EXOTIC SPECIES OCCURRENCE IN MEADOWS ALONG AN ELEVATIONAL GRADIENT IN THE COLORADO FRONT RANGE

by

GABRIELLE L. KATZ

B.A., Brown University, 1991

A thesis submitted to the
Faculty of the Graduate School of the
University of Colorado in partial fulfillment
of the requirement for the degree of
Master of Arts
Department of Geography
1995

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Nina Williams
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July 26, 1995

Dear Nina and Lori,

Thank you so much for allowing me to sample the meadow near El Dorado Mountain last summer. Here is a copy of my thesis -- finally finished and approved! I hope you find it useful. The City Open Space meadow is coded as site L-3 in all of the Tables and Figures. You might want to take a look at Table 5.1 (p. 63) which lists all of the exotic species and their frequencies in each meadow, and at Appendix C (pages 95 - 97) which lists the same information for native species.

If you have any questions or comments feel free to contact me at the above address or at home: 494-9214. I will be starting the Ph.D. program in the Geography Department this fall, so I'll probably be in touch with you in the future with regards to the invasion ecology of Russian olive in riparian areas of Colorado. Again, thanks for everything!

Sincerely,

Gabrielle Katz

Gabrielle Katz

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Exotic species occurrence in meadows along an elevational gradient in the Colorado Front Range.

Thesis directed by Associate Professor Susan W. Beatty

Exotic species invasions can impact native species diversity and the maintenance of native ecosystems. The basic characterization of the patterns of exotic species occurrence represents an important contribution towards understanding the invasion process. Along elevational gradients, environmental conditions and plant species composition change dramatically. This study examines the distribution of exotic species in meadows along an elevational gradient in the Colorado Front Range.

The questions addressed in this study are as follows. (1) Does exotic species occurrence (species richness, cover and composition) change along an elevational gradient? (2) Do native and exotic species occurrence exhibit the same elevational trends? (3) Are there relationships between native and exotic abundance that are independent of elevation?

Exotic and native species exhibit opposite elevational trends in abundance. Exotic species richness and cover decline with increasing elevation. However, exotic species composition does not appear to be influenced by the elevational gradient. In contrast to the exotic occurrence pattern, native species richness and cover increase with increasing elevation. Native species composition in the nine meadows is influenced strongly by elevation. When the whole data set is pooled, and elevation is not considered, native and exotic occurrence are negatively correlated. Thus, even at small scales native and exotic species often exhibit mutually exclusive abundance patterns.

Although currently there are few exotic species in the subalpine meadows that I sampled, this situation could change in the future. With increased human mobility and increased use of high elevation environments for recreation and residential

development, more species introductions are likely. There may still be sufficient time for managers to protect alpine and subalpine areas from these influences. At lower elevations, where exotic species are already relatively abundant, managers should focus their efforts on the control of particularly threatening individual exotic species.

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CHAPTER 1

INTRODUCTION

There has been much recent research on the subject of biological invasions (Drake et al. 1989, Groves & Burdon 1986, Macdonald et. al 1986, Mooney & Drake 1986), and on the implications of exotic species invasions for biological conservation (Hobbs & Huenneke 1992, Huenneke & Thomson 1995) and management (Coblentz 1990, Soulé 1990, Westman 1990). Invasions by exotic species have resulted in alterations of the nutrient cycling regimes, trophic structures, and disturbance regimes of invaded areas (D'Antonio & Vitousek 1992). Biological invasions have also been associated with the loss of native species diversity (McIntyre & Lavorel 1994a, 1994b). Research has focused on a range of topics concerning the patterns, processes, and effects of invasion. In this context, sound description of the patterns of abundance of exotic species is an important prerequisite to the development of general theories of the invasion process. Interestingly, while increasing attention is being paid to the issue of biological invasions, in many cases basic patterns remain poorly characterized. For example, very few workers have examined the patterns of plant invasion along elevational gradients (Frankel 1977, Forcella and Harvey 1983).

1.1 Exotic Species Invasions -- Generalizations

1.1.1 Patterns of Exotic Occurrence

Several patterns have been described concerning the distributions of exotic plant species along environmental gradients and in patchy landscapes. In California, Frankel (1977) found that the occurrence of exotic species on roadsides declined with increasing elevation (cited in Mooney et. al 1986). Similarly, Forcella and Harvey

(1983) examined species composition along a complex environmental gradient of elevation in western Montana, and found that alien species richness declined with increasing elevation. Weaver, et al. (1990) also found that exotic richness declined from the subalpine to the alpine in the Northern Rocky Mountains.

The role of landscape heterogeneity in influencing species patterns is becoming an increasingly popular area of research. Tyser and Worley (1991) examined the role of roads and trails as establishment corridors for exotic species in Glacier National Park, Montana. They found that, in general, exotic species richness declined with distance away from such travel routes. Brothers and Spingarn (1992) described patterns of exotic species invasion into forest fragments surrounded by agricultural fields in Indiana. In this system, the frequency of alien species declined with distance into a forest patch.

1.1.2 Invasibility

In seeking to make generalizations about biological invasions, many workers have attempted to characterize the attributes of communities which make them susceptible or resistant to invasions. Several workers have suggested that the invasibility of a community is related to the amount of bare ground found within it. Baker (1986) identified grasslands, riparian habitats, waterways, roadsides, trodden paths, sand dunes, and some open forests as communities particularly susceptible to invasion by exotic species. The characteristic common to these communities was the fact that they all had openings in the vegetation cover which could serve as establishment sites for invaders. Similarly, Crawley (1976) concluded that one of the key characteristics of an invasible community was that it had "low average levels of plant cover" (p.432), although he added frequent disturbance as another important attribute. In recent years, the efficacy of such broad-based generalizations has come into question, with some workers arguing that general principles of invasion do not exist at all (D'Antonio 1993).

In efforts to understand biological invasions, increasing attention is being given to the attributes of individual native plant species and communities. The morphology and phenology of the native species, for example, as well as the evolutionary history of a community may both be important factors influencing the invasibility of a community. Mack (1989) compared the attributes of temperate grasslands vulnerable (Australia, South America, and western North America) and resistant (Eurasia, southern Africa, and central North America) to invasion. He argued that dominance by caespitose grasses was an extremely important community attribute of the grasslands vulnerable to plant invasion. Such dominance, in turn, was intrinsically related to the fact that large ungulates were absent from vulnerable grassland communities throughout the Holocene. Rhizomatous grasses tend to be much more resilient in the face of grazing by large ungulates than are bunch grasses. Rhizomatous forms can reproduce vegetatively if their flowers are removed by grazing, and they often form dense mats which restrict the establishment of other plants.

For the most part, Mack's (1982, 1989) studies seek to explain grassland invasions with an emphasis on a single species (*Bromus tectorum*) and in light of a specific introduced disturbance (cattle grazing). As such, Mack's insights represent a step down in generality from those described above. Other authors have suggested that generalizations are impossible, and that every invasion must be viewed as a unique interaction between a particular exotic species and a particular suite of natives. D'Antonio (1993) found distinct differences in the factors influencing the invasion dynamics of *Carpobrotus edulis* (iceplant) into three coastal plant communities in California. She stated that "invasion by *Carpobrotus* is a context-specific process. Any attempt to predict future invasions must take into account the identity of the plants and animals in the communities being entered" (p.92). It appears that this context-specific approach is yielding positive results, as workers seek to fine-tune their understanding of the dynamics of specific invasions.

1.2 Limits to Invasion

It is reasonable to assume that certain initial conditions must be met in order for invasion to be possible. First, seeds of non-native species must be present at a location, if non-natives are to become established. Second, the germination requirements of the exotics must be met. For example, microsites suitable for the germination of non-natives must exist in the native community. Harper (1965) asserted that "weeds" often have very subtle and precise germination requirements. He described experiments in which several *Plantago* species exhibited very distinct species-specific preferences for particular types of germination microsites (e.g. different depression depths, or degrees of shelter). Once these two pre-conditions are met, it is theoretically possible for a non-native species to become established in a native community. Such establishment, however, is by no means assured. Establishment will depend upon such factors as the local climate and the resistance of the native vegetation. Successful invasion will also require successful reproduction by the non-native species in the native community. Clearly, invasions may be limited at any of these stages, from seed arrival to germination, establishment, and reproduction. Below, I will discuss three factors which may limit exotic species invasions in mountain environments, (1) climate, (2) site isolation, and (3) the native biota.

1.2.1 Climate

The climate in which a native community is found will play a significant role in determining whether or not an invasion will be successful. It seems likely that the more similar the climate of a new environment is to that of a species' original environment, the easier it will be for that species to invade. This reasoning was used, in part, by

Mack (1986) to explain the spectacularly successful invasion of *Bromus tectorum* (cheatgrass) into the intermountain grasslands of the United States. The intermountain climate consists of cool, wet autumns and winters, with hot, dry summers. These conditions closely resemble those of a large area stretching from Spain to Turkmenistan (p.193). Consequently, Mack argued, plants which evolved in this region of Europe/Asia were "pre-adapted" to the general climatic conditions of the intermountain west. It is important to note that climatic "pre-adaptation" is not necessarily a prerequisite to invasion. For example, Beatty and Licari (1992) described the successful invasion of *Foeniculum vulgare* into native plant communities on Santa Cruz Island, California despite the dissimilarity of the climates of California and Europe. In California, *F. vulgare* exploits a non-native "niche", that of growth during the summer when native species are dormant.

Within climatic regions, year-to-year variability seems to have a large impact on species invasions. Hobbs and Mooney (1991) investigated the influence of rainfall variability on the invasion of Californian serpentine grasslands by the introduced annual *Bromus mollis*. They found that *B. mollis* could invade and establish in grassland sites during periods of fairly high rainfall. The onset of drought conditions, however, resulted in the rapid decline of *B. mollis* populations. During dry periods, individual plants either died soon after establishment, or were unable to set seed due to lack of water. The authors characterized the successful invasion of *B. mollis* at the beginning of their study as an "invasion episode" linked directly to a period of favorable climatic conditions.

Along elevational gradients, climate can change relatively quickly over short distances. Here, factors such as the length of the growing season, number of frost-free days, snowpack, wind intensity, mean annual temperature and amount of annual precipitation will influence the patterns of invasion at relatively small scales. While there is much anecdotal evidence for the fact that the abundance of alien species tends to decline with increasing elevation, few quantitative studies have been done. In the few cases where such a pattern has been described, explanation of its causes has proven difficult. Forcella and Harvey (1983) found that exotic species abundances declined in undisturbed sites with increasing elevation. It is important to note, however, that this pattern was the result of at least two factors. Climate most definitely had an effect, and the authors did link their patterns qualitatively to such climatic factors as the number of months without frost, and mean July temperature. On the other hand, biotic influences confounded the climatic effect in this study. The two higher elevation sample zones consisted of forest communities (*Abies lasiocarpa* and *Pseudotsuga menziesii*) which probably had fairly closed canopies, while the mid-montane zone consisted of a *Pinus ponderosa* forest which was probably much more open. The low elevation sites in this study were located in a grassland community, which presented an entirely different life form altogether. Differences in community structure and dominant life form can influence the success or failure of an invader, and therefore they obscured the influence of climate in this study.

Investigations involving experimental introductions of alien populations into native communities offer an opportunity to gain insight into patterns of non-native establishment. Pierson and Mack (1990) described the demography of populations of *Bromus tectorum* introduced into forests along an elevational gradient in eastern Washington. They found that although recruitment was high, *B. tectorum* had low survivorship and fecundity when introduced into mountain forests. The authors attributed these patterns to "the intolerance of cheatgrass to the constraints imposed by the forests' environment" (p.423). Further, they identified low soil and air temperatures, along with persistent snow cover, as factors likely to have influenced the failed establishment of this grass. Differences in seasonal weather also appeared to have a significant effect on annual mortality and on the proportions of different causes of mortality (e.g. desiccation, and "winter death"). Interestingly, the authors did not discount shading as having an effect. It appeared that an array of interlocking factors, both climatic and biotic, limited the establishment of this species in mountain forests. These factors varied in intensity and influence from season to season, and from year to year.

1.2.2 Site Accessibility

As mentioned previously, seed is required if an exotic species is to become established in a new community. Proximity to seed sources will be an aspect of native communities influencing invasion. According to the theory of Island Biogeography (MacArthur & Wilson 1967), the farther an island is from the mainland (source of immigrants), the lower will be its rate of colonization or invasion. This theory has been applied to several situations beyond that of actual oceanic islands. For example, the theory has been applied to fragmented scrub landscapes, forest patches, and caves (McCoy & Mushinsky 1994). The theory may also be applied to alpine and subalpine mountain environments (MacArthur 1972). According to Forcella and Harvey (1983), "subalpine environments are analogous to small islands resting upon a vast sea of low elevation landscapes. The probability that alien weeds tolerant of subalpine conditions will reach such limited sites is low" (p.108). Further, mountain meadows below timberline are island-like habitat patches within the predominately forested mountain environment.

If mountain environments are indeed analogous to islands, then perhaps the paucity of aliens at high elevations is due to lack of seed. Pierson and Mack (1990) directly addressed this question with respect to *B. tectorum.* The authors concluded that the absence of this grass in mature forests was due to environmental constraints "rather than a simple lack of opportunity to reach forest sites" (p.523). Unfortunately, the study included no analysis of the soil seed bank, so it is unclear whether or not *B. tectorum* seeds were indeed reaching their sites by natural means. I have found no studies which adequately distinguish between the influences of site isolation and environment on exotic establishment patterns. Brothers and Spingarn (1992), for example, concluded that in central Indiana "it seems likely that most of the available aliens are prevented from invading these forests by some combination of low light availability, lack of disturbed substrate, and poor dispersal" (p.97). Clearly, the influences of dispersal distance and environmental restriction are often confounded, as is the case in both mountain and forest systems. Efforts to tease out their relative importance are needed.

The seeds of exotic species may enter native communities along very specific pathways. Tyser and Worley (1992) showed that, due to both accidental and intentional roadside introductions of non-native species, roadsides may serve as sources of seed for the surrounding vegetation. Other workers have also recognized that roadsides serve as establishment sites for exotics. Weaver, et al. (1990) stated that they "sampled only roadside sites because these have a high probability of inoculation; that is, species absences there are likely due to the physical-biological environment rather than lack of seed" (p.208). Seeds of non-native species arrive at roadsides and trails via intentional plantings, human vectors (e.g. in clothing), domesticated animals (e.g. in fur and feces), and vehicles (e.g. in tires and wheels). Stream channels may also serve as corridors for exotic species establishment. DeFerrari and Naiman (1994) found that exotic species richness, density and cover were all significantly higher in riparian zones than in uplands in two watersheds on the Olympic Peninsula, Washington. It is debatable, however, whether or not roadsides and stream channels actually serve as source areas from which exotic species can invade intact native vegetation. Given the differences in habitat between roadsides and intact forest, or between riparian zones and upland forests, it is possible that exotic species adapted to the corridor environments are unable to inhabit adjacent areas. Dispersal to "islands" may be facilitated by corridors of alien establishment, but more work is needed in order to verify this relationship.

1.2.3 Competition & Herbivory

The native flora and fauna may both limit the ability of non-native plant species to invade a community. Native species may outcompete invaders for limiting resources such as water, light or soil nutrients. For example, in the forests described by Brothers and Spingarn (1992), the native trees may have exploited so much of the available light that they excluded exotics from the forest interior. Similarly, Beatty and Licari (1992) found that *Foeniculum vulgare* establishment did not extend very far (~ 10 meters) into California chaparral communities. Here, the chaparral vegetation may have monopolized all available resources, rendering it impossible for *F. vulgare* to establish even when disturbed microsites were available. Native herbivores can also limit invasions into non-native plant species. D'Antonio, et al. (1993) examined the factors influencing the invasion of *C. edulis* into California maritime chaparral. Through experiments involving herbivore exclosures, they found that herbivory by native rabbits and deer severely limited *C. edulis* establishment in both burned and unburned chaparral. It is clear that the native biota is able, in some cases, to exclude exotic species from certain communities.

1.3 Disturbance

Disturbance plays a very important role in the invasion process (e.g. Fox & Fox 1986, Hobbs 1989, Hobbs & Huenneke 1992). Disturbance may influence the availability of exotic propagules, alter the availability of germination microsites or safe-sites in the native community, impact the vigor and regeneration of native species, or produce a host of other effects. It is likely that both natural and anthropogenically altered disturbance regimes influence invasion patterns, although most studies are conducted on communities at least marginally affected by human intervention. Human alteration of disturbance regimes rarely influences a single disturbance factor. For example, fire suppression in the western United States is often accompanied by the introduction of exotic grazers, or by road and trail construction. Separating out the influence of a single factor on alien invasion is often difficult.

1.3.1 Fire

Much recent research addresses the role of fire in influencing species diversity (Collins 1987, Howe 1994), regenerating native ecosystems, and altering the probability of non-native invasion (D'Antonio 1993). The effects of fire are extremely context specific, and will depend heavily on the evolutionary history of the native and non-native vegetation, and the timing, intensity and recurrence interval of burns.

