each climax region in the Front Range. In addition, he hypothesized how each stand would change over time from these data and the scientific literature. Marr (1961) predicted the successional trajectory for the ponderosa pine stand to be an open park-like stand of ponderosa pine (*Pinus ponderosa*) and the successional trajectory for the Douglas-fir/ponderosa pine stand to be composed of equal dominance of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine. In addition, Marr (1961) hypothesized the aspen stand to become an Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies bifolia*) steady state stand and he predicted the kobresia meadow stand would remain a dry meadow climax community. Kooiman and Linhart (1986) continued this analysis by resurveying the general area of Marr's study sites for each climax region in 1981 to examine changes in the herbaceous communities studied almost thirty years prior.

Study Area

The study area is situated along an elevational gradient between the drainage basins of North Boulder Creek and Left Hand Creek within Boulder County (Marr 1961). The foothills (ponderosa pine stand) and alpine (kobresia meadow stand) zones are separated by approximately 1550 m in elevation and 22 km in horizontal distance. The relative boundaries of the four climax regions and study sites are provided in Marr (1961) for the east slope of the Front Range in Boulder County, Colorado. Within each study site, Marr (1961) selected ridge-top stands to study based on their proximity to environmental measurement stations and their apparent representation of homogenous herbaceous communities 'typical' of the Front Range. Kooiman permanently marked these ridge-top stand locations with iron stakes in 1981 based upon written records (Marr 1961), field visits, and personal communication with Marr (Kooiman & Linhart 1986).

Methods

Field methods

We resurveyed the permanently marked ridge-top stands in each climax region during 1996. The exact methodology used by Kooiman & Linhart (1986) was replicated to permit accurate comparison between the two surveys. We collected data on the frequency, abundance, and percent ground cover of herbaceous plants in fifty plots measuring 85 × 100 cm at each ridge-top stand. An 85 × 100 m wooded frame, divided into 10 equal cells, was positioned on top of every plot in each stand. These fifty plots were systematically located every two meters alternating to the left and right of a 100 m surveying line. We recorded all species present in each cell and considered a species as present if it had one or more individuals rooted within the cell.

In addition, we attempted to locate species encountered during the 1981 survey that were not present in the plots during the 1996 survey. We surveyed each stand at least twice a month throughout the growing season to detect species appearing at different times. Field work began in mid-May and continued through early September 1996, with a progressively later starting date with increasing elevation due to the later persistence of snow cover.

We conducted forest structure analyses at the ponderosa pine, Douglas-fir/ponderosa pine and aspen stands. A long thin plot of variable size, dependent on tree density, was overlaid on the existing sampling area used to study the herbaceous communities. A 1000 m^2 sample area was used for the ponderosa pine and Douglas-fir/ponderosa pine stands and a 400 m^2 plot was sampled for the aspen stand. Long thin plots have been shown to return consistently higher species richness values than the Whittaker plot and more accurately reflect the total species richness recorded in a complete plant survey of an area (Stohlgren 1994). At each plot, all live and dead trees greater than 4 cm diameter at breast height (dbh) were recorded by species and diameter. Seedlings and saplings were also recorded in each plot. Seedlings were defined as stems less than 1 m in height and saplings as stems greater than 1 m in height and less than 4 cm dbh. All stumps and fallen trees were recorded and identified to species within each plot. Additional notes of ecological data were also collected such as the presence of dwarf mistletoe (*Arceuthobium vaginatum* ssp. *cryptopodum*) and the type of seedlings and saplings growing under dead mature trees. Canopy cover percentages were taken at each stand using the Buckner cover-point projector (Buckner 1985). Two hundred sampling points were taken within each stand to determine canopy cover.

Data analyses

We analyzed the structure of the herbaceous communities using identical parameters measured by Kooiman & Linhart (1986) to allow for comparison between 1981 and 1996. These parameters included species richness, species diversity, species frequency, distribution of frequency classes, and species composition. The Shannon–Weiner diversity index (Magurran 1988) was used to measure diversity and species frequency was determined based on the number of individuals within a plot. Voucher specimens for each species were collected and deposited in the University of Colorado Herbarium (COLO). The Latin nomenclature follows Weber & Wittmann (1994, 1996). A list of all the species present during the 1996 survey is located in Korb (1997).