When native plant communities are adapted to fire, alteration of fire regimes may alter the invasibility of such communities. It is fairly well agreed that both the tallgrass and shortgrass prairies of the central and western United States experienced frequent fires before European settlement. Fires resulting from lightning strikes probably occurred throughout the evolutionary history of these communities, while anthropogenic fire may have assumed more importance during approximately the last 1,000 years. Periodic fire helps to maintain tallgrass prairies by suppressing shrubs and trees, and by stimulating grasses and forbs (Howe, 1994). Since European settlement, however, fire frequency has declined dramatically. In a study of the effects of fire on native tallgrass prairie in Oklahoma, Collins (1987) demonstrated that burning treatments increased the cover of the "matrix-forming" (dominant) grasses, *Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans,* and *Sporobolus asper*. Further, fire reduced the cover of the non-native annual grass, *Bromus tectorum.*

The timing of fire events relative to the life-cycles of the affected species is an important factor influencing resultant patterns. Collins (1987) burned his plots in Oklahoma in mid-April. According to Howe (1994), however, lightning fires on the Great Plains occur predominantly in midsummer. Howe (1994) reported the results of anthropogenic burns conducted in a "prairie restoration" in Wisconsin during March and July. He found that burn timing significantly influenced species response. Early-flowering species, such as *Agropyron repens*, were strongly favored by July burns. Late-flowering species, such as *Andropogon gerardii*, were favored by March burns and by the absence of fire. While this study indicates that fire season influences the composition of native prairies, its results can be extrapolated to include non-native species.

Clearly, both native and alien plant species may fall into any flowering guild (early, mid, and late season). Interestingly, thirty-five "volunteer" species, including fourteen aliens, survived in Howe's plots. The aliens represented all three flowering guilds. Based on this information, it appears that predicting the influence of fire season on invasion by exotics will be difficult. If there is only one exotic species of interest, then the problem is less intractable, although native community effects should not be ignored. It appears that fire effects will be species-specific, since each species has its own phenology and evolutionary history.

1.3.2 Soil Disturbance

Several investigators have addressed the role of soil disturbance in facilitating exotic species invasions. Soil disturbance can result from the activities of native animals, introduced animals, physical geomorphic processes, or directly from human activities such as road-building. Hobbs (1989) conducted experiments in five different Australian plant communities and found that soil disturbance enhanced the establishment of the exotic annual grass *Avena fatua* in all of them. Hobbs and

Mooney (1991) examined the role of gopher disturbance in the invasion dynamics of California serpentine grasslands. They found that *Bromus mollis* was able to invade un-manipulated grassland vegetation (control plots) by establishing on gopher mounds. Once established in these microhabitats, *B. mollis* was able to produce abundant seed and to spread. McIntyre and Lavorel (1994a) found that the degree of soil disturbance at a site had a significant impact on exotic species richness in Australian tableland grasslands. In an analysis of 120 sites, the authors found that exotic species richness increased with increasing soil disturbance. Here, soil disturbance was predominantly the result of human activities, namely vehicle and machinery use. In these studies, it appears that exotic species were able to take advantage of the decreased competition, and increased nutrient availability (e.g. light) on disturbed sites.

The frequency of soil disturbance will have an important impact on species patterns. Weaver, et al. (1990) examined a range of human-induced soil disturbance frequencies and types in the vicinity of Grand Teton National Park, Wyoming. They classified road shoulders as constantly disturbed, roadside ditches as periodically disturbed, and roadcuts as disturbed only once, and then analyzed species composition, constancy, frequency, and cover in each of these disturbance zones. The authors found that the frequency and cover of exotic species increased from roadcuts to roadside ditches, which corresponded to an increase in disturbance frequency. This pattern, however, did not extend to the road shoulder. Here, exotic richness declined from the values found in the ditch. The authors attributed this pattern to the increased influence of trampling at the road shoulder. Although certain species, such as those with flexible, stemless, and creeping plant forms, as well as those with short life cycles or "growth in the off-season", were able to increase in this zone, "brittle-stemmed species" tended to be eliminated due to the effects of trampling (p.211). Despite the further increases in "water and sun" (p.210) on the road shoulder, exotic species establishment was limited there. It seems that there is a trade-off between the positive results of soil disturbance, and the negative aspects of experiencing the process itself.

1.3.3 Nutrient Enhancement

Direct resource enhancement has been shown to influence invasion patterns. McIntyre and Lavorel (1994a, 1994b) found that water enrichment, which resulted from the modification of drainage patterns during road construction, had an effect on species composition. Using linear models derived from their field data, the authors found that exotic species richness significantly increased in sites with increased water enrichment in Australian tableland grasslands (McIntyre and Lavorel, 1994a). In this ecosystem, mesic sites have been rare over evolutionary time, leading to a dearth of native species adapted to well-watered conditions. In experimental manipulations, Hobbs (1989) found that fertilization, in combination with soil disturbance, greatly augmented the establishment and growth of two non-native grasses in native Australian plant communities. Similarly, Huenneke, et al. (1990) found that fertilization enhanced the invasion of non-native annual grasses into native vegetation in California serpentine grasslands. Here, in fertilized plots, exotic grasses were able to invade and dominate in patches originally dominated by native annual forbs. Such patterns may have been the result of direct species responses to nutrient applications, or to altered competitive balances between species.

1.3.4 Grazing

The impacts of grazing on species composition and exotic species invasion are varied and complex. Such impacts depend upon grazing intensity, grassland type, history and location, and the identity of the potential invaders. Moreover, grazing impacts occur over a range of spatial and temporal scales. Milchunas, et al (1992) distinguished between two different time-scales of herbivore impact. Short-term effects included injury and defoliation-induced mortality of individual plants, while long-term effects included alterations of water and mineral nutrient cycling dynamics, which in turn may influence competition and population processes (p.520). Milchunas and Lauenroth (1993) analyzed a 236-site data set to assess the general effects of grazing. They found that annual net primary production, the evolutionary history of grazing of a site, the level of consumption, and years of treatment were all important variables influencing species and community responses to grazing. Although generalizations have proven difficult, it is useful to discuss grazing impacts in terms of the evolutionary history of the grassland in question.

The introduction of non-native grazers into plant communities which evolved in the absence of grazing can strongly influence community patterns and susceptibility to invasion. Mack (1989) asserted that one of the two "quintessential characteristics of temperate grasslands vulnerable to plant invasion" was "the lack of large, hooved, congregating mammals in the Holocene or longer" (p.156). When native communities are not adapted to disturbance and grazing by large mammals, the introduction of such animals can be devastating. For example, the introduction of cattle into the intermountain west of North America by European settlers was largely responsible for the rapid and almost complete demise of the native bunchgrass community there. Native grasses, such as *Agropyron spicatum*, are very susceptible to the direct effects of ungulate grazing. In addition, the effects of trampling are severe (Mack 1982). In this situation, the stage is set for the invasion of exotic species adapted to grazing.

In plant communities which evolved in the presence of large grazers, introduced cattle can inhibit the invasion of the native vegetation by exotic species. Milchunas, et al (1992) described the impact of cattle on experimental plots in grasslands of the shortgrass steppe region in North America. Plant communities in this region "have been subjected to heavy grazing by large ungulates and semiarid conditions since the uplift of the rocky Mountains and the end of glaciation 10,000 years ago" (p.520).

This shortgrass community contains perennial grasses which are adapted to herbivory. In sowing experiments, the researchers found that germination, emergence, and survivorship of five opportunistic exotic annuals were lower in grazed than in ungrazed plots. The authors attributed these patterns to higher levels of competition on grazed sites, with a concomitant decrease in the availability of safe-sites for annuals.

Grazing may differentially affect different species or groups of species within a community. For example, Belsky (1992) found that grazing prevented tall-statured grass species from out-competing short-statured grass species in the Serengeti National Park, Tanzania. In addition, due to the build-up of dense vegetation, rhizomatous grass species began to replace stoloniferous ones when protected from grazing. Huenneke, et al. (1990) also found differences in species composition between grassland plots within and outside of cattle exclosures. In this experiment, conducted in Californian serpentine grasslands, both native and non-native grasses increased in abundance in the exclosures, while native annual forbs declined. The authors suggested that, in this ecosystem, grazing may facilitate the persistence of native forbs because cattle remove grass biomass (both native and exotic) and thereby enhance the germination, emergence, and establishment of native forbs.

1.4 Elevational Gradients

The study of environmental gradients has a long history in ecology and biogeography. Elevation is a complex environmental gradient along which many environmental and climatic factors vary (Peet 1988). For example, the frost-free season decreases, temperature decreases, seasonality of precipitation changes, and total precipitation increases with increasing elevation in the Colorado Front Range (Barry 1973). Disturbance regimes also vary along this elevational gradient (Peet 1988). Although it is recognized that vegetation changes along this complex gradient, interpretations have differed as to the nature of this change.

Early workers in Colorado classified the vegetation of the Rocky Mountains according to elevational zones. Distinct communities were described, usually based on characteristics of the dominant tree species. Ramaley (1927) described five "life zones" of Colorado: the plains (to 1,829 meters), foothills (1,829 -- 2,439 meters), montane (2,439 -- 3,048 meters), sub-alpine (3,048 -- 3,506 meters), and alpine (above 3,506 meters). Marr (1967) renamed the foothills zone the lower montane, and the montane the upper montane, identified the elevational ranges of ecotones between the life zones, and adjusted some of the boundary elevations. Marr (1967) also characterized the vegetation assemblages typical of each zone as "climax" communities (Marr 1967, Kooiman & Linhart 1986).

According to Peet (1988), there are several problems with the elevational zonation approach to vegetation classification. First, the assumption that mountain vegetation is comprised of distinct bands (Ramaley 1927, Marr 1967, MacArthur 1972) is usually incorrect. Rather, vegetation composition appears to vary continuously along elevational gradients. The second difficulty with the elevational zonation approach is the fact that vegetation in mountain areas is influenced by environmental factors other than elevation. In the Rocky Mountains, for example, disturbance history, site moisture and soils also have an important influence on vegetation composition.

More recently, workers have analyzed vegetation along environmental gradients using the techniques of gradient analysis. Whittaker (1975) described the distributions of individual species along moisture gradients in Oregon and Arizona. He related the distributions to Ramensky and Gleason's individualistic hypothesis of plant distributions, and to the their concept of community continuity, that communities intergrade continuously along environmental gradients (p. 115). Peet (1981, 1988) employed a combination of ordination, gradient analysis, and classification to describe the vegetation of the Colorado Front Range. The resulting community mosaic diagram provides a detailed classification of Front Range forest vegetation in relation to both elevation and site moisture. While Peet's (1981) description is undoubtedly more accurate than those of Ramaley (1927) and Marr (1967), the simplicity of the earlier models makes them still useful as shorthand descriptions of Front Range vegetation.

Compared to the forest communities of the Colorado Front Range, mountain meadows have received very little study. Meadows occur at all elevations throughout the mountains. These treeless patches are dominated by grasses, sedges and forbs (Peet 1981). Several early workers described the herbaceous vegetation of some Colorado parks and meadows (Ramaley & Elder 1912, Reed 1917, Ramaley 1919), but recent work has been relatively scarce (Wilson 1969, Mutel 1973, Peet 1981). Attempts to classify Front Range vegetation usually have not included herbaceous communities. Marr (1967) mentioned the occurrence of meadows within the forest "climax regions" he described, but he did not discuss them in any detail. Peet (1981) included understory vegetation in his analysis of Front Range forests, but he did not include meadows.

Several explanations have been offered to account for the locations of meadows in otherwise forested systems. These explanations have generally focused on soil texture, soil drought, excess soil moisture, and disturbance (Peet 1988). Daubenmire (1968) described the occurrence of "grassland climaxes" at generally forested high elevations in Idaho on sites where soil drought was significant. Similarly, Root and Habeck (1972) suggested that tree seedlings were unable to establish in grassy balds in the Bitterroot Mountains of Montana because of annual summer drought. In contrast, Allen-Diaz (1991) suggested that the distribution of meadows in the Sierra Nevada of California was related to the presence of shallow water tables. It is possible that both extremes of moisture availability may contribute to meadow persistence. Mutel (1972) asserted that montane meadows in the Front Range were probably maintained by a combination of high water levels on some edges, and soil drought on others. Both conditions tend to inhibit tree invasion.

It is possible that the factors influencing meadow persistence vary with elevation (Peet 1988). Several workers have implicated disturbance as a factor responsible for the creation of meadows in subalpine areas. Grassland may dominate after fire in subalpine Rocky Mountain forests in Colorado (Stahelin 1943), and in the Medicine Bow mountains of Wyoming (Billings & Mark 1957). Once established, such meadows may persist due to the competitive abilities of the herbaceous species (Stahelin 1943), and because of the increased climatic severity of treeless environments (Billings & Mark 1957, Mutel 1972).

There is probably considerable variability in the longevity and stability of mountain meadows. Where meadow vegetation is the result of edaphic factors which favor herbaceous species, and preclude tree growth, such patches may be very persistent. Benedict (1982) argued that many meadows were at least as stable as the surrounding vegetation, and that the locations of meadows were often geologically determined. Where meadow vegetation is the result of a disturbance such as fire, however, trees may encroach on the meadows over relatively short time scales. Veblen and Lorenz (1986) discussed the active invasion of montane meadows by trees. While there is still controversy over the causes and stability of mountain meadows, at any point in time they are clearly present as distinct habitat patches within most mountain ecosystems.

1.6 Objectives

Since mountain meadows are patches of a single habitat type found at all elevations of the Colorado Front Range, they offer a valuable opportunity to investigate the effects of elevation on exotic species occurrence. In this study, patterns of exotic species abundance are not confounded by differences in overstory canopy density. The purpose of this study is to document the occurrence of exotic species in meadows at three elevations, and to compare species richness, cover, and composition between elevations. The specific research questions I address are: (1) Do the richness and cover of exotic species change along the elevational gradient?; (2) Do native and exotic cover and species richness exhibit the same elevational trends?; (3) Are there any general relationships between native and exotic species abundances?

CHAPTER 2

STUDY AREA

This study was conducted in nine meadows in the Front Range of Colorado. Eight meadows were located in Boulder County, and one meadow was situated just south of the county line in Jefferson County. The sites were located in three elevational zones, corresponding approximately to the lower montane, upper montane, and subalpine zones of Marr (1967). The lower montane meadows were located at approximately 1980 meters elevation, the montane meadows at 2590 meters, and the subalpine meadows at 3050 meters. The meadow designations are based on elevation only, and not on an analysis of the dominant tree species around them.

2.1 Physical Region

The Colorado Front Range is part of the Southern Rocky Mountain physiographic province (Benedict 1991). The Continental Divide forms the backbone of the Front Range (Marr 1967), where it reaches its easternmost extent on the entire North American continent (Weber 1965). The eastern slope of the Front Range rises abruptly from the plains, extending from the grasslands at elevations of 1710 meters to alpine peaks of over 4268 meters within a horizontal distance of less than 32 kilometers (Marr 1967).

Vegetation changes dramatically along this steep elevational gradient (Ramaley 1927, Marr 1967, Peet 1981, 1988). Grassland ecosystems dominate at both the lowest and highest elevational extremes -- prairie grassland below lower treeline, and alpine tundra above upper treeline. In general, coniferous forests dominate the middle elevations, although deciduous aspen stands and treeless meadows are also common.

The different approaches which have been taken to classifying Front Range vegetation are discussed in the introduction.

2.2 Climate

Climate varies significantly with elevation in the Colorado Front Range. Barry (1973) described these climatic changes along a transect on the eastern slope. He found that the mean duration of the frost-free season decreased from 125 days in the lower montane, to 104 days in the upper montane, 59 days in the subalpine, and 47 days in the alpine. The diurnal temperature range was highest at low elevations, and decreased markedly in the alpine. Peet (1981) constructed climate diagrams for the same transect described by Barry (1973). He found a decrease in mean annual temperature from 8.3 ° C in the lower montane, to 5.6 ° C in the upper montane, 1.7 ° C in the subalpine, and -3.3 ° C in the alpine. Mean annual precipitation increased from 532 mm in the lower montane, to 540 mm in the upper montane, 657 mm in the subalpine, and 1050 mm in the alpine. Below the alpine, which received predominantly winter precipitation, maximum precipitation occurred in May.

2.3 Disturbance

Front Range ecosystems are subject to a diverse array of disturbances. Peet (1988) stated that "fire, wind, insects, disease, ungulate browsing, avalanches, landslides, extreme weather, volcanism, and of course, humans all have major impacts on the landscape" (p.69). Historically, fire has probably been the most important natural disturbance (Peet 1988), with fire frequency declining with increasing elevation. Humans have modified fire regimes, and have introduced new types of disturbance to the Front Range. In particular, the introduction of cattle has had a major impact on many Front Range ecosystems.

The Colorado Front Range has been influenced by human activities for a long time. Early campsites were present at timberline and in alpine areas of the Front Range as early as 6,000 years BC (Veblen & Lorenz 1991). Before European settlement, Native Americans hunted both in the mountains and on the adjacent plains, and may have set periodic fires in both areas (Peet 1988, Veblen & Lorenz 1991). During the mid-19th century, European settlers came to the Colorado Front Range, and initiated a period of increased disturbance associated first with trapping, and then with mining and exploration (Veblen & Lorenz 1991). The "gold rush" in the Colorado Front Range began in 1858 (Veblen & Lorenz 1991). During the settlement era, from 1859 to 1920, fire frequencies were higher in much of the Front Range than they had been prior to European arrival (Veblen & Lorenz 1986, Goldblum 1990). Since the 1920's, however, fire frequencies have decreased in much of this area (Veblen & Lorenz 1986, Goldblum 1990). This reduction in fire frequency is due to many factors including fire suppression and reduced fuel levels due to grazing (Peet 1988). As the size of the human population increases along the Colorado Front Range, many areas are experiencing increased pressures from both development and recreational activities.

2.4 Study sites

A summary of the physical characteristics of the nine study sites is presented in Table 2.1. I sampled three meadows in each of three elevational zones. Within each zone, the elevations of the meadows are within approximately 100 meters of one another. Elevations were determined from U. S. Geological Survey topographic maps. A map of the study area is presented in Figure 2.1.

The nine meadows chosen for this study were selected to be as similar to one another as possible in terms of all factors other than elevation. All nine meadows are (1) relatively mesic, (2) of similar size (long axis ~ 100 meters, short axis ~ 50 meters), (3) free of tree stumps or any signs of logging, (4) adjacent to roads or trails, and (5) have been grazed by cattle. Criteria 4 and 5 were included in order to maximize the probability that the sites would be inoculated by exotic seed (Weaver, et al. 1990). Ideally, all physical site factors and land-use histories would be constant between the meadows, and I could then examine only the influence of elevation on species patterns. In reality, there is some variability in edaphic conditions among the nine meadows. In particular, I did not control for soil types when choosing the study sites. The study design attempts to compensate for such differences by including three replicate meadows in each elevational zone.

Table 2.1: Description of the nine study sites.

Meadow	Elevation (meters)	Topographic Position	Aspect	Slope Steepness	Slope Configuration
S-1	3109	valley	SE	3 - 4 %	concave/straight
S-2	2926	lower slope	S	25 -30 %	straight
S-3	3109	upper slope	NW	~ 2 %	straight
M-1	2591	lower slope	NE	1 - 2 %	concave/straight
M-2	2683	lower slope	E	0 - 5 %	straight
M-3	2591	valley	SW	2 - 3 %	concave
L-1	1982	upper slope	NE	1 - 20 %	concave
L-2	2097	middle slope	E	5 - 20 %	straight
L-3	1966	middle slope	E	1 - 5 %	straight

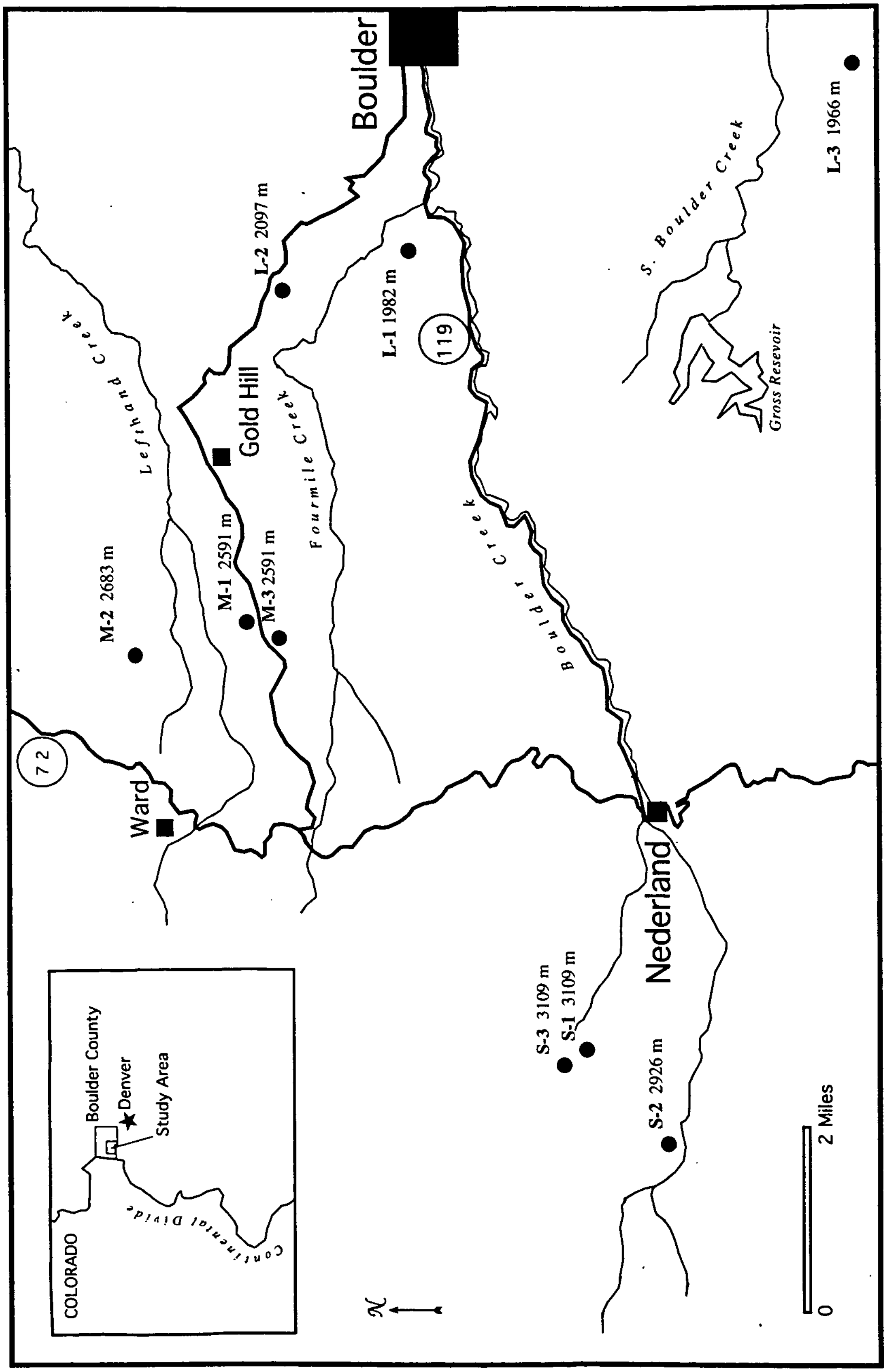


Figure 2.1: Map of study area.

2.4.1 Lower Montane Sites

(L-1) Betasso Preserve. This study site is located in the Betasso Preserve (section 28, T1N, R71W), which is managed by the Boulder County Parks and Open Space Department. The site is located just north of the Canyon Loop Trail, where the trail first turns east along a fairly flat ridge. The approximate elevation of the site is 1982 meters. The site is oblong, with a north-east aspect, and a concave shape. The slope of the long axis of the meadow, along trend, is 20%, according to field measurements. The slope, perpendicular to trend, averages 2.5% towards the meadow center.

The area around Betasso Preserve has been impacted by Europeans since the 1870's (Schooland 1980, cited in Boulder County Parks & Open Space, #1). Initially, these impacts included sawmills, mining operations, and the construction of small towns and roads. Eventually, much of the area became rangeland for livestock. Most of Betasso Preserve was operated as a ranch by the Betasso family from 1915 until 1976. Cattle wintered on the ranch, and ate alfalfa which was hayed from a meadow on the Preserve.

(L-2) Bald Mountain Scenic Area. This study site is also located on land managed by the Boulder County Parks and Open Space Department. Bald Mountain Scenic Area is located in the southeast quarter of section 16, T1N, R71W on County Highway 52. The predominant vegetation types in the Scenic Area are meadow, ponderosa pine parkland, and ponderosa pine forest. The study site itself is located immediately south of the parking area and picnic tables. The site is situated at approximately 2027 meters above sea level, and it has an eastern aspect. While the predominant slope is towards the east, at the southern end of the site the slope increases to the south.

The history of European impacts on the Scenic Area extends at least to 1886, when grazing leases were granted on Bald Mountain (BCPOS, #2). In 1896, a mineral lease was granted for the area. Mining-related impacts include small exploratory pits, piles of tailings, and small-scale logging (BCPOS, #2).

(L-3) El Dorado Mountain. This site is located on land belonging to the City of Boulder Open Space Department. The site is located on the county line between Boulder and Jefferson Counties, in section 31, T1S, R70W and section 6, T2S, R70W. The site is oblong and oriented with its long axis almost exactly north-south. It slopes ~ 2.5 % to the east. The elevation is approximately 1966 meters. This site is currently grazed by cattle on an annual basis, although cows were not yet present during the time that I sampled (late June).

2.4.2 Upper Montane Sites

All three of the Upper Montane field sites are on Forest Service land, administered by the Roosevelt National Forest.

(M-1) Switzerland Trail. This site is located on the north-east corner of the intersection of the Gold Hill road (County road 52) and the Switzerland Trail (County road 93) in the north-east quarter of section 16, T1N, R72W. The elevation is approximately 2591 meters. The meadow slopes slightly (~ 2 %) to the east.

(M-2) Gold Lake. This site is located on the south side of County road 102, between the Peak to Peak Highway (State road 72) and Gold Lake in section 5, T2N, R72W. The elevation is approximately 2683 meters. The long axis of this meadow is oriented with an azimuth of 108 °, and the slope down this length ranges from 2% to 5% (down to the east). This site is part of a current grazing allotment. However, it was not grazed during the summer of 1994. Although cattle were absent during the sampling season, dung from the previous year was still present in the meadow. An old road is visible along the northern side of the meadow. This road has been seeded with *Festuca saximontana*. No transect lines came within 10 meters of the abandoned road.

(M-3) Gold Hill Road. This site is located on the south-west corner of the intersection of the Gold Hill road and the Switzerland Trail in the central portion of section 16, T1N, R72W. The elevation is approximately 2591 meters. The meadow slopes approximately 2.5% to the south-west, and is very wet at its southern end. The transects at this site were all located in the drier eastern end of the meadow.

2.4.3 Subalpine Sites

(S-1) Caribou Flat. This site is located on Caribou Flat in section 8, T1N, R73W. The elevation is approximately 3109 meters. The meadow slopes 3% -- 4% towards the south-east (azimuth of 155°). Although this site is on private land which is not leased for grazing, it is actively grazed by cattle which stray from adjacent Forest Service land. Aside from the actual presence of cattle, evidence of grazing includes trampled areas, dung, and grazed vegetation.

(S-2) Devil's Thumb. This site is located immediately east of the boundary of the Indian Peaks Wilderness Area in the Roosevelt National Forest. The site is adjacent to the Devil's Thumb Trail, accessed from the Hessie Trailhead on Boulder County road 111. The elevation is approximately 2926 meters. This meadow is oriented east-west, with an azimuth of 290 °. The meadow has a southern aspect, with slopes ranging from 25% to 30%.

(S-3) Roberts Placer. This site is located on Caribou Flat, north of site S-1, in the same section. The elevation is 3109 meters. The long axis of this meadow is oriented with an azimuth of 327 °. Cattle were present in this meadow during the sampling season, as in S-1. In addition, there is a high degree of ant activity in this meadow, and ant hills were often encountered along the transect lines. There is clear evidence of mining activity on the edges of the meadow, in the form of exploratory pits and piles of excavated rock.

CHAPTER 3

METHODS

3.1 Study design

This study was conducted in nine meadows, three at each of three elevations, 1980 meters (lower montane), 2590 meters (montane) and 3050 meters (subalpine) (Figure 2.1). At each of the three elevational zones sampled, the elevations of the replicate meadows are all within approximately 100 meters of one another. The nine meadows are all within an 8 kilometer wide east-west strip on the east slope of the Colorado Front Range.

3.2 Vegetation Sampling

During the summer of 1994, I sampled vegetation along line transects placed within each meadow. In each meadow, 150 meters were sampled. The transects were placed so as to capture as much within-meadow spatial pattern as possible (Figure 3.1). In most cases, a single long transect (100 to 150 meters) was placed down the long axis of the meadow, and three shorter transects were established perpendicular to that axis and distributed evenly along its length. Depending upon the size of the meadow, and the consequent lengths of the established transects, some transects were sampled continuously, and some were sampled only every other meter. The only criterion was that the total number of sampled meters in each meadow equal 150. The transect lines did not come within 10 meters of the meadow edge. In most cases this edge was defined by roads, trails, or a forest border.

The transects were labeled in a consistent manner. The long, central transect was labeled ‘A’, with the perpendicular transect lines labeled ‘B’, ‘C’, ‘D’, and only in site LM-3, ‘E’. The meadows were also given codes. The subalpine sites are distinguished as S-1, S-2, S-3. The mid-montane sites are M-1, M-2, and M-3, and the lower montane sites are coded L-1, L-2 and L-3. Therefore, transects can be uniquely identified by a combination of the meadow code and the transect letter. For example, L-2-B is transect B in site L-2.

I sampled the vegetation occurring along meter tapes which were stretched out on the transect lines. I estimated vegetation cover using the line intercept method (Kent & Coker, 1992). For each individual meter, I estimated the cover, in centimeters, of each species present. All species determinations were made according to Weber (1990). If species determinations could not be made in the field, specimens were taken to the University of Colorado Herbarium for identification. Each species was classified as either native or exotic according to Harrington (1954) and Weber (1990). In addition to plant cover, I also estimated the cover of bare ground in each meter. Since there can be considerable species overlap, even in herbaceous systems such as these, the total cover values of each meter usually sum to more than 100 centimeters.

3.3 Vegetation Analysis

In order to examine first order patterns in the data, ordinations were conducted using the DECORANA program to perform Detrended Correspondence Analysis (DCA) (Hill 1979, Hill & Gauch 1980). Indirect ordination techniques, such as DCA, examine the similarity of the floristic composition of vegetation samples (Kent & Coker, 1992). When the results are graphed, points which occur close together in the ordination space are more similar to one another in terms of species composition than are points which are far apart. Despite several valid criticisms of the technique (Palmer, 1993), DCA remains a very useful way to summarize complex multidimensional data. Once the data are reduced, possible underlying causes may be subjectively inferred from the observed patterns. For ease of interpretation, I used whole transect lines as sample sites in the ordination analysis. This reduced the number of samples from 1350 (meters) to 37 (transects).

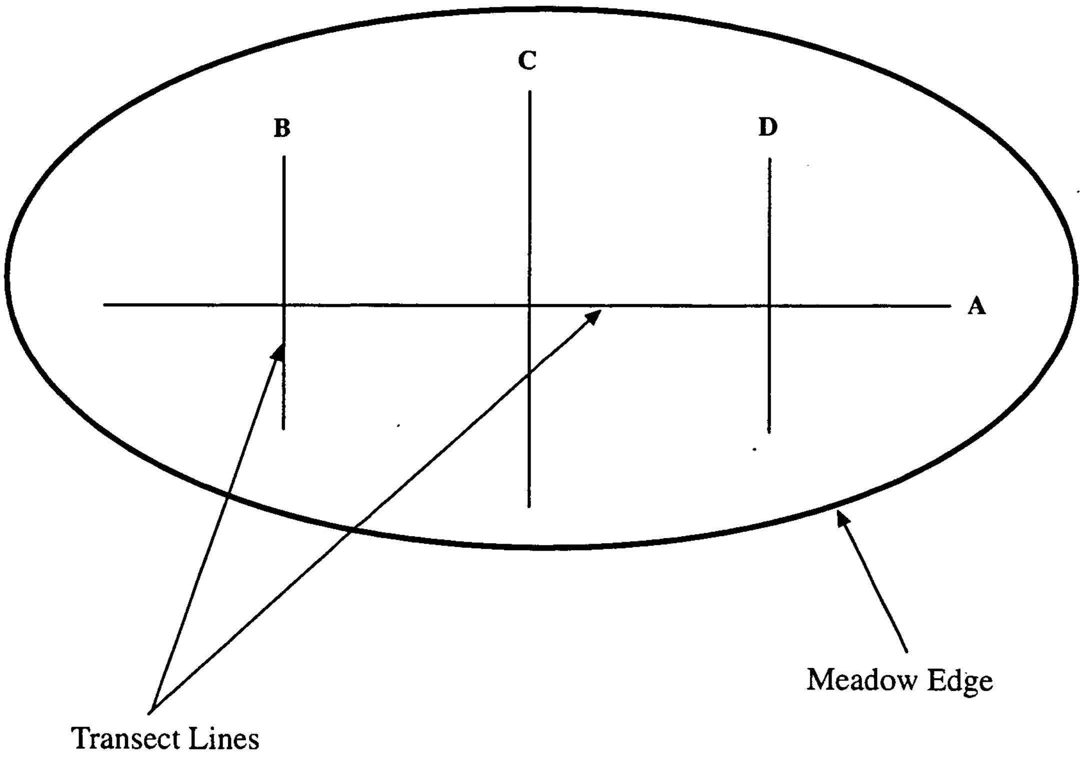


Figure 3.1: Meadow sampling design.

To compare species richness and plant cover among elevations, statistical methods were used. I used the SPSS computer program (SPSS 1990) to perform all of the following statistical tests. In these analyses, a single meter is a sample point, with its own associated values of plant cover (total, native and exotic), cover of bare ground, and species richness (total, native, and exotic) calculated as the number of species of each type occurring in the meter. For the examination of total species richness, native species richness, total plant cover and native plant cover, parametric statistics were used. Here, the data were pooled within each of the three elevations (n = 450) and these were compared using a standard Analysis of Variance (ANOVA). All pairwise comparisons were tested for significance using Duncan's multiple range tests. For comparisons of exotic species richness and exotic cover between elevations, nonparametric statistics were used. Here, since many of the sampled meters at each elevation contained no exotic species, the samples were severely skewed towards zero and did not meet the assumptions of parametric methods (Sokal & Rohlf 1981). To test for significant differences in exotic richness and cover between elevations, all data were pooled within each zone (n = 450) and Kruskal-Wallis ANOVA's were used. To compare specific elevational pairs, Kolmogorov-Smirnov two-sample tests were employed.

To test for positive and negative relationships between the various factors measured, I used Pearson product-moment correlation analysis. The purpose of this analysis was to determine the strength and direction of the relationships, if any, between exotic cover and richness per meter and other variables such as native species richness, native cover, and cover of bare ground per meter. In these analyses, I first looked for relations in the whole data set (n = 1350), pooling data from all of the meadows. In addition, similar correlations were determined within each of the three elvational zones (n = 450) and within each individual meadow (n = 150).

Chi-square analysis was used to test for associations between native and exotic species and various life form characteristics. I coded all species as native or exotic, annual or perennial, and as either a (1) bunch grass, (2) rhizomatous grass, (3) annual grass, (4) legume, (5) bulb-former, (6) forb, (7) sedge or rush, or a (8) tree or shrub. I then used chi-square tests to determine whether there were significant associations between native and exotic species and any of these attributes.