Forest structure, density, and dominance were determined using data recorded from the long thin plots in the lower three elevational stands. Stand structure was determined by dividing species into diameter classes based on 5 cm intervals. Relative density was calculated by dividing the number of individuals of a species by the total number of individuals within the plot. Relative dominance was determined by dividing the dominance of a species by the total dominance of all species within the plot. Dominance is defined simply as stem cover or basal area (Mueller-Dombois & Ellenberg 1974).

Statistical analyses

We calculated Spearman's rank correlation coefficients as nonparametric measures of association to determine the similarity in species composition of the herbaceous communities between 1981 and 1996. We included only species with frequency values of at least 20% in these analyses. In addition, we calculated 95% confidence intervals for the Shannon–Weiner diversity indices and individual species' frequency values to determine significant changes for these parameters between 1981 and 1996.

Table 1. Spearman's rank correlation coefficients for herbaceous species with a frequency of at least 20% in the plant communities between the 1981 and 1996 surveys. Q is the number of species used for the non-parametric statistical test.

Location	Q	Spearman's rank	Significance
Ponderosa pine stand	13	0.65	0.02
Douglas-fir/ponderosa pine stand	19	0.56	0.02
Aspen stand	19	0.34	0.20
Kobresia meadow stand	28	0.81	0.001

Results

Ponderosa pine stand at 2200 m

Rank correlation coefficients for the herbaceous species indicated that their was a significant relationship ($p = 0.02$) between the composition of herbaceous communities in the 1981 and 1996 surveys (Table 1). Species richness and diversity indices remained relatively constant (Table 2). The distribution of frequency classes was also comparable between the two surveys: a high percentage of the herbaceous species was present in frequency classes below 20% and a low percentage of the species was found in frequency classes above 40%.

Significant changes for individual species were evident. Variation in frequency over time for individual species and turnover in species composition were evident between the 1981 and 1996 surveys (Appendix A). Overall, the frequencies of herbaceous species in this community increased steadily in frequency percentages over time. Six species showed a minimum 10% increase in frequency between the 1981 and 1996 surveys. Two of these species, *Anisantha tectorum* and *Poa compressa* showed significant differences between 1981 and 1996 at the 95% confidence level (Appendix A).

The species with the most dramatic change in this herbaceous community was *A. tectorum,* an exotic species that is abundant on disturbed ground (Weber & Wittmann 1996). *Anisantha tectorum* increased from 10% to 62% between 1981 and 1996 (Appendix A).

The forest structure of the ponderosa pine stand showed that Douglas-fir was the dominant tree species (dbh >4 cm) within the stand in 1996. Douglas-fir had the highest relative density (58%) and highest relative dominance (80%) compared to other tree species present within the stand. Rocky Mountain juniper

Table 2. Shannon–Wiener diversity indices calculated from presence data of species in the plots. Q is the number of species; H' is the estimated diversity index; $H' >$ is the jackknife estimate; C. I. is confidence interval; H'_{min} and H'_{max} are the minimum and maximum values of H' for Q species. S.E. is the standard error.

Location	Year	Q	H'	Jacknife $H' >$ 95% C.I. (S.E.)	H'_{min}	H'_{max}
Ponderosa pine stand	1981	36	3.05	3.15 2.95–3.32 (0.084)	2.14	3.58
	1996	38	3.15	3.22 3.11–3.33 (0.057)	2.22	3.64
Douglas-fir/ponderosa pine stand	1981	40	3.24	3.30 3.21–3.39 (0.046)	2.29	3.69
	1996	41	3.29	3.33 3.24–3.42 (0.045)	2.30	3.71
Aspen stand	1981	45	3.25	3.31 3.18–3.43 (0.062)	2.46	3.81
	1996	29	2.92	2.97 2.84–3.10 (0.065)	1.85	3.37
Kobresia meadow stand	1981	41	3.29	3.31 3.25–3.37 (0.031)	2.30	3.71
	1996	35	3.18	3.20 3.15–3.25 (0.025)	2.10	3.56

(*Sabina scopulorum)* and ponderosa pine were similar for relative density and dominance values within the stand (Table 3). Douglas-fir represented 64% of the regenerating individuals (seedlings and saplings), while ponderosa pine comprised only 9% of the regenerating individuals. In constrast, ponderosa pine represented 90% of the non-regenerating individuals (stumps and fallen trees) for this stand. The total tree canopy cover for this stand was 12%.