CHAPTER 4

RESULTS

4.1 Flora

Native species far out-number exotics in the nine meadows I studied. In the entire study, 128 native species, and 23 exotic species were identified. Appendix A lists all of the species and indicates their presence or absence in each of the nine meadows. Appendix B lists all species according to family. Thirty-nine families are represented, the most common being the Asteraceae (34 species) and the Poaceae (30 species). Appendix C lists all of the native species according to their elevational ranges and indicates their frequencies in each on the nine meadows. Table 5.1 consists of a comparable listing of the exotic species.

Native species and exotic species differ in terms of longevity. According to a chi-square test of association, there is no significant tendency for exotic species to exhibit an annual or a perennial habit (Table 4.1). Of the exotic species, 7 are annual (~30%) and 16 are perennial (~70%). Native species, on the other hand, have a significant tendency to be perennial (Table 4.2). Of the natives, 8 (~6%) are annual, and 120 (~94%) are perennial. Compared to native species, then, proportionally more exotic species are annuals.

Table 4.1: Chi-square test for the association of exotic species with habit.

Habit:	Observed:	Expected:	Residual:
Annual	7	11.5	-4.50
Perennial	16	11.5	4.50

Chi-square = 3.522, df = 1, Significance = .061

Table 4.2: Chi-square test for the association of native species with habit.

Habit:	Observed:	Expected:	Residual:
Annual	8	64	-56
Perennial	120	64	56

Chi-square = 98.00, df = 1, Significance < .001

Native and exotic species sort out differently in terms of life form characteristics (Table 4.3). For example, proportionally more exotic species (34.7%) than natives (17%) are grasses. Further, while all of the native grasses are perennial bunch-formers, exotic grasses are predominantly either rhizomatous perennials or annuals. I did not identify any native annual grasses in this study.

Table 4.3: Frequencies of native and exotic species of different life forms.

	Native:		Exotic:	
Form:	Number	Percent	Number	Percent
Bunch Grass	22	17%	1	4.3%
Rhizom. Grass	–	–	5	21.7%
Annual Grass	–	–	2	8.7%
Legume	10	7.8%	2	8.7%
Bulb-former	3	2.3%	–	–
Forb	74	57.8%	13	56.5%
Sedge/Rush	13	10%	–	–
Tree/Shrub	6	4.7%	–	–
Total:	128	–	23	–

I was unable to identify all of the species I encountered along the transect lines. For the entire data set, 119 out of the 270 morphospecies encountered remain unidentified. Of the 119 unknown species, however, 75% occur only 10 times or fewer in the entire data set (1350 observations). The unidentified species usually consisted of either basal leaves of plants which did not flower during the field season or grass blades without flowers. Importantly, according to a simple oneway ANOVA, there were no significant differences in the mean number of unknown species per meadow among the three elevations (n=3, p=.42). The mean number of unknowns per meadow was 15.6 in the subalpine, 16.6 in the montane, and 8.6 in the lower montane. The number of unknown species in the data set is probably artificially high, since unidentified species were labeled uniquely in each meadow. Unless otherwise specified, I did not include the unidentified species in any of the analyses presented here.

4.2 Species Ranges

Three exotic species (13%) were present in the subalpine zone in this study (Table 5.1). None of these was limited to the subalpine zone, and all three (*Phleum pratense*, *Taraxacum officinale*, and *Poa compressa)* also occurred at both of the lower elevations. For comparison, of the 128 native species encountered, a total of 49 (38%) occurred in the subalpine zone, eight (6% of 128) of which were found at all three elevations, and 37 (29% of 128) of which were found only in the subalpine zone (Appendix C). While proportionally more exotic species than natives were present over the entire elevational range, proportionally fewer exotic species than natives were present in the subalpine zone.

Of the three exotic species present at all three elevations, none was very abundant in the subalpine zone. While *Phleum pratense* and *Poa compressa* did exhibit high frequencies at the two lower elevations, none of the exotic species had a frequency of over 20% in any of the three subalpine meadows (Table 5.1). In contrast, of the eight native species found at all three elevations, three species had frequencies of over 20% in at least one subalpine meadow. Further, two native species, *Achillea lanulosa* and *Juncus arcticus*, had frequencies of over 20% in at least one meadow at each of the three elevations (Appendix C).

Most species, whether native or exotic, did not exhibit broad elevational ranges. Of the exotic species, 17 (74%) were confined to a single elevation. In comparison, 83 native species (65%) were confined to single elevation. Similar proportions of exotic and native species were confined to a single meadow. Twelve exotic species (52%) and 68 native species (53%) were present in one meadow only. Therefore, while proportionally more exotic species than natives were present over the entire elevational range sampled, proportionally more exotics were also present at one elevation only. In contrast, proportionally more native species than exotics extended over at least two elevations.

4.3 General Associations Between Native & Exotic Occurrence

Analysis of the entire data set, which consists of 1350 observations, provides insight into general relationships between exotic species occurrence and other measured variables. Table 4.4 contains correlation coefficients describing the relationships between eight variables. Both native cover and native richness are strongly negatively correlated with exotic cover. Exotic cover and exotic richness are strongly positively correlated with one another. Likewise, native cover and native richness are positively correlated, although the relationship is not as strong. Total cover, total richness, and cover of bare ground show weak relationships with both exotic cover and exotic richness. Both total cover and total known cover are strongly negatively correlated with the cover of bare ground. In contrast, total known richness is only weakly negatively correlated with the cover of bare ground.

Table 4.4: Entire data set (n= 1350) matrix of correlation coefficients between eight variables. Note that both total cover (cover of all plants (cm) per meter) and total known cover (cover of only identified species (cm) per meter) are included. Notation: ** indicates that P < .01, * indicates P < .05, **bold** indicates r > .5 or r < -.5.

	Total Cover	Known Cover	Exotic Cover	Native Cover	Bare Ground	Known Richness	Exotic Richness	Native Richness
Total Cover	1.00							
Known Cover	**.87****	1.00						
Exotic Cover	.30**	.28**	1.00					
Native Cover	.43**	**.55****	**-.65****	1.00				
Bare Ground	**-.85****	**-.77****	-.22**	-.42**	1.00			
Known Richness	.22**	.27**	-.07**	.28**	-.15**	1.00		
Exotic Richness	.28**	.26**	**.77****	-.46**	-.22**	.22**	1.00	
Native Richness	.03	.09**	**-.54****	**.55****	-.01	**.80****	-.41**	1.00

The strength of the correlations between the eight variables differs among elevations (Tables 4.5, 4.6, & 4.7). For example, the correlation between exotic cover and native cover is strongly negative in the montane (r = -.61) and lower montane (r = -.61) zones, but not very strong in the subalpine zone (r = -.17). The weak correlation in the subalpine zone is most likely due to the very low number of exotic species there, and their very low cover values. Further evidence of the relative lack of exotic species in the subalpine zone is the extremely high correlation between native richness and total richness there (r = .98). Further, while in the subalpine zone the relationship between native richness and exotic cover is non-significant, there is a significant negative correlation between native richness and exotic cover in the montane (r = -.46) and lower montane (r = -.30) elevational zones.

Table 4.5: Subalpine zone (n = 450) matrix of correlation coefficients between eight variables. Notation as in Table 4.4.

	Total Cover	Known Cover	Exotic Cover	Native Cover	Bare Ground	Known Richness	Exotic Richness	Native Richness
Total Cover	1.00							
Known Cover	**.92****	1.00						
Exotic Cover	- .09	-.06	1.00					
Native Cover	**.92****	**.99****	-.17**	1.00				
Bare Ground	**-.92****	**-.84****	.12*	**-.84****	1.00			
Known Richness	-.10 *	-.09 *	.07	-.11*	.15**	1.00		
Exotic Richness	-.09	-.06	**.77****	-.15**	.11*	.15**	1.00	
Native Richness	-.08	-.08	-.08	-.07	.13**	**.98****	-.05	1.00

Table 4.6: Montane zone (n = 450) matrix of correlation coefficients between eight variables.

	Total Cover	Known Cover	Exotic Cover	Native Cover	Bare Ground	Known Richness	Exotic Richness	Native Richness
Total Cover	1.00							
Known Cover	**.79****	1.00						
Exotic Cover	.29**	-.23**	1.00					
Native Cover	.41**	**.62****	**-.61****	1.00				
Bare Ground	**-.84****	**-.66****	-.16**	-.41**	1.00			
Known Richness	.27**	.48**	-.16**	**.52****	-.23**	1.00		
Exotic Richness	.10*	.12*	**.60****	-.39**	-.08	.22**	1.00	
Native Richness	.22**	.41**	-.46**	**.71****	-.18**	**.87****	-.29**	1.00

Table 4.7: Lower montane zone (n=450) matrix of correlation coefficients between eight variables.

	Total Cover	Known Cover	Exotic Cover	Native Cover	Bare Ground	Known Richness	Exotic Richness	Native Richness
Total Cover	1.00							
Known Cover	**.95****	1.00						
Exotic Cover	.36**	.37**	1.00					
Native Cover	.48**	**.52****	**-.61****	1.00				
Bare Ground	**-.89****	**-.86****	-.35**	-.42**	1.00			
Known Richness	.52**	.49**	.19**	.24**	.47**	1.00		
Exotic Richness	.46**	.43**	**.62****	-.21**	.42**	**.68****	1.00	
Native Richness	.30**	.29**	-.30**	**.52****	.27**	**.76****	.04	1.00

In addition to the differences in correlations among elevations, there are also notable differences in the magnitudes of the various correlation coefficients among the nine individual meadows (n = 150, Tables 4.8 and 4.9). For example, exotic cover is strongly positively correlated with exotic richness in all three subalpine meadows, and in two montane meadows. However, in one montane meadow (M-1) the correlation is not particularly strong. Meadow M-1 is fairly unique in that it is largely dominated by a single exotic species, *Tithymalus uralensis* (leafy spurge). If high values of exotic cover result from the influence of a single (or few) ubiquitous species, then high exotic cover will not translate into high values of exotic richness. In the lower montane zone, exotic cover and richness are not strongly correlated.

Table 4.8: Within-meadow (n = 150) correlation coefficients between exotic cover and six other variables. Notation as in Table 4.4.

	Correlation Coefficient with Exotic Cover:								
	Lower Montane			Montane			Subalpine		
	L-1	L-2	L-3	M-1	M-2	M-3	S-1	S-2	S-3
Native Cover	**-.77****	-.36**	**-.59****	-.36**	-.38**	**-.57****	.01	-.33**	-.11
Native Rich.	-.46**	-.24**	-.44**	-.17*	-.32**	-.39**	.10	-.09	-.22**
Exotic Rich.	.16	.38**	.35**	.42**	**.58****	**.65****	**.83****	**.75****	**.81****
Total Cover	-.15	.20*	.41**	**.71****	.15	.06	.10	-.19*	.02
Total Rich.	-.30**	-.00	-.15	.06	-.04	-.05	.24**	.14	-.05
Bare Grnd	.08	-.15	-.31**	-.45**	-.07	.00	-.13	.26**	.00

Table 4.9: Within-meadow (n= 150) correlation coefficients between exotic richness and five other variables. Notation as in Table 4.4.

	Correlation Coefficient with Exotic Richness:								
	Lower Montane			Montane			Subalpine		
	L-1	L-2	L-3	M-1	M-2	M-3	S-1	S-2	S-3
Native Cover	-.01	-.03	-.26**	-.02	-.29**	-.30**	.02	-.31**	-.06
Native Rich.	-.01	.03	-.25**	.08	-.32**	-.17*	.16*	-.08	-.21**
Total Cover	.16	.18*	.08	.40**	.02	.12	.09	-.21*	.04
Total Rich.	**.54****	**.56****	.48**	**.55****	.16	.34**	.33**	.22**	0
Bare Grnd	-.07	-.06	0	-.12	-.07	-.05	-.08	.24**	0

4.4 Species Composition -- Ordination Analysis

In order to examine the patterns of species distributions among the study sites, I performed ordination analyses of three data sets -- species composition and percent cover of (1) all species together, (2) native species alone and (3) exotic species alone. I used individual transect lines as samples in this analysis, and the total cover value (sum of cover in all meters along the transect) for each species along the transect line as its importance value. Ordination is a very useful technique for summarizing complex data, and for identifying the underlying factors which influence species distribution patterns. The ordination axes produced in the analysis are interpreted as representing real gradients influencing species establishment patterns. I performed ordinations for native and exotic species separately in order to determine whether their distributions are related to the same factors.

The results of the ordinations performed on all species and on native species alone are very similar (Figs. 4.1 and 4.2). In both cases, the meadows can easily be grouped by elevation in the ordination space. For the ordination of native species, the first axis has an eigenvalue of .899, and the second axis has a value of .687. For all species together, these values are .875 and .576. The meadows are clearly segregated by an elevational gradient, expressed diagonally in the ordination space. Since the ordinations of all species together and native species alone exhibit the same patterns, it appears that native species are strongly influencing overall species distribution patterns. This is not surprising since most of the species encountered in this study are native.

The ordination results for exotic species alone are presented in Figures 4.3 and 4.4. Figure 4.3 presents the scatterplot for the ordination of exotic species using all of the nine meadows in the analysis. It is apparent that site M-1 is very different from all of the other sites, and this results in the compression of most of the points at the low end of axis one. In order to focus more closely on the patterns on the left side of the graph, I also present the scatterplot of the ordination performed on all sites except for M-1 (Figure 4.4). The patterns are very similar between the two graphs, although they are easier to see in Figure 4.4.

The ordination of only exotic species yields a pattern strikingly different from the previous two. First, the ordination axes explain less of the variation in the data. The first axis has an eigenvalue of .648, while the second has an eigenvalue of only .357. Second, the axes do not reflect the elevation gradient in any obvious way, and the sites cannot easily be grouped by elevation in the ordination space. Attempts to correlate the first axis scores with other physical variables, such as cover of bare ground and a topographic-moisture rating, yielded very poor results. While I have been unable to identify the underlying factors represented by the ordination axes, it is clear that exotic species do not sort out along the elevation gradient as do natives.

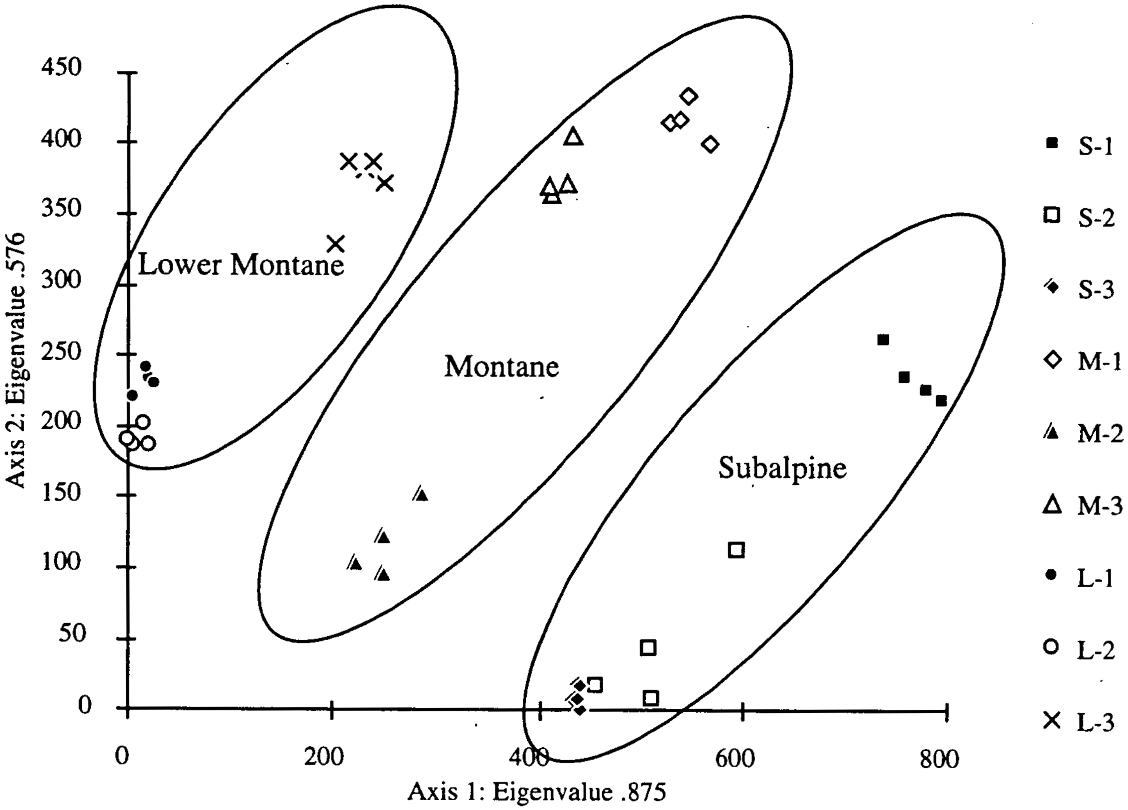


Figure 4.1: Scatterplot of DCA results for all known species. Sample points are transect lines. Notation is as follows: S-1, S-2, S-3 = subalpine sites; M-1, M-2, M-3 = montane sites; L-1, L-2, L-3 = lower montane sites.