Douglas-fir/ponderosa pine stand at 2700 m

The results from this stand were similar to the results of the pure ponderosa pine stand. Rank correlation coefficients for the herbaceous species at this stand showed their was a significant relationship ($p = 0.02$) between the composition of herbaceous communities between the 1981 and 1996 surveys (Table 1). Species richness and diversity indices remained relatively constant (Table 2). The distribution of frequency classes for herbaceous species had a high percentage of species present in frequency classes below 20% and a low percentage of species found in frequency classes above 40% in both years.

The greatest changes in this stand were the variation in frequency over time for individual species and turnover in species composition (Appendix A). Overall, frequencies of herbaceous species in this community increased in frequency percentages over time. Nine species showed a minimum 10% increase in frequency between the 1981 and 1996 surveys. *Lupinus argenteus* and *Solidago multiradiata* showed significant differences between the 1981 and 1996 sur-

Table 3. Absolute density (trees/hectare), relative density (%), and relative dominance for standing live and dead trees (dbh > 4 cm) at the ponderosa pine, Douglas-fir/ponderosa pine and aspen stands.

Stand Location (tree species)	Absolute density (trees/hectare)	Relative density (%)	Relative dominance (%)
Ponderosa pine stand			
Ponderosa pine (live)	60	18.0%	9.0%
Ponderosa pine (dead)	10	3.0%	3.0%
Douglas fir (live)	190	58.0%	80.0%
Rocky Mt. juniper (live)	70	21.0%	8.0%
Douglas-fir/ponderosa pine stand			
Ponderosa pine (live)	70	16.0%	4.0%
Douglas-fir (live)	360	80.0%	93.0%
Limber pine (live)	20	4.0%	3.0%
Aspen stand			
Subalpine fir (live)	600	10.0%	4.0%
Engelmann spruce (live)	875	14.0%	23.0%
Lodgepole pine (live)	550	9.0%	21.0%
Aspen (live)	2550	41.0%	32.0%
Aspen (dead)	1650	26.0%	20.0%

The sample area for the ponderosa pine and Douglas-fir/ponderosa pine stands was 1000 m^2 and the sample area for the aspen stand was 400 m^2.

veys at the 95% confidence level (Appendix A). These two species showed the most dramatic change in this community with a 32% increase in frequency.

Douglas-fir was the dominant tree species (dbh > 4 cm) within this stand in 1996, similar to the ponderosa pine stand. Douglas-fir had the highest relative density (80%) and highest relative dominance (93%) compared to the other tree species present within the stand (Table 3). Ponderosa pine was the next most dominant species within the stand followed by limber pine (*Pinus flexilis).* Ninety-seven percent of the regenerating individuals were Douglas-fir, with only three percent from ponderosa pine. The total tree canopy cover for this stand was 11%.

Aspen stand at 3050 m

This herbaceous community exhibited the most significant change in comparison with the other three communities. Rank correlation coefficients for the herbaceous species illustrated that their was no significant relationship ($p = 0.20$) between the composition of herbaceous communities in the 1981 and 1996 surveys (Table 1). Similarly, there was no significant correlation ($p > 0.05$) for diversity measurements between the two years. In addition, there were large changes in species richness, frequency percentages for individual species, and a large turnover in species composition (Table 1 and Appendix A).