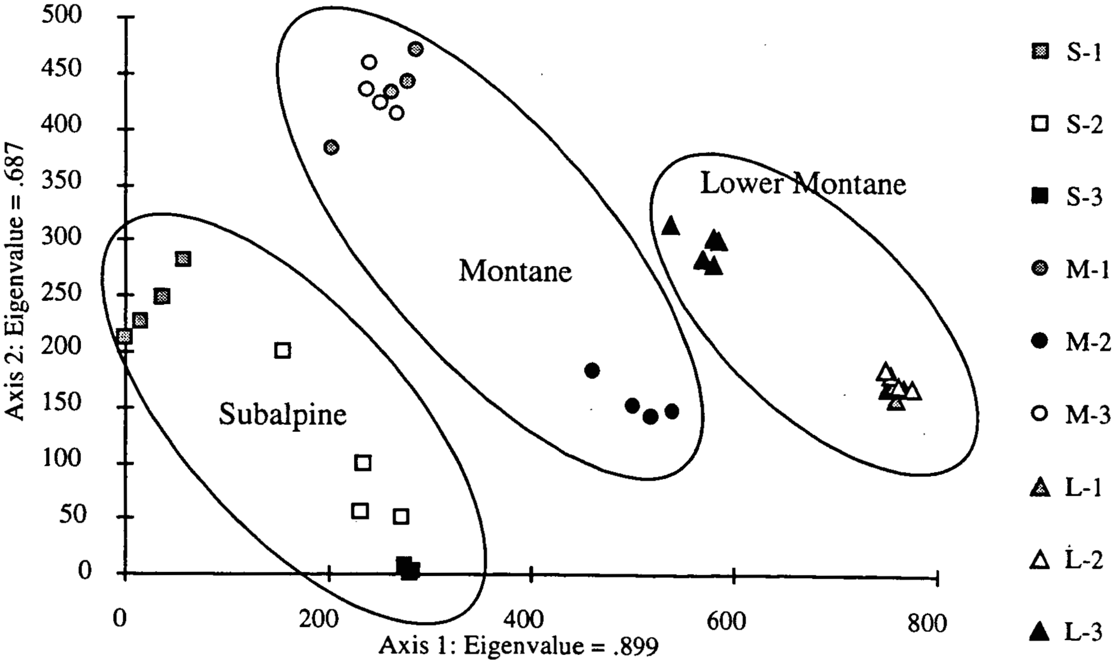


Figure 4.2: Scatterplot of DCA results for native species only. Notation as in Figure 4.1.

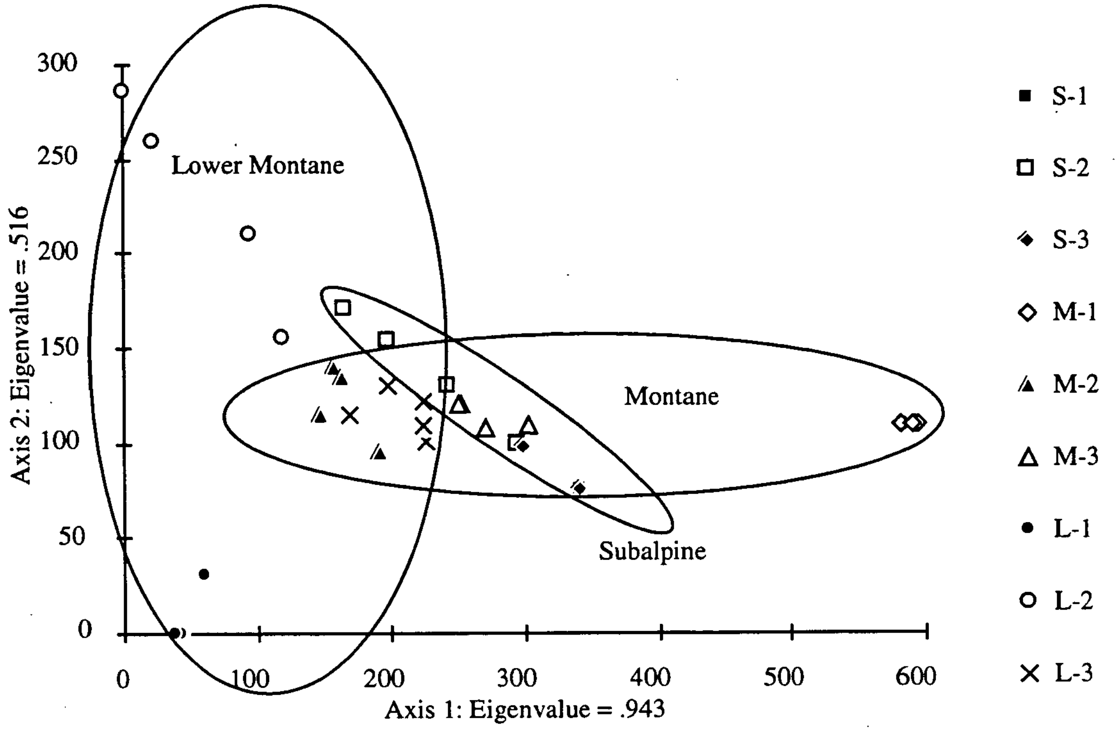


Figure 4.3: Scatterplot of DCA results for exotic species only. Notation as in Figure 4.1.

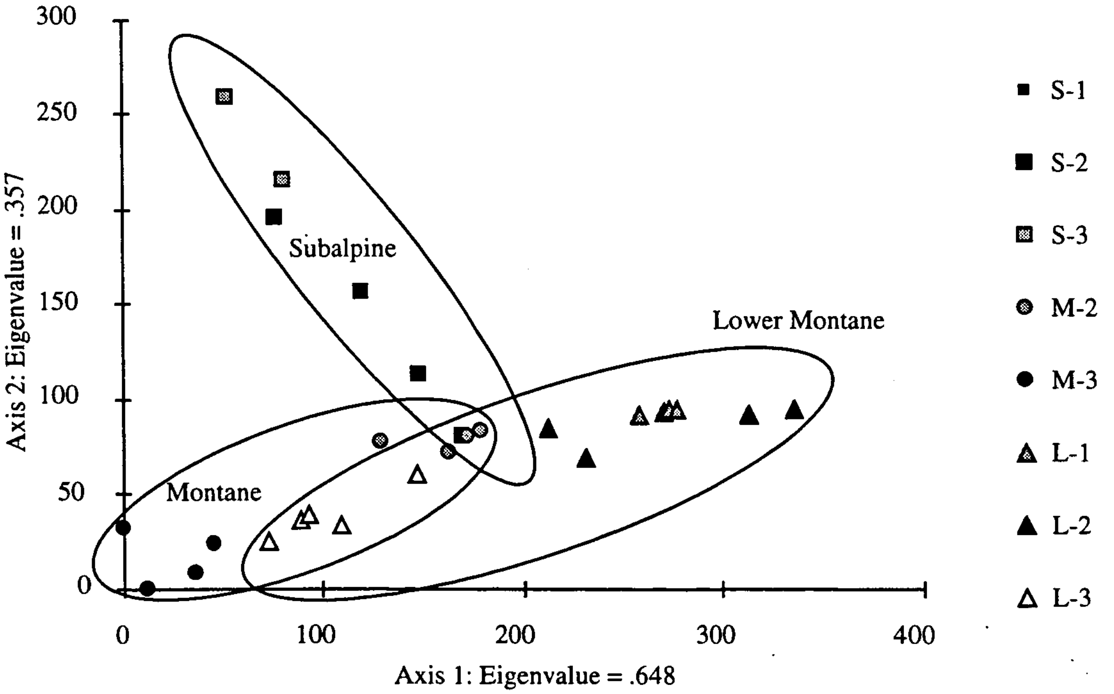


Figure 4.4: Scatterplot of DCA results for exotic species only and excluding site M-1. Notation as in Figure 4.1.

4.5 Species Diversity & Equitability

4.5.1 Total Diversity

Species diversity was calculated using the Shannon-Wiener diversity index. The Shannon-Wiener index is a community-level measure which combines information about species richness and relative abundance (Kent & Coker, 1992). A single diversity value is calculated for each site using the equation $H' = -\Sigma\, pi(log(pi))$, where pi is the relative importance of species i. Equitability (or evenness) is calculated as $E = H'/Hmax$, where $Hmax = log(s)$, and s is the number of species. Both average total species diversity and average total species equitability appear to increase with increasing elevation (Table 4.10). However, according to a simple oneway ANOVA, the differences are not significant at the .05 level (Table 4.11). Indeed, examination of the individual meadow diversity and evenness values (Tables 4.12 and 4.13) indicates that there is quite a bit of variability within each elevational zone.

Table 4.10: Mean species diversity (H') and equitability (E) for each elevation

	Lower Montane		Montane		Subalpine	
	H'	E	H'	E	H'	E
All Known Species:	.93	.61	1.05	.68	1.08	.72
Native Species:	.82	.59	1.02	.72	1.07	.73
Exotic Species:	$.49^{a}$	.53	.40	.52	$.11^{b}$	.26

Within a single row, diversity values with different superscripts are different at the .05 level using Duncan's multiple range test, n = 3.

4.5.2 Native & Exotic Diversity

Qualitatively, native and exotic species diversity show opposite elevational trends (Table 4.10). However, according to both an ANOVA and Duncan's multiple range tests, there are no significant differences in native species diversity or equitability among elevations (Table 4.11). Both the diversity of native species, and native equitability, have their lowest values in the lower montane. The levels of native diversity and evenness appear to be very similar between the montane and the subalpine, and these values are slightly higher than those of the lowest elevational zone. In contrast to native diversity, exotic species diversity reaches its highest values in the lower montane zone. Here, a Duncan's multiple range test indicates that there is a significant difference between subalpine and lower montane exotic diversity (Table 4.10). Interestingly, the montane and lower montane zones are qualitatively quite similar in terms of their exotic species diversity and evenness values. In this case, the subalpine zone appears to be distinct in its low values. There are no significant differences in exotic equitability between elevations (Table 4.11).

Table 4.11: Analysis of Variance table for differences in total, native, and exotic species diversity and evenness between elevations.

	Source	df	ss	F	P
Total Diversity:	Elevation	2	.0382	.4627	.6503
	Error	6	.2475		
Total Evenness:	Elevation	2	.0186	.8719	.4652
	Error	6	.0640		
Native Diversity:	Elevation	2	.1052	1.3950	.3180
	Error	6	.2261		
Native Evenness:	Elevation	2	.0546	2.3070	.1806
	Error	6	.0710		
Exotic Diversity:	Elevation	2	.2430	3.5166	.0976
	Error	6	.2073		
Exotic Evenness:	Elevation	2	.3585	3.8760	.0831
	Error	6	.2775		

The lack of statistical significance for most of the elevational diversity and equitability patterns could be due to two factors. First, the small sample size (n= 3) for the comparisons among elevations undoubtedly makes it difficult to distinguish differences. Here, since diversity and equitability are community level attributes calculated for whole meadows, the data set is constrained to nine values. Second, the high degree of variability in species diversity and evenness within each elevational zone may account for the absence of significant elevational trends. Examination of Tables 4.12 and 4.13 yields some interesting observations. At each elevation there can be a considerable range in diversity and equitability values among the three meadows. In addition, there is considerable overlap in values among elevations. The fact that these values are scattered so widely indicates that species diversity and equitability in these Front Range meadows are probably strongly influenced by factors other than elevation.

Table 4.12: Total, native and exotic species diversity (H') values for each meadow

Lower Montane			Montane			Subalpine		
L-1	L-2	L-3	M-1	M-2	M-3	S-1	S-2	S-3
All Species:								
.64	1.04	1.12	.85	1.13	1.17	.92	1.11	1.23
Native Species:								
.52	.86	1.08	.91	1.03	1.10	.91	1.09	1.22
Exotic Species:								
.16	.62	.71	.37	.45	.38	.00	.24	.09

Table 4.13: Total, native, and exotic species evenness (E) values for each meadow.

Lower Montane			Montane			Subalpine		
L-1	L-2	L-3	M-1	M-2	M-3	S-1	S-2	S-3
All Species:								
.44	.69	.71	.61	.69	.75	.68	.69	.80
Native Species:								
.38	.61	.69	.76	.64	.76	.69	.69	.81
Exotic Species:								
.23	.73	.62	.41	.75	.40	.00	.50	.30

4.6 Species Richness

4.6.1 Total Richness

Total richness of all known species exhibits the combined input of the separate native and exotic patterns (Figure 4.5). While the trend is for total richness per meter to increase with increasing elevation, according to Duncan's multiple range tests the subalpine and montane values are not significantly different at the .05 level (Tables 4.14 and 4.15). Total species richness, however, is significantly higher in the subalpine and montane zones than it is in the lower montane zone.

Table 4.14: Total known species richness (number of species/meter)

Elevation:	Mean:	Std. Dev:	n:
Subalpine	5.51^a	1.85	450
Montane	5.21^a	1.82	450
Lower Montane	4.87^b	1.98	450

Numbers with different superscripts are different at the .05 level according to Duncan's multiple range test.

Table 4.15: Analysis of Variance table for differences in total species richness (number of species/meter) and native species richness between elevations , n = 450.

	Source	df	ss	F	P
Total Richness	Elevation	2	92.91	13.1	<.0001
	Error	1347	4790.24		
Native Richness	Elevation	2	1596.94	269.16	<.0001
	Error	1347	3995.92		

Table 4.16: Mean total species richness (number of species/meter) for each meadow. n = 150. Values in parentheses are standard deviations.

Lower Montane			Montane			Subalpine		
L-1	L-2	L-3	M-1	M-2	M-3	S-1	S-2	S-3
3.08 (1.08)	5.18 (1.66)	6.34 (1.58)	4.47 (1.72)	6.14 (1.66)	5.01 (1.66)	4.88 (1.64)	4.85 (1.46)	6.80 (1.73)

4.6.2 Native Richness

Native and exotic species exhibit opposite richness patterns across the elevational gradient (Figure 4.5). Richness of native species increases with increasing elevation. A simple oneway ANOVA of native richness per meter (n=450) yields significant differences among all three elevations (Tables 4.17). Although the trend in the data is the same, the ANOVA performed on values of whole-meadow richness (n=3) yields no significant differences (Table 4.18). The values for mean whole-meadow native richness for the subalpine, montane, and lower montane zones are 30, 28, and 24 respectively (Table 4.18).

Table 4.17: Native species richness (number of species/meter) of each elevation calculated from the pooled meter data within each elevation.

Elevation	Mean	Std. Dev.	n
Subalpine	5.36^{a}	1.83	450
Montane	3.65^{b}	1.85	450
Lower Montane	2.73^{c}	1.45	450

Numbers with different superscripts are different at the .05 level according to Duncan's multiple range test.

Table 4.18: Native species richness of each elevation calculated from whole-meadow richness values (number of native species/meadow).

Elevation	Mean*	Std. Dev.	n
Subalpine	30	8.18	3
Montane	28	12.00	3
Lower Montane	24	1.73	3

* A simple oneway ANOVA indicates that no values are significantly different at the .05 level.

Table 4.19: Mean native species richness (number of native species/meter) for each meadow. Values in parentheses are standard deviations, n= 150.

Lower Montane			Montane			Subalpine		
L-1	L-2	L-3	M-1	M-2	M-3	S-1	S-2	S-3
1.77 (.91)	3.55 (1.37)	2.87 (1.42)	2.36 (1.44)	4.63 (1.73)	3.95 (1.59)	4.78 (1.57)	4.65 (1.43)	6.64 (1.77)

4.6.3 Exotic Richness

Exotic species richness declines with increasing elevation. The median richness value in the subalpine zone is 0, while in the montane zone this value is 1.00 and in the lower montane zone it is 2.00 (Table 4.21). In the subalpine zone, the maximum exotic richness for any meter is 2.00. In the montane zone, the maximum is 5.00, and in the lower montane zone it is 7.00. Since the exotic richness values do not meet the assumptions necessary for parametric statistics, I used non-parametric methods in this part of the analysis. A Kruskal-Wallis ANOVA performed on exotic richness by elevation, indicates that there is a significant elevational effect (Table 4.20). Kolmogorov-Smirnov two-sample tests between all elevational pairs indicate that all three distributions are significantly different from one another with $p < .001$ (Table 4.21).

Table 4.20: Kruskal-Wallis oneway ANOVA table for differences in exotic richness (number of exotic species/meter) between elevations.

Elevation:	Lower Montane	Montane	Subalpine
n:	450	450	450
Mean Rank:	930.03	807.67	288.80

Adjusted chi-square: 741.07; Significance: <.0001

Table 4.21: Median, 25th percentile, 75th percentile, and modal values of exotic richness (number of exotic species/meter) for each elevation, calculated from the pooled meter values within each elevation, n = 450.

Elevation*:	1st Quartile	Median	3rd Quartile	Mode
Subalpine	.00	.00	.00	.00
Montane	1.00	1.00	2.00	1.00
Lower Montane	1.00	2.00	3.00	1.00

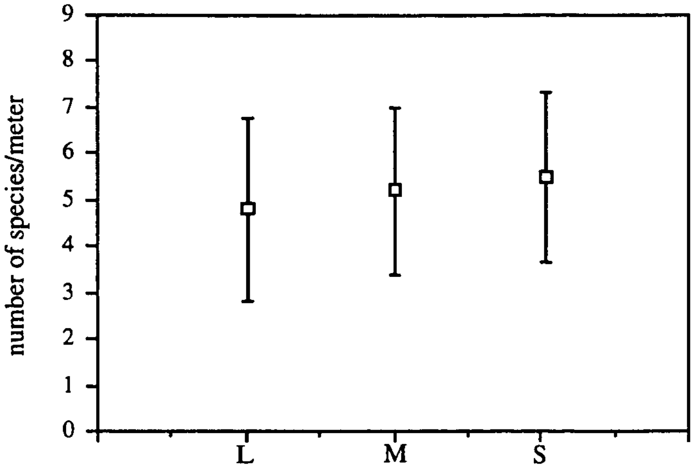
* all three distributions are significantly different according to Kolmogorov-Smirnov two-sample comparisons, $p < .001$.

Table 4.22: Median, 1st quartile, 3rd quartile, and modal values of exotic richness for each meadow, n= 150.