The distribution of frequency classes for the herbaceous species in 1981 and 1996 was similar to the results in the two lower elevation stands. However, the frequencies of herbaceous species in this community steadily decreased in frequency percentages over time. In both years, there was a high percentage of species in frequency classes below 20% and a low percentage of species above 40%. Twelve species decreased in frequency by at least 10% between the two years (Appendix A). In contrast, only two species, *Calamagrostis canadensis* and *Carex foenea,* increased at least 10% across the two surveys. Eight of these species showed significant difference between 1981 and 1996 at the 95% confidence level (Appendix A). *Lupinus argenteus* and *Taraxacum officinale* exhibited the greatest change in this herbaceous community between 1981 and 1996 with both of these species decreasing 46% between the two surveys (Appendix A).

Aspen (*Populus tremuloides*) was the dominant tree species (dbh > 4 cm) within the stand. Live aspen had the highest relative density (41%) and highest relative dominance (32%) compared to the other tree species present within the stand (Table 3). Dead standing aspen was the next most abundant species with a relative density of 26%. Regenerating individuals were dominated by subalpine fir (42%) and Engelmann spruce (37%). The remaining regenerating individuals were almost equally divided between lodgepole pine (*Pinus contorta*) and aspen. Total tree canopy cover for this stand was 84%.

Kobresia meadow stand at 3750 m

Changes in this herbaceous community were the least evident between 1981 and 1996 in comparison with the other herbaceous communities. Rank correlation coefficients for the herbaceous species indicated that there was a significant relationship ($p = 0.001$) between the composition of herbaceous communities in the 1981 and 1996 surveys (Table 1). Species richness and diversity indices remained relatively constant (Table 2) and there was only a small turnover in species composition. The distribution of frequency classes contrasted with those of the three lower elevation stands. Overall, there was a lower percentage of species frequency classes below 20% than species in frequency classes of 40% or greater. *Acomastylis rossii* ssp. *turbinata* and *Oreoxis alpina* were the most prominent species at this stand across both surveys with frequencies of 98% (Appendix A). There was no general pattern for the frequencies of herbaceous species in this community, with about half the species increasing and half declining between the two surveys.

Variation in frequencies of individual species occurred between 1981 and 1996. Nine species increased in frequency by at least 10% between the two surveys and seven species decreased in frequency by at least 10% (Appendix A). Six of these species showed significant difference between 1981 and 1996 at the 95% confidence level (Appendix A). The species with the largest change in this herbaceous community between 1981 and 1996 was *Carex albonigra,* which increased 46%.

Discussion and conclusion

Ponderosa pine stand at 2200 m

In 1961, Marr classified this stand as a seral community that would eventually be an open park-like climax stand of ponderosa pine. He based this conclusion on three types of evidence: the basic processes of succession, scientific literature pertaining to this type of stand, and the data from his study on the abundance of ponderosa pine stumps and seedlings (Marr 1961). The 1996 results for the ponderosa pine stand contradicts this successional trajectory suggested by Marr. Marr's prediction probably would have been fairly accurate if disturbance regimes (e.g., fire, insect outbreaks) in this area had remained constant.

Fire has been recognized as an important natural disturbance that permits the continuous existence of open park-like ponderosa pine stands in the montane zone of the southern Rockies (Goldblum & Veblen 1992; Hadley 1994; Peet 1988; Veblen & Lorenz 1986, 1991). Human-set fires have been prevalent in the Front Range for as long as 8000 years (Benedict 1975; Husted 1965). In the late 1860's, during the mining era of the Front Range, wildfires and logging were extensive as indicated through repeat photography and stand age-structure data from forest studies in this region (Veblen & Lorenz 1991). Mining districts outlawed human-set fires in the late 19th century and since the 1920's fire frequency has greatly decreased (Veblen & Lorenz 1986).

Fire suppression in this region has greatly influenced changes in forest stand structure in the montane zone. For example, the shade tolerant Douglas-fir is increasingly abundant in areas where previously, during the settlement era, seedling and saplings of this species would have been eliminated by surface fires (Hadley 1994; Keane et al. 1990; Peet 1981). Consistent with this trend is the observation that the establishment and regeneration of ponderosa pine seedlings and saplings has greatly decreased with fire suppression (Keane et al. 1990). We predict that a Douglas-fir steady-state stand with little presence of ponderosa pine and Rocky Mountain juniper will exist at this stand in the next fifty years if fire suppression persists in the future. Another plausible trajectory for this stand is that a stand replacing crown fire will occur due to increased fuel loads that will allow for ponderosa pine reestablishment or another completely new successional trajectory.