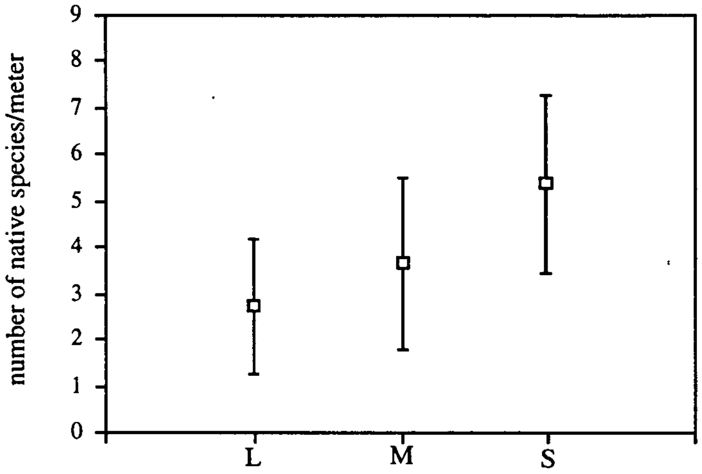
Site:	1st Quartile	Median	3rd Quartile	Mode
Subalpine:				
S-1	.00	.00	.00	.00
S-2	.00	.00	.00	.00
S-3	.00	.00	.00	.00
Montane:				
M-1	2.00	2.00	3.00	2.00
M-2	1.00	1.00	1.00	1.00
M-3	.00	1.00	2.00	1.00
Lower Montane:				
L-1	1.00	1.00	2.00	1.00
L-2	1.00	2.00	2.00	2.00
L-3	3.00	3.00	4.00	3.00

4.6.4 Within-Elevation Variability in Species Richness

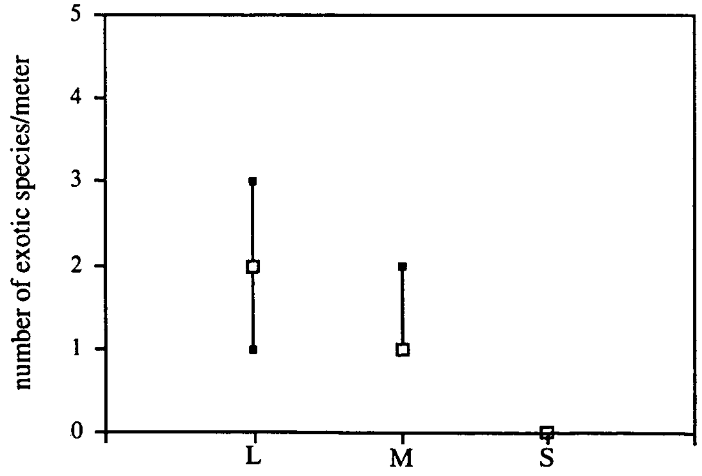
In addition to the robust trends in native and exotic species richness along the elevational gradient in this study, there are also significant differences in the richness values among the meadows of a single elevation (see Tables 4.16, 4.19, and 4.22, and Figure 4.6). In some cases, patterns are apparent in the relative magnitudes of native and exotic richness for particular meadows. For example, site M-1 exhibits low native species richness and high exotic richness compared to the other two montane meadows. Although the between-meadow differences are not great enough to obscure the broader elevational patterns, they are certainly worthy of note.



(a) Mean total species richness of each elevation. Error bars are ± 1 standard deviation.

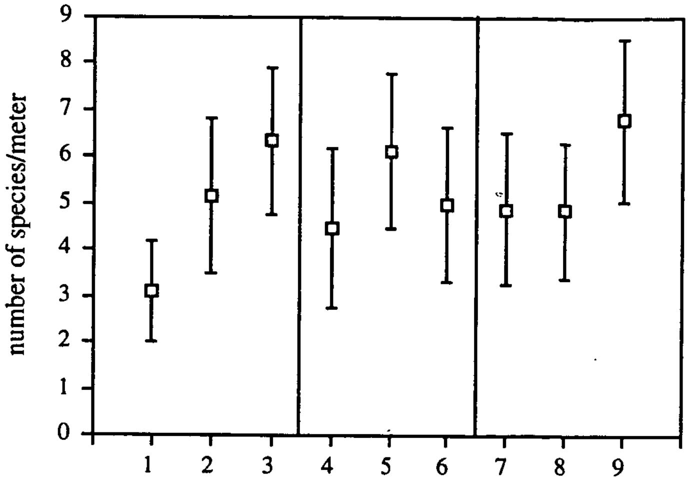


(b) Mean native species richness of each elevation. Error bars are ± 1 standard deviation.

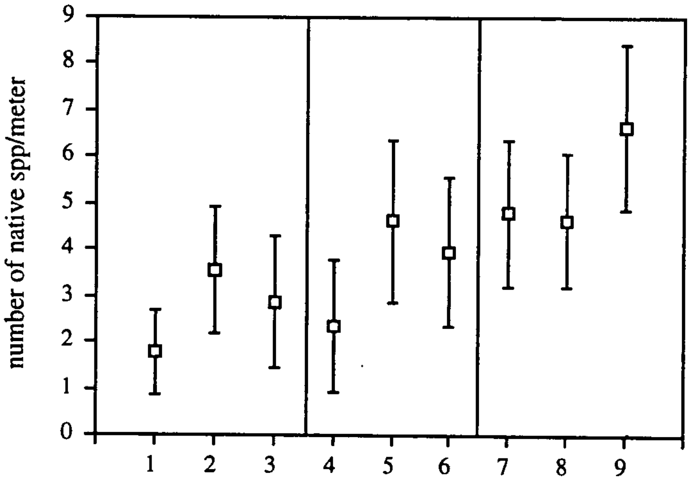


(c) Median exotic species richness of each elevation. Error bars are 1st and 3rd quartiles.

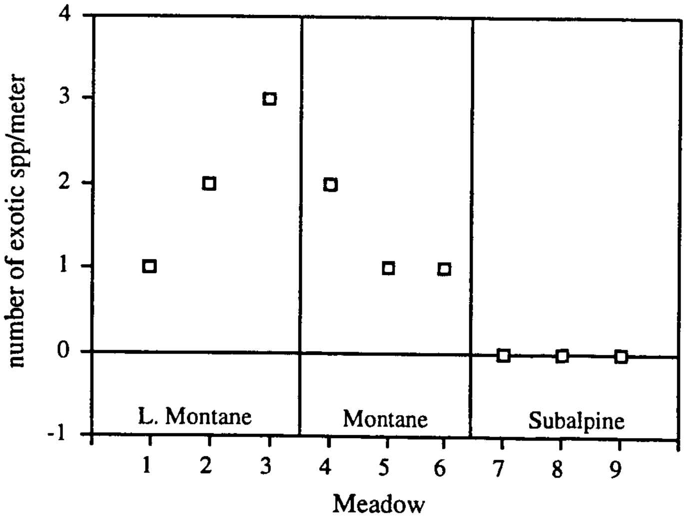
Figure 4.5: Total, native, and exotic species richness (number of species/meter) of each elevation, n = 450. L = lower montane, M = montane, S = subalpine.



(a) Mean total species richness of each meadow. Error bars are ± 1 standard deviation.



(b) Mean native species richness of each meadow. Error bars are ± 1 standard deviation.



(c) Median exotic species richness of each meadow. See Table 4.22 for quartile values.

Figure 4.6: Total, native, and exotic species richness (number of species/meter) for each meadow, n = 150. Meadows are numbered as follows: lower montane: 1 = L-1, 2 = L-2, 3 = L-3; montane: 4 = M-1, 5 = M-2, 6 = M-3; subalpine: 7 = S-1, 8 = S-2, 9 = S-3.

4.7 Cover

4.7.1 Total Cover

Total plant cover and the cover of bare ground do not exhibit simple elevational trends. Total plant cover per meter is lower in the subalpine zone than it is in the montane and lower montane zones. (Table 4.23, note that calculations include the cover of unidentified species). However, mean plant cover in the montane zone is greater than in the lower montane zone. Not surprisingly, the mean cover of bare ground per meter exhibits the reverse of the pattern observed for total plant cover (Table 4.24). Bare ground declines from the lower montane to the montane zone, but increases again in the subalpine zone. The lowest value for the cover of bare ground coincide with the highest values of total plant cover.

Table 4.23: Total plant cover (cm/meter) for each elevation, calculated from the pooled meter data within each elevation.

Elevation:	Mean:	Std Dev:	n:
Subalpine	66.08^a	17.55	450
Montane	78.27^b	17.16	450
Lower Montane	70.75^c	18.39	450

Numbers with different superscripts are different at the .05 level according to Duncan's multiple range tests. Note that calculations include the cover of unidentified species.

Table 4.24: Cover of bare ground (cm/meter) for each elevation, calculated from the pooled meter data within each elevation.

Elevation:	Mean:	Std. Dev:	n:
Subalpine	39.29^a	15.97	450
Montane	31.60^b	11.33	450
Lower Montane	36.88^c	13.89	450

Numbers with different superscripts are different at the .05 level according to Duncan's multiple range tests.

4.7.2 Native Cover

The cover per meter of native species increases with increasing elevation. The mean cover of native species per meter is 35.12 cm in the lower montane zone and

60.59 cm in the subalpine zone (Table 4.25). A Duncan's multiple range test indicates that the means of all three elevations are distinct at the .05 level.

Table 4.25: Cover of native species (cm/meter) in each elevation, calculated from the pooled meter data within each elevation.

Elevation:	Mean:	Std. Dev:	n:
Subalpine	60.59^{a}	18.90	450
Montane	42.81^{b}	25.10	450
Lower Montane	35.12^{c}	21.59	450

Numbers with different superscripts are different at the .05 level according to Duncan's multiple range tests.

Table 4.26: Mean cover values (cm/meter) and standard deviations for bare ground, all plant species, and only native species for each meadow, n = 150.

	Bare Ground		Total Cover		Native Cover	
Site:	Mean	Std Dev	Mean	Std Dev	Mean	Std Dev
Subalpine:						
S-1	29.5	(10.12)	75.22	(11.82)	68.96	(14.18)
S-2	36.43	(16.34)	70.35	(18.45)	67.14	(19.22)
S-3	51.95	(11.55)	52.69	(12.84)	45.67	(12.95)
Montane:						
M-1	30.93	(9.09)	81.07	(16.48)	21.93	(16.96)
M-2	31.96	(10.96)	76.56	(15.19)	55.17	(17.87)
M-3	31.9	(13.56)	77.17	(19.32)	51.33	(25.02)
Lower Montane:						
L-1	46.83	(10.35)	57.87	(11.39)	27.81	(18.22)
L-2	36.83	(14.06)	70.49	(17.67)	50.18	(20.25)
L-3	27	(8.86)	83.89	(15.37)	27.37	(17.88)

4.7.3 Exotic Cover

In contrast to the observed patterns for the cover of native species, the cover of exotic species per meter decreases significantly with increasing elevation. Since the cover values of exotic species are strongly skewed towards zero, I used distribution-free statistics in this part of the analysis. A Kruskal-Wallis non-parametric ANOVA of exotic cover among the three elevations, yields a chi-square value of 804.24 (Table 4.27). This value is significant at less than the .0001 level, indicating that at least one pair of distributions is significantly different. Pairwise comparisons conducted with the

Kolmogorov-Smirnov two-sample test indicate that all elevational pairs are significantly different (Table 4.28).

Table 4.27: Kruskal-Wallis oneway ANOVA table for differences in exotic cover between elevations, calculated using the pooled meter data from each elevation zone.

Elevation:	Lower Montane	Montane	Subalpine
n:	450	450	450
Mean Rank:	957.21	801.40	267.88

Adjusted chi-square: 804.24; Significance: < .0001

Table 4.28: 1st quartile, median, 3rd quartile, and modal values of exotic cover (cm/meter) for each elevation, calculated using the pooled meter data from each elevation zone.

Elevation*:	1st Quartile	Median	3rd Quartile	Mode	n
Subalpine	.00	.00	.00	.00	450
Montane	10.00	20.00	35.00	15.00	450
L. Montane	18.75	30.00	45.00	25.00	450

* All three distributions are significantly different according to Kolmogorov-Smirnov two-sample comparisons, $p < .001$.

In order to determine whether differences in exotic cover among elevations were merely a function of differences in total cover, I calculated the proportion of exotic cover (exotic cover/total plant cover) in each meter. Like the exotic cover values, the proportion data do not meet the assumptions of parametric statistics. Distribution-free methods, however, indicate that the proportion of exotic cover per meter is highest in the lower montane zone, and decreases with increasing elevation (Tables 4.29 and 4.30). According to Kolmogorov-Smirnov two-sample tests, all elevational pairs are significantly different in terms of the proportion of exotic cover per meter (Table 4.30).

Table 4.29: Kruskal-Wallis oneway ANOVA table for differences in the proportion of exotic cover per meter between elevations, calculated using the pooled meter data from each elevation zone.

Elevation:	Lower Montane	Montane	Subalpine
n:	450	449	450
Mean Rank:	946.02	809.50	269.78

Adjusted chi-square: 786.86; Significance: < .0001

Table 4.30: 1st quartile, median, 3rd quartile, and modal values of the proportion exotic cover (cm cover of exotic species/cm total plant cover) per meter, calculated using the pooled meter data from each elevation zone.

Elevation*:	1st Quartile	Median	3rd Quartile	Mode	n
Subalpine	.00	.00	.00	.00	450
Montane	.14	.29	.59	.00	449
L. Montane	.27	.48	.71	.50	450

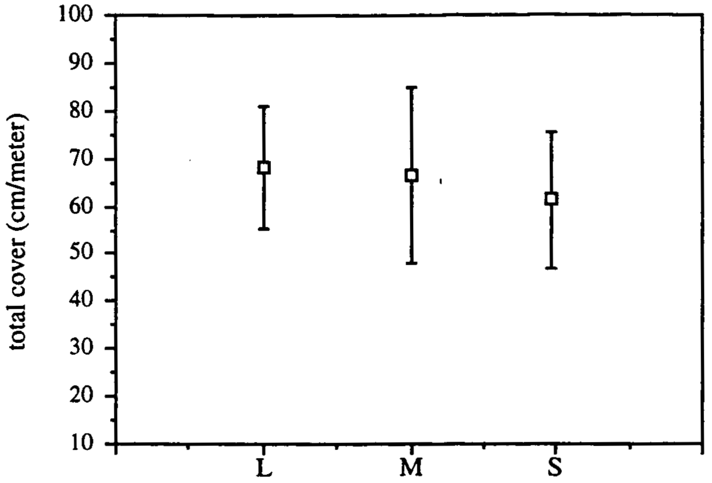
* All three distributions are significantly different according to Kolmogorov-Smirnov two-sample comparisons, p < .001.

Table 4.31: Median, 1st quartile and 3rd quartile values of exotic cover (cm/meter) and proportion exotic cover (cm exotic cover/cm total plant cover per meter) for each meadow, n = 150.

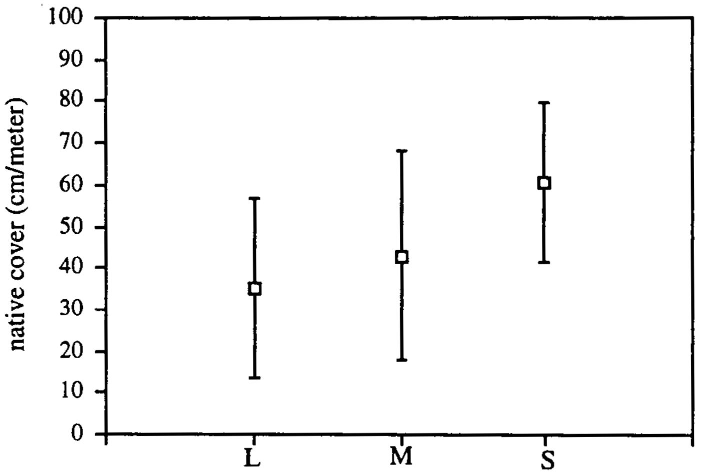
	Exotic Cover			Proportion Exotic Cover		
Site:	1st Quartile	Median	3rd Quartile	1st Quartile	Median	3rd Quartile
Subalpine:						
S-1	.00	.00	.00	.00	.00	.00
S-2	.00	.00	.00	.00	.00	.00
S-3	.00	.00	.00	.00	.00	.00
Montane:						
M-1	20.00	40.00	55.00	.49	.67	.84
M-2	9.50	15.00	20.00	.12	.21	.31
M-3	.00	10.00	25.00	.00	.17	.45
Lower Montane:						
L-1	20.00	30.00	40.00	.33	.50	.75
L-2	10.00	15.50	25.00	.13	.26	.37
L-3	40.00	50.00	62.25	.50	.66	.82

4.7.3 Within-Elevation Variability in Plant Cover

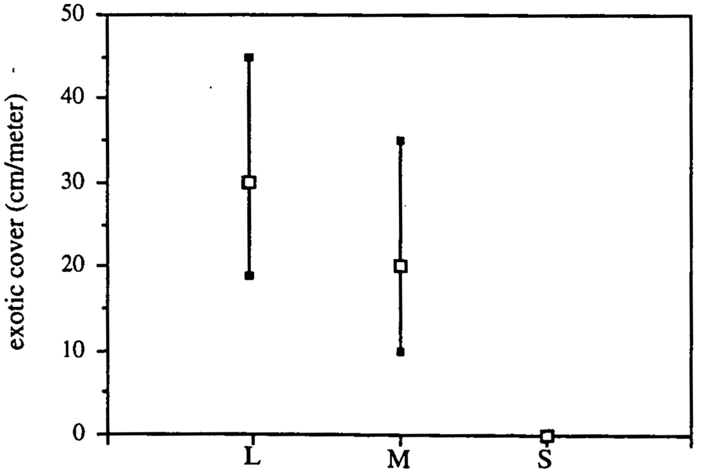
Within each elevational zone, the meadows can show considerable variation in cover values. For example, the proportion of exotic cover per meter ranges widely among meadows within the montane and lower montane zones (Figure 4.7, Tables 4.26 and 4.31). While these variations are not big enough to obscure the general elevational trends, they are interesting to note. There seem to be other important factors influencing vegetation patterns in these meadows besides elevation.