Douglas-fir/ponderosa pine stand at 2600 m

Marr (1961) classified this stand as a seral community that would eventually change into a stand composed of equal dominance of Douglas-fir and ponderosa pine. The 1996 results for the Douglas-fir/ponderosa pine stand were inconsistent with Marr's original hypothesis. Similar to the ponderosa pine stand, Marr's successional trajectories may have been fairly accurate if the natural disturbance regimes of this area had remained constant.

Peet (1981) observed that fire suppression had resulted in an increase in Douglas-fir saplings and a decrease in ponderosa pine saplings in Douglas-fir/ponderosa pine forests in the southern Rockies. He also detected an increase in fuel loads, which would potentially result in devastating fires and new successional pathways for similar stands (Peet 1981). We predict that a Douglas-fir steady-state stand with little or no occurrence of ponderosa pine will exist at this stand if fire suppression continues to persist into the future. Limber pine will continue to senesce, as suggested by size structure analysis (Korb 1997) and the successional role of this species in this habitat. Low regeneration of ponderosa pine was present at this stand and all evidence was highly infested with dwarf mistletoe suggesting that these seedlings and saplings will probably senesce. Similar to the ponderosa pine stand, a stand replacing crown fire could result in new successional pathways for this community if fire suppression activities persist in this area.

Aspen stand at 3050 m

Numerous studies have shown a gradual replacement of aspen and lodgepole by Engelmann spruce and subalpine fir in the subalpine zone of the southern Rockies (Aplet et al. 1988; Peet 1981; Romme & Knight 1981; Veblen 1986; Whipple & Dix 1979). Size structure analysis and historical past written records (Marr 1961) support that both aspen and lodgepole pine were early successional species at this stand. Specifically, stump evidence and the ages of aspen dated by Marr (1961) suggest that this aspen stand probably began development following a period of logging approximately 95 years ago. Our data support Marr's (1961) hypothesis that an Engelmann spruce/subalpine fir steady-state stand will exist in the future at this stand. Size structure analysis in 1996 (Korb 1997) and well-known successional phases of subalpine forests (Parker & Parker 1983; Peet 1988; Veblen et al.1991) suggest that aspen will continue to senesce and eventually die out. Likewise, the probability of a continued presence of lodgepole pine is low at this stand.

Kobresia meadow stand at 3750 m

The 1996 kobresia meadow stand results were consistent with the successional trajectory suggest by Marr (1961) that this stand represented a dry meadow alpine climax community. However, similar to the two lower elevational stands, Marr neglected to incorporate anthropogenic disturbances into his hypothesis for the successional trajectory of this stand.

The alpine vegetation on Niwot Ridge has been studied in greater detail than any other alpine area in the Rocky Mountains (Billings 1988). Species composition at the kobresia meadow stand in the 1996 survey was similar to the dry meadow community found on Niwot Ridge in other studies (May and Webber 1982; Walker et al. 1994). A detailed study of the dry meadow community on Niwot Ridge indicated that interannual variation in the most limiting factors (i.e., low temperatures, high winds, short growing season, low nutrient availability, soil moisture) controlled the response of this community to changes over time (Walker et al. 1994).

Nutrient and water availability are the most limiting factors that reduce plant biomass production of alpine tundra species in the southern Rockies (Bowman et al. 1993, 1995; Isard 1986; Walker et al. 1994). Nitrogen has often been cited as the most common nutrient limiting plant growth (Bowman et al. 1993). Over the past few decades in the Colorado Rocky Mountains, atmospheric nitrogen has increased six-fold as a result of anthropogenic sources (Bowman et al. 1995). This increase of nitrogen availability in dry meadow communities on Niwot Ridge may have dramatic long-term effects resulting in changes in individual species abundance and species composition (Bowman et al. 1993).