(a) Mean total plant cover of each elevation. Error bars are ± 1 standard deviation.

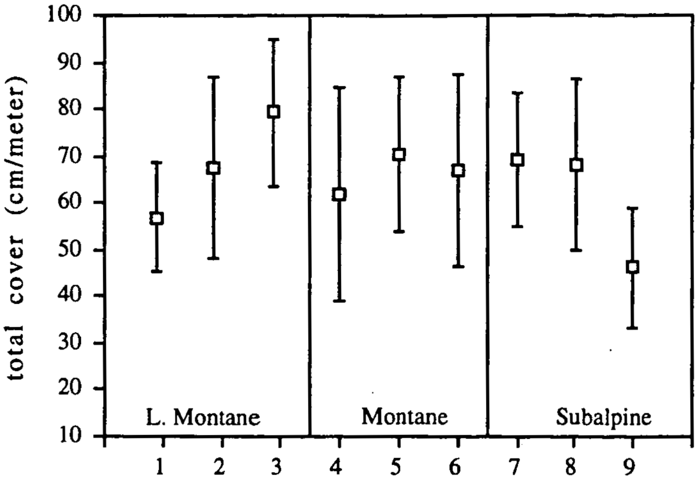


(b) Mean native plant cover of each elevation. Error bars are ± 1 standard deviation.

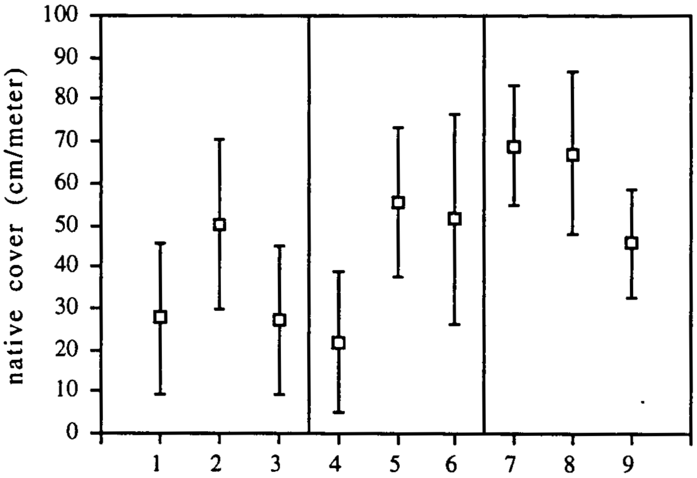


(c) Median exotic plant cover of each elevation. Error bars are 1st and 3rd quartiles.

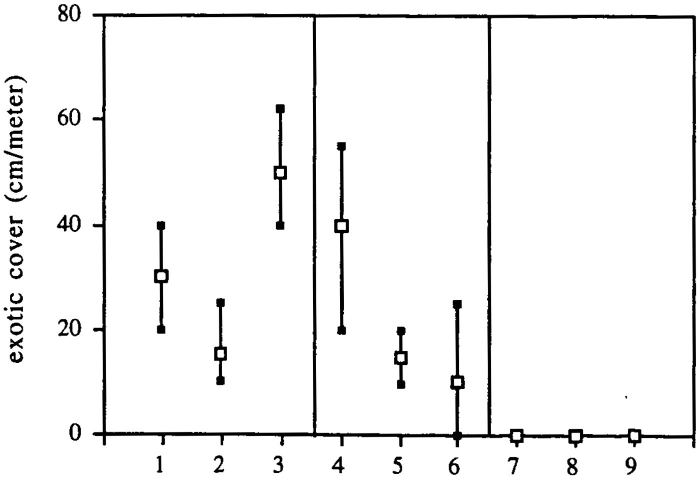
Figure 4.7: Total, native, and exotic plant cover (cm plant cover/meter) for each elevation. n = 450. S = subalpine, M = montane, L = lower montane.



(a) Mean total plant cover of each meadow. Error bars are ± 1 standard deviation.



(b) Mean native plant cover of each meadow. Error bars are ± 1 standard deviation.



(c) Median exotic plant cover of each meadow. Error bars are 1st and 3rd quartiles.

Figure 4.8: Total, native, and exotic plant cover (cm plant cover/meter) of each meadow. n = 150. Meadows are numbered as in Figure 4.5.

CHAPTER 5

DISCUSSION

5.1 General Relationships Between Exotic & Native Species

The richness of exotic species is negatively correlated with both the cover and richness of native species in this study (Table 4.4). Additionally, exotic species cover is strongly negatively correlated with both native cover and richness (Table 4.4). Similarly, McIntyre and Lavorel (1994) found that native and exotic species richness were inversely related in Australian grasslands. There are several possible explanations for this pattern. Native and exotic species may respond differently to small-scale (~1 meter) abiotic environmental influences and disturbances. In addition, native and exotic species may competitively exclude one another from small areas. Such exclusion could be influenced by site characteristics, or it could simply reflect chance aspects of the timing of seed arrival and plant establishment. For example, early arrivals might have an advantage over late-comers. While I cannot distinguish between these various factors in the present study, the observed relationships most likely result from a combination of influences.

In some cases, based on the characteristics of the species involved, it is possible to speculate about the factors influencing the negative correlation between native and exotic establishment. For example, *Anisantha tectorum* (cheatgrass, also called *Bromus tectorum*) may competitively exclude native species from sites which it occupies. However, this exclusion depends upon the ability of this grass to germinate early and occupy space. In particular, *A. tectorum* can establish quickly after soil disturbance or fire, and can then compete successfully with native species for soil water (Link et. al 1990, Melgoza et. al 1990, Melgoza & Nowak, 1991). Such competition may prevent the establishment of native plants (Link, et. al 1990). I have observed qualitatively that *A. tectorum* tends to establish on very disturbed sites in the lower montane zone. For example, it is abundant directly adjacent to trails on patches trampled heavily during winter, and in grazed areas underneath shade trees where cattle probably congregate and trample vegetation annually. Although this study did not investigate the role of competition, my results are consistent with the possibility that some exotic species do competitively exclude natives from certain areas.

5.2 Characteristics of the Exotic Flora

5.2.1 Strategies of Exotic Species

Many ecologists have tried to describe the general characteristics of invasive or "weedy" species. In island biogeography theory, good colonizers have been described as being r-selected (MacArthur & Wilson 1967). According to this theory, successful colonizers tend to have high population growth rates, early reproduction, small seed size, short life-spans, and relatively low tolerance for competition. In the context of biological invasions, exotic species do not always colonize disturbed or open areas, but sometimes become established in fairly intact native vegetation. Bazzaz (1986) distinguished between *colonizers*, which entered "unoccupied" habitats, and *invaders* which entered "relatively intact vegetation" and dominated or displaced it (p.97). Baker (1986) suggested that successful invaders should have (1) generalized pollination systems, (2) appropriate seed dispersal systems, (3) breeding systems which allow for seed production and genetic recombination (e.g. self-pollination, and no strong inbreeding depression), and (4) the capacity for strong vegetative reproduction. Since in many ecosystems there is a continuum of site conditions, from disturbed to undisturbed, it is likely that a range of plant strategies, from those associated with colonization to those associated with invasion, may be successful.

For the most part, recent research has not supported earlier generalizations about the characteristics of successful invaders (Newsome & Noble 1986, D'Antonio

1993). Newsome and Noble (1986) suggested that, rather than being generalists, plant invaders in Australia tended to be "specialists" which could exploit only "particular opportunities for invasion" (p.15). Crawley (1987) reviewed the characteristics of the "top twenty" British aliens, and found no general life-history patterns, breeding systems, or modes of dispersal. The only common characteristic that Crawley identified was the tendency of good perennial invaders to form dense thickets. (This is in accordance with Baker's attribute (4) above, and with Baker's (1965) comments on the importance of "vigorous vegetative reproduction" in weeds (p.165)). Thus, according to Crawley (1987), successful invaders were "thicket-forming plants capable of prolonged site pre-emption, and of preventing the establishment of other species beneath them" (p.450). Some recent studies support this observation. For example, *Foeniculum vulgare* (fennel) and *Carpobrotus edulis* (iceplant), both successful invaders into California coastal plant communities, seem to share this morphology (Beatty & Licari, 1992, D'Antonio 1993). In my study, however, *Tithymalus uralensis* (leafy spurge) is the only exotic species which clearly fits this description. The species is vigorously rhizomatous and can spread clonally over large areas (Whitson, et. al, 1992). It is present in only one meadow (M-1), but at that site it is nearly ubiquitous (frequency = 94.6%).

My results suggest that site pre-emption can be achieved by strategies other than vegetative reproduction. In the lower montane zone, annual exotic species may achieve site pre-emption without forming dense perennial thickets. At this elevation, annuals can often dominate disturbed or open sites; when a site becomes available for colonization, they can germinate early and monopolize nutrients before perennial species are established. This can result in the long-term occupation of a site by annual species, especially if nutrient levels remain high (McLendon & Redente, 1992). In the montane and subalpine zones, I found no annual exotic species. At these elevations, the exotic grasses are all rhizomatous perennials. Here, an annual life form is not a successful strategy for invasion, perhaps due to the limited growing season. The strategies of site occupation employed by successful invaders appear to vary along the elevational gradient I studied. While vegetative reproduction appears to be an important strategy for perennial exotics at higher elevations, in the lower montane zone annual exotic species can dominate sites by establishing early year after year.

5.2.2 Elevational Ranges of Exotic Species

Proportionally more exotic species than natives were present over the entire elevational gradient that I sampled. The only three exotic species found in the subalpine zone were also present at both lower elevations (Table 5.1). However, exotic species did not achieve high frequencies in the subalpine zone (Table 5.1). While most species, whether native or exotic, were confined to a single elevation, this was true for proportionally more exotic species than natives (Appendix C, Table 5.1). In contrast, proportionally more native species than exotics were present at two elevations. Therefore, while more exotic species than natives may tend to be either broadly distributed along this elevational gradient or else present at only one elevation, native species tend to inhabit an intermediate proportion of the elevational gradient.

The ability of a species to tolerate the wide range of conditions characteristic of this elevational gradient could be associated with several factors, including both genetic differentiation and phenotypic plasticity. Specifically, plant species may inhabit broad environmental ranges by forming genetically distinct populations (ecotypes) adapted to local conditions (Clausen et. al 1940 & 1948, Rice & Mack 1991, Ricklefs 1990), or through a high degree of flexibility in phenotype (Williams et al. 1995, Rice & Mack 1991, Levin 1986).

Table 5.1: Frequencies of exotic species occurrences in each meadow. Frequency was determined from presence in the 150 sampled meters (maximum frequency = 150). Note that a frequency of 30 = 20%. Species are arranged into groups of common elevational range. See Appendix C for a comparable listing of native species.

	Lower Montane			Montane			Subalpine		
	L-1	L-2	L-3	M-1	M-2	M-3	S-1	S-2	S-3
Species of all elevations:									
Taraxacum officinale	0	0	27	7	19	2	14	8	23
Phleum pratense	0	0	129	6	39	97	0	1	0
Poa compressa	11	63	124	3	126	27	0	21	1
Species of the lower montane & montane zones:									
Plantago lanceolata	0	0	22	10	0	0			
Poa pratensis	147	22	89	0	42	0			
Tragopogon dubius	9	2	8	0	0	1			
Species of the montane zone only:									
Bromopsis inermis				103	0	9			
Elytrigia repens				28	0	0			
Tithymalus uralensis				142	0	0			
Trifolium spp				18	0	0			
Acetosella vulgaris				0	0	4			
Agrostis gigantea				0	0	6			
Hieracium aurantiacum				0	0	4			
Linaria vulgaris				0	0	8			
Species of the lower montane zone only:									
Anisantha tectorum	4	63	0						
Silene antirrhina	25	79	1						
Bromus japonicus	0	12	70						
Camelina microcarpa	0	3	1						
Alyssum minus	0	0	10						
Convolvulus arvensis	0	0	7						
Medicago lupulina	0	0	1						
Neolepia campestris	0	0	9						
Potentilla recta	0	0	22						

It is unclear whether native resident species and exotic invaders are differentiated between these two strategies. For example, Baker (1965) suggested that in undisturbed communities native species should consist of finely adapted ecotypes, and that invading weeds should possess "general purpose" genotypes that pre-adapt them to grow under a range of conditions (p.165). Consistent with this prediction, Clausen et. al (1948) found distinct genetic differentiation among "climatic races" of native species of *Achillea*. Further, Williams et al. (1995) attributed the wide elevational range of the introduced grass *Pennisetum setaceum* (fountaingrass) on Hawaii to phenotypic plasticity. However, Bazzaz (1986) indicated that some invaders exhibited ecotypic differentiation, and Rice and Mack (1991) attributed the broad ecological range of *Anisantha tectorum* to a combination of genetic differentiation among populations and phenotypic plasticity. The question of the relative importance of these two strategies among native and exotic species in general remains unanswered.

In contrast to the paucity of exotic species in the subalpine zone in this study, Weaver, et al. (1990) identified thirty-four exotic species growing in timberline environments of the Northern Rocky Mountains. While most of the exotics identified in their study were found on disturbed roadsides, the authors found that six species, including both *Phleum pratense* and *T. officinale*, were present in intact meadows. *Poa compressa*, however, was confined to roadside shoulders and ditches in their study. The differences in the results of these two studies undoubtedly arise from the differences in the sites sampled. Since roadsides experience very high levels of disturbance, they are probably not directly comparable to the meadows sampled here. The meadows that I studied are influenced by cattle grazing, the activities of small mammals, and the recreational activities of humans, but they are not subjected to the intense and repeated disturbances associated with roadside areas. Subalpine exotic richness is more consistent between the two studies if only intact meadows are compared.

In many cases, it should be possible to predict the distributions of particular exotic species along an elevation gradient based on current understandings of the species' tolerance ranges. For example, *Anisantha tectorum* was confined to the lower montane in this study. This result is not surprising since *A. tectorum* is considered to be adapted to conditions of limited moisture. In particular, this grass exhibits early growth of deep roots which allows it to exploit soil moisture earlier in the season and at greater depths than many native species (Link, et. al 1990). In addition, Pierson and Mack (1990) found that at high elevation sites, the growing season was too short for *A.*

tectorum to reproduce successfully. In general then, the distribution of *A. tectorum* described here conforms to current expectations.

It has been suggested that disturbance may extend the elevational range of some exotic species (Forcella & Harvey, 1983). A comparison of my findings with those of other studies, is generally consistent with this theory. Several of the exotic species which were limited to lower elevations in this study were observed by Weaver et al. (1990) to grow on disturbed sites in the subalpine zone. Of the eleven exotic species I recorded in the montane zone but not in the subalpine, Weaver et al. (1990) found five (*Bromopsis inermis*, *Poa pratensis*, *Tragopogon dubius*, *Trifolium* spp, and *Acetosella vulgaris*) at timberline. Of the twelve exotic species I observed in the lower montane zone but not in the subalpine, Weaver et al. (1990) found three (*Poa pratensis*, *Tragopogon dubius*, and *Medicago lupulina*) in their timberline sites. However, all of these species, except for *P. pratensis*, were confined to highly disturbed roadsides and roadcuts at timberline. In addition, although *Anisantha tectorum* is confined to the lower montane in this study, Pierson and Mack (1990) mentioned that this grass was common along roadsides, and in agricultural fields and pastures at relatively high elevations of the Intermountain Region. It appears that, while these exotic species have not invaded the relatively intact high elevation meadow communities that I sampled, given ample opportunity they can establish in some areas of the subalpine zone. The existence of highly disturbed sites, such as roadsides, may enable certain exotic species to establish at higher elevations than would otherwise be possible. Since I did not analyze the soil seed bank or the seed rain at my sites, however, my data do not unequivocally support the disturbance theory. The possibility exists that there is a difference in seed availability between my sites and those of other studies.

The observed distributions of exotic species along elevational gradients depend upon the types of communities being studied. While the present study examines meadow communities, other studies have addressed different ecosystems. Kooiman and Linhart (1986) described the herbaceous species composition of four stands along an elevation gradient in the Colorado Front Range. They analyzed the understories of three forest stands -- a lower montane ponderosa pine stand, an upper montane douglas-fir/ponderosa pine stand, and a subalpine aspen stand, and they sampled an alpine kobresia meadow. Interestingly, Kooiman and Linhart (1986) found only three exotic species in their entire study. Of these, *Anisantha tectorum* and *Tragopogon dubius* were both confined to the lowest elevation and *Taraxacum officinale* was found only in the subalpine. No exotic species were identified beneath the upper montane douglas-fir/ponderosa pine canopy or in the alpine meadow. Two aspects of their results are relevant here. First, there was no simple linear trend of exotic occurrence with respect to elevation in their study. Exotic species were distributed discontinuously, with none in the mid-elevation forest stand. Second, if these results are comparable with those of my study, then it appears that exotic species may be able to establish more easily in meadow communities than in forest understories at the same elevations.

It is possible that, in addition to the influence of the elevational gradient in mountain ecosystems, patterns of herbaceous exotic species occurrences are influenced by a gradient of light availability among different communities, ranging from dense forests to open meadows. Differences in the densities of the tree canopies in different forests probably have a significant influence on the ability of exotic species to establish in the forest understories. For example, Kooiman and Linhart (1986) reported a very high frequency (64%) of *T. officinale* in the subalpine aspen stand which they sampled. In contrast, Forcella and Harvey (1983) found no exotic species growing in the understory of the subalpine spruce/fir forests which they sampled in Montana. Here, since the aspen stand was undoubtedly more open than the conifer stand, perhaps higher light levels at the height of the understory enabled *T. officinale* establishment there. In the present study, three exotic species were present in the subalpine meadows, although their frequencies were less than 20% (Table 5.1). In accordance with these observations, Frankel (1977) found higher percentages of exotic species along roadsides in communities which lacked closed tree canopies, than along roadsides in forests (cited in Mooney et. al 1986, p.259).

5.3 Elevational Trends

5.3.1 Species Composition

The native species composition of these Front Range meadows is strongly influenced by elevation. Detrended Correspondence Analysis indicates that native species clearly respond to the complex environmental gradient represented by elevation (Figure 4.2). Native species assemblages appear to change gradually over a range of elevation. That is, in terms of species composition and relative abundances of species, meadows of the lower montane are more similar to meadows of the montane than they are to meadows of the subalpine. Meadows of the montane are intermediate between those of the lower montane and those of the subalpine, and so forth. The species changes are not abrupt, and sharply delineated "life zones" are not apparent. However, native species do appear to sort out individualistically along the elevation gradient studied here.

Elevation does not appear to strongly influence the exotic species composition of the Front Range meadows I studied. In contrast to the patterns observed for native species, exotic species composition and relative abundances do not respond to elevation in any obvious way. The axes produced by the Detrended Correspondence Analysis do not seem to represent elevation (Figures 4.3 & 4.4). For example, sites L-1 and L-2 are close together in the ordination space in Figure 4.3. Much of this similarity is driven by the presence of *A. tectorum* and *Silene antirrhina* (axis one ranks are 375 and 338 respectively) at both of these sites (Table 5.1). Site LM-3, however, is widely separated from the other two lower montane sites. These results could be due to several factors including, (1) site history, (2) environmental conditions, (3) seed dispersal.

The patterns of exotic species establishment may be the result of site history. That is, the exotic species composition of these meadows may reflect aspects of land use history which I cannot account for. While L-1 was once a ranch, and L-2 was only leased for grazing, perhaps certain common aspects of historic land use influence the present suite of exotic species. In addition, aspects of the disturbance histories of each site will play an important role. For example, if L-1 and L-2 experienced recent fires, this may have facilitated the establishment of *A. tectorum* at those sites.

Environmental factors which I did not measure may account for the patterns of distribution of exotic species in this study. Peet (1988) stated that after elevation, the "topographic-moisture gradient" and soils are the second and third most important complex environmental variables influencing vegetation patterns. Although I chose the nine meadows to be as similar as possible in terms of topographic influences on site moisture, slight differences in moisture availability between sites may be having an important impact on species patterns. In addition, I did not analyze the soils in the meadows I sampled. It is certainly possible that differences in soils, particularly in terms of texture and nutrient status, may have a significant influence on the observed patterns. For example, McIntyre and Lavorel (1994) found that exotic richness increased on sites of increasing soil fertility.

Differences in seed dispersal to the nine meadows may also influence exotic establishment patterns. That is, the assumption that all nine meadows are equally accessible to all exotic seed may be incorrect. It is possible that the distributions of particular exotic species in this study are the results of the haphazard introduction of propagules to the study sites. Such introductions may depend on chance alone, or they may result from the differential success of different types of dispersal in reaching the various sites. While it may be reasonable to suppose that roads and trails serve as effective routes for the dispersal of exotic seed (Weaver et al. 1990), I did not test this assumption with an analysis of the actual pool of seeds present at my study sites.

5.3.2 Exotic Occurrence

Along the elevational gradient examined in this study, native and exotic species exhibit inverse trends of occurrence in mountain meadows. Both native species richness and native cover increase with increasing elevation. In contrast, both exotic species richness and exotic cover decline with increasing elevation. The observation that the occurrence of exotic species declines markedly with increasing elevation is consistent with anecdotal reports as well as with previous work (Frankel 1977, Forcella & Harvey 1983). Frankel (1977) found that the percentage of aliens in the roadside flora of California decreased with increasing elevation (cited in Mooney et. al 1986, p.259). Forcella and Harvey (1983) examined 'Eurasian weed' establishment along an elevational gradient in Montana. They found that weed establishment declined from the low elevation grasslands to the subalpine forests in their study. Importantly, this study is not directly comparable with mine because Forcella and Harvey (1983) did not examine all exotic species. Rather, they excluded forage species such as *Dactylis glomerata*, *Phleum pratense*, *Poa pratensis*, *Medicago sativa*, *Trifolium pratense* and *T. repens*, which they did not consider to be weedy (Forcella & Harvey, 1983, p.103).

Native species may be better adapted to the changing environmental conditions associated with increasing elevation than are exotics. The meadows examined in this study were chosen to be as comparable as possible in terms of environmental conditions, disturbance types, and accessibility to plant seeds. If this assumption of meadow comparability holds true, then the observed patterns of native and exotic establishment should be due to differences among elevations only. If this is the case, then native species tend to be better adapted to the conditions of the subalpine zone than are the available exotics. Exotic species, according to this argument, tend to be pre-adapted to the conditions of the lower montane and to some extent, the montane zones of the Colorado Front Range. Most exotic species in the study area cannot tolerate the harsh conditions of the subalpine. Possible explanations for the observed decrease in exotic species occurrence with increasing elevation include those which focus on (1) island biogeography theory, (2) community stability, and (3) historical dispersal.

First, since plant species inhabit high mountain ranges all over the world, there should be a large number of exotic species capable of tolerating the conditions of the Colorado subalpine. It has been suggested, however, that such species are unlikely to ever reach suitable foreign habitats. In this context, mountain environments can be thought of as islands separated by large expanses of dissimilar habitat (MacArthur 1972, Forcella & Harvey 1983). For example, the mountains of Colorado are bordered to the east and west by expanses of low elevation rangeland. Plant species adapted to high elevations must disperse through low elevation environments before they find areas to which they are pre-adapted. It is likely that such species will be unsuccessful if dispersal requires establishment and reproduction in the intermediate areas (Forcella & Harvey 1983). Exotic species which are adapted to the specific range of conditions found at high elevations, then, are unlikely to disperse either out of their native habitats or into similar habitats elsewhere.

In this context, exotic invasion into mountain environments can be thought of as being limited by dispersal at a global scale. Historically, this may have been true. Ramaley (1909) listed ninety-five naturalized European plant species in Colorado and stated that most were introduced "through their seeds being mixed with seed-grain, lawn-grass and garden-seeds, or in livestock food, while a few escape from cultivation" (Ramaley 1909, p.494). Many exotic species are agricultural and garden weeds, probably not adapted to high-elevation climates. Further, Ramaley stated that "most of the species have come to Colorado from the eastern United States and not directly from Europe" (Ramaley 1909, p.494). Many of the species introduced into

Colorado, then, must first have been able to establish in eastern habitats. This observation is consistent with the idea that, at least historically, species pre-adapted to high elevations elsewhere were unlikely to disperse to such habitats in Colorado.

Second, it is possible that low elevation herbaceous plant communities are more susceptible to invasion because they are more dynamic than higher elevation assemblages. Kooiman and Linhart (1986) examined species turnover along an elevational gradient in the Colorado Front Range using plots sampled in both 1953 and 1981. They found high species turnover at their lowest elevation site (2200 meters, ponderosa pine understory), and few changes in their sites at 2600 meters (douglas-fir/ponderosa pine understory) and 3700 meters (alpine meadow) over that time. If lower elevation meadow communities have higher rates of species turnover compared to higher elevations, opportunities for exotic establishment might decrease with increasing elevation. If this is the case, then for a constant rate of exotic introduction across an elevational gradient, there might be greater exotic establishment at low elevations.

A third explanation for the relative lack of exotic species at high elevations in Colorado focuses on ancient dispersal. It is possible that many 'exotic' species capable of living at high elevations are already part of the local flora due to dispersal 2 to 3 million years ago (Axelrod & Raven 1985). According to Billings (1988), due to Pleistocene migrations arctic species accounted for 91 out of 194 plant species sampled in the alpine zone of the Beartooth Mountains in Wyoming and Montana. Notably high numbers of arctic species also occurred in the Colorado alpine (Billings, 1988). In turn, the arctic flora is truly circumpolar, and has been so since before the glaciations of the Pleistocene (Bliss, 1988). According to Weber (1965), the Southern Rockies held the "greatest concentration of circumpolar species at their southernmost limits" on the North American continent (p.453). Further, he stated that the modern flora of high elevations in this area represented "remnants of what must have been a more or less continuously distributed high-mountain flora extending from this area across Beringia into the mountains of Central Asia" (p.457). It is likely then, that due to past land connections at high northern latitudes, high elevation environments in North America and Europe/Asia share similar floras.

5.3.3 Native Species Richness

The richness of native species increases with increasing elevation in this study. This pattern is in direct contrast to those described in many published studies. Stevens (1992) reviewed several studies which found that the richness of co-occurring tree species declined with increasing elevation in Alaskan old growth forests, Pacific Costa Rican forests, and in sub-xeric forests of Tennessee. Bird diversity has been found to decrease with increasing elevation on Mt. Karimui, New Guinea (MacArthur 1972), and on the Amazonian slope of the Peruvian Andes (Brown 1988). In fact, some authors consider it a general rule that species diversity decreases with increasing elevation (MacArthur 1972, Brown 1988). This generalization, however, is not universally accepted.

Several studies have suggested that species richness does not follow a simple linear trend along elevational gradients. Two separate studies of the same elevational transect in the Colorado Front Range found a consistent unimodal pattern of species richness. In his study of Front Range ecosystems, Marr (1967) found maximum species richness at mid-elevations. Twenty-eight years later, Kooiman and Linhart (1986) found that species richness was still highest beneath the canopy of the subalpine aspen stand, and that it declined to lower values at both higher and lower elevations. This unimodal pattern is not confined to Front Range plant communities. Whittaker (1965) observed that the species richness of herbs in the Siskiyou Mountains of Oregon increased and then declined with increasing elevation. Rosenzweig et al. (1993) reviewed research that indicated that, within equally sized areas, bird species richness is highest at mid-elevations in the Neotropics, and that tropical ferns and bryophytes exhibited the same pattern. Since I did not sample the entire elevational gradient present in the Colorado Front Range, my results are not inconsistent with a general unimodal pattern of species richness along elevational gradients. It is possible that the species richness of mountain meadows declines at elevations above the subalpine, in which case my results would support the unimodal model.

In detailed studies of heterogeneous landscapes, it is difficult to make generalizations about elevational trends in species richness. In his study of the forest vegetation of the Colorado Front Range, Peet (1978) did not find a simple relationship between elevation and species richness. Instead, Peet (1978) found the highest values of species richness in the grasslands and *Pinus ponderosa* shrublands of the lower montane, in the mesic forests of the montane, and in the krumholtz islands of the alpine. Similar results were reported by Allen et. al (1991) for forests at other latitudes in the Rocky Mountains. In contrast to my findings, these studies reported low richness values for most of the subalpine. The most likely explanations for this discrepancy are the facts that Peet (1978, 1981) and Allen et. al (1991) primarily examined forest communities, and that they sampled a very broad range of sites. By including more vegetation types and sampling a more diverse range of sites than I did, they incorporated more complexity into their findings.

In terms of simple elevational species richness trends, there are several possible explanations for the discrepancy between my results and those of the other studies mentioned. First, the present study was not designed to be an exhaustive investigation of species richness. While the line intercept sampling method allows for a good general characterization of the species composition and cover of a site, it is likely that rare and patchily distributed species will be missed. On the other hand, my data would only misrepresent an elevational trend if the probability of not sampling representatively changed between elevations. I have no reason to believe that this is the case. While it is possible that my data do not accurately represent site richness, it is very unlikely that this effect biases my results.

A second possible reason for the difference between my results and those of previous investigations is the fact that I am examining herbaceous systems. Most other studies of species richness along elevational gradients seem to have examined either tree or bird communities. The limiting factors influencing organisms vary with elevation. Since different organisms respond differently to these limiting influences, it is perhaps not surprising that trees and herbs show different richness patterns along a complex environmental gradient. According to Whittaker (1965), "there is no reason why species-diversity relations for different strata or fractions of the community, subject to different environmental factors and modes of population limitation, should parallel one another". Indeed, Whittaker (1965) observed that the elevational trends in the species richness of trees and shrubs were opposite to those of herbs in the Siskiyou Mountains of Oregon. He found that herbaceous species richness initially increased with increasing elevation, and then declined above 1600 meters, while tree and shrub species richness both exhibited linear declines with increasing elevation.

Third, the latitudinal and climatic setting of an elevational gradient should influence species richness patterns. The key environmental factors which constitute the complex gradient of elevation most likely vary across the globe. In the tropics, where moisture is abundant, temperature is the primary climatic variable changing with elevation. This may not be the case in western North America, where moisture is quite limited at low elevations, but increases with increasing elevation (Barry 1973, Peet 1981). It is likely that, since the characteristics of elevational gradients vary globally, species richness patterns should likewise be expected to vary.

It is possible that as precipitation increases over the elevational gradient that I studied, productivity also increases, and this may influence species richness. Several workers have noted the relationship between species richness and primary productivity

(Rosenzweig & Abramsky 1993, Tilman & Pacala 1993, and references therein). Specifically, in many ecosystems species richness exhibits a "hump-shaped" pattern across a gradient of increasing productivity (Rosenzweig & Abramsky 1993, p.52). According to Rosenzweig & Abramsky (1993), "elevation is probably a good inverse index of productivity in the wet tropics " (pp.53-54). Therefore, a unimodal pattern of species richness in that context may be related to high productivity at low elevations and lower productivity at high elevations. In the Colorado Front Range, the relationship between elevation and productivity may not be simple. Here, moisture and temperature may tend to have opposite influences on productivity. Due to increased moisture, productivity should actually increase with elevation. On the other hand, decreasing temperature should increasingly limit productivity as high elevations are reached. While elucidation of the impacts of these two factors is beyond the realm of this study, my results do emphasize the fact that elevational gradients vary globally.

A fourth possible explanation for the increase in native species richness with increasing elevation centers on the contrast between native and exotic species richness patterns. Exotic species richness decreases with increasing elevation. Native richness, however, shows the opposite trend, increasing with increasing elevation. Since native and exotic species richness are inversely correlated in this study, and since this effect is independent of elevation, it is possible that the abundance of exotic species in the lower montane is associated with the relative paucity of native species there. In the present study, I cannot determine whether this pattern results from biotic interactions between native and exotic species or whether it is the result of environmental or other site factors. Certainly, other studies have found evidence for the actual or potential competitive displacement of native species by exotics (Melgoza et. al 1990, D'Antonio & Mahall 1991, Huenneke & Thomson 1995) and the possibility exists that such displacement is occurring here.

CHAPTER 6

CONCLUSION

Exotic species invasions can impact native biological communities and species diversity. Exotic species invasions have caused extinctions, the loss of habitat, changes in resource supply rates, modification of trophic structure, and the alteration of disturbance regimes in native communities (D'Antonio & Vitousek 1992). While many workers agree on the importance of this area of study, in many cases the basic patterns of invasion are unknown. In particular, very few studies have examined the invasion of exotic species along environmental gradients (Frankel 1977, Forcella & Harvey 1983)

This study documents the patterns of exotic species occurrence in nine mountain meadows along an elevational gradient in the Colorado Front Range. Exotic species richness and cover decline with increasing elevation. This pattern may be due to (1) the inability of exotic species adapted to high elevations elsewhere to reach suitable (island-like) Front Range environments, (2) the greater rates of species turnover at low elevations in the Front Range, or (3) ancient dispersal prior to the Holocene. The patterns of exotic species composition between the nine study sites cannot be explained by elevation alone. Superimposed on the significant elevational trends, there is considerable variability in exotic species richness, cover, and composition among meadows of the same elevation. The variability in exotic occurrence among the study sites may be due to differences in physical site factors, site histories, or landscape factors such as distance from seed sources.

Native species richness increases with increasing elevation in this study. This pattern may result from the unique responses of herbaceous species to the complex environmental gradient of elevation. With increasing elevation in the Front Range, precipitation increases (Barry 1973, Peet 1981), and this may influence native herbaceous species diversity. Alternatively, the low values of native species richness at lower elevations may be related to the high values of exotic species richness and cover there. It is possible that exotic species are displacing natives at low elevations.

D'Antonio (1993) stated that biological invasion was a "context-specific process. While this statement may be true, in many cases it does not preclude the prediction of exotic distributions. Along the elevational gradient I studied, exotic species occurrence varies considerably. In some cases this variation can be predicted based on (1) the environmental changes along the gradient, and (2) the known tolerance limits and characteristics of the exotic species present. Predictive capability is limited in cases where the individual exotic species have not been well-studied.

Exotic species are present at all three of the elevations I studied. Although presently they are most abundant at the lower elevations, this situation is not necessarily stable. Two factors suggest that in the future, more exotic species may invade high elevations in this region. First, although historically exotic species adapted to high elevations elsewhere were probably unlikely to ever disperse to Front Range subalpine and alpine areas, this may change in the future. With increased human mobility and with growth in the recreational use of high elevation areas, it is likely that new opportunities for the dispersal of plant species will become available. As more species are intentionally and unintentionally "translocated" among habitats (Newsome & Noble 1986), more invasions will occur. Second, a comparison of my results with those of other studies (Forcella & Harvey 1983, Weaver et. al 1990), indicates that disturbance extends the elevational ranges of many exotic species. With human population growth in this area, and increased