Implications for determining successional trajectories

The results of this study illustrate the importance for incorporating disturbance into successional trajectories. Specifically, researchers need to understand that measurements characterizing a stand at one point in time represent a 'snap-shot' view of the ecosystem and this information along with successional trends supported in the scientific literature do not necessarily represent the future trajectory for these ecosystems. Marr's hypothesized trajectories for these stands were based upon 'snap-shot' characterizations of the ecosystem and general successional pathways described for these communities in the scientific literature. Marr (1961) subscribed to the polyclimax theory of Tansley (1935) where there was more than one possible climax for a stand under similar climatic conditions. In addition, he also acknowledged that '*All stands are dynamic internally*; there are a myriad of processes going on in every stand as long as its exists; if they should cease, the stand would disintegrate, this fact is true of a climax as well as a successional stand' (Marr 1961). However, despite his recognition that ecosystems are dynamic, Marr failed to incorporate anthropogenic disturbances into his successional trajectories that made his hypothesized successional pathways for these communities unrealistic. We would argue that the role of disturbance is crucial to understanding successional trajectories because successional endpoints may never be reached due to disturbance. Furthermore, disturbances can have different influences on a community depending on the scale, intensity, and frequency of the disturbance. This will then affect what species will occupy certain successional habitats or even specific patches within the habitats resulting in a mosaic of diverse communities across the landscape (Bazzaz 1996).

Long-term ecological studies

Understanding the causal effects of anthropogenic influences on natural communities has gained great interest in the past few decades, which has led to an increase in the desire for investigators to conduct long-term ecological studies. However, because of lack of funding from granting agencies for long-term studies, time constraints and the need for individuals to continually publishing new work, almost 70% of field experiments span across two years or less (Tilman 1989). Therefore, it is crucial that individual investigators clearly document all components of their research so that cause-and-effect relationships in ecological studies can be interpreted properly when these studies are repeated over time even if the original study was not intended to be a long-term study. This will allow researchers to gain a greater insight into the natural ecological processes occurring in different systems and will allow the influence of anthropogenic disturbances on these systems to be better understood.

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Appendix A. The frequencies of herbaceous species that were present at a frequency of at least 20% in 1981 or 1996 are provided. The 95% confidence limits for a binomial distribution are given in parentheses. Asterisks are next to individual species that had significant ($p \leq 0.05$) differences in frequency between the two years.

	1981	1996
Ponderosa pine stand (2200 m)		
*Anisantha tectorum**	10 (3–22)	62 (47–75)
Artemisia ludoviciana	18 (9–31)	28 (16–42)
Carex pensylvanica ssp. *heliophila*	72 (58–84)	82 (69–91)
Collinsia parviflora	30 (18–45)	30 (18–45)
Drymocallis fissa	22 (12–36)	16 (7–29)
Gayophytum nuttallii	30 (18–45)	32 (20–47)
Leucopoa kingii	22 (12–36)	34 (21–49)
Mertensia lanceolatum	16 (7–29)	28 (16–42)
Phacelia heterophylla	24 (13–38)	14 (6–27)
*Poa compressa**	0 (0–7)	20 (10–34)
Scutellaria brittonii	38 (25–53)	42 (28–57)
Senecio integerrimus	28 (16–42)	34 (21–49)
Solidago missouriensis	30 (18–45)	40 (26–55)
Douglas-fir/ponderosa pine stand (2600 m)		
Achillea lanulosa	20 (10–36)	34 (21–49)
Aletes acaulis	36 (23–51)	32 (20–47)
Amerosedum lanceolatum	34 (21–49)	54 (39–68)
Artemisia ludoviciana	54 (39–68)	68 (54–80)
Astragalus tenellus	18 (9–31)	28 (15–40)
Boechera sp.	22 (12–36)	4 (0–14)
Carex pensylvanica ssp. *heliophila*	76 (62–87)	82 (69–91)
Drymocallis fissa	36 (23–51)	34 (21–49)
Gayophytum sp.	24 (13–38)	18 (9–31)
Gilia pinnatifida	12 (5–24)	20 (10–36)
Harbouria trachypleura	34 (21–49)	24 (13–38)
Koeleria macrantha	16 (7–29)	28 (16–42)
Leucopoa kingii	50 (36–64)	44 (30–59)
*Lupinus argenteus**	2 (0–11)	34 (21–49)
Packera fendleri	28 (16–42)	44 (30–59)
Penstemon virens	72 (58–84)	76 (62–87)
Phacelia heterophylla	24 (13–38)	16 (7–29)
Scutellaria brittonii	14 (6–27)	28 (16–42)
*Solidago multiradiata**	20 (10–36)	52 (37–66)
Aspen stand (3050 m)		
*Achillea lanulosa**	74 (60–85)	38 (25–53)
Anticlea elegans	16 (7–29)	20 (10–34)
*Antennaria parviflora**	24 (13–38)	2 (0–11)
*Aster foliaceus**	20 (10–34)	0 (0–6)
*Calamagrostis canadensis**	6 (1–14)	32 (20–47)
Campanula rotundifolia	28 (16–42)	24 (13–38)
*Carex foenea**	0 (0–5)	44 (30–59)
Chamerion danielsii	90 (78–97)	78 (65–88)
Fragaria virginiana ssp. *glaua*	86 (73–94)	84 (72–93)
Juncus arcticus ssp. *ater*	34 (21–49)	16 (7–29)

Appendix A (Continued)

	1981	1996
*Lupinus argenteus**	52 (37–66)	6 (0–6)
Orthilia secunda ssp. *obtusata*	18 (9–31)	22 (12–36)
Potentilla pulcherrima	50 (36–64)	36 (23–51)
Pseudocymopteris montanus	34 (20–47)	34 (20–47)
Rosa woodsii	28 (16–42)	14 (6–27)
Selaginella densa	34 (21–49)	28 (16–42)
Solidago multiradiata	32 (20–47)	22 (12–36)
*Taraxacum officinale**	64 (49–77)	18 (9–31)
*Thermopsis divaricarpa**	26 (15–40)	0 (0–6)
Kobresia meadow stand (3750 m)		
Acomastylis rossii ssp. *turbinata*	98 (89–100)	98 (89–100)
Bistorta bistortoides	90 (78–97)	98 (89–100)
*Bistorta vivipara**	26 (15–40)	0 (0–6)
Campanula uniflora	98 (89–100)	90 (78–97)
*Carex albonigra**	12 (5–24)	58 (43–66)
Carex rupestris ssp. *drummondiana*	4 (0–14)	24 (13–38)
Eremogone fendleri	34 (21–49)	52 (37–66)
*Eritrichum aretiodes**	42 (28–57)	12 (5–24)
Erysimum capitatum	38 (25–53)	46 (32–61)
Helicotrichon mortonianum	52 (37–66)	54 (39–68)
Kobresia myosurioides	92 (81–99)	94 (83–100)
Lidia obtusiloba	58 (43–66)	54 (39–68)
Lloydia serotina	92 (81–99)	86 (73–94)
Mertensia lanceolatum	40 (26–55)	56 (41–70)
Oreoxis alpina	98 (89–100)	98 (89–100)
Phlox sibirica ssp. *pulvinata*	90 (78–97)	86 (73–94)
Poa glauca ssp. *rupicola*	66 (51–79)	92 (81–99)
Polemonium viscosum	34 (21–49)	32 (20–47)
Potentilla nivea	40 (26–55)	54 (39–68)
*Potentilla ovina**	0 (0–6)	24 (13–38)
Potentilla rubricaulis	38 (25–53)	14 (6-27)
Rydbergia grandiflora	8 (2–19)	20 (10–34)
Selaginella densa	88 (76–95)	70 (56–82)
Silene acaulis	26 (15–40)	6 (1–17)
Taraxacum ceratophorum	52 (37–66)	60 (49–77)
*Thlaspi montanum**	22 (12–36)	0 (0–6)
Trifolium dasyphyllum	88 (76–95)	98 (89–100)
*Trifolium nanum**	40 (26–55)	6 (1–17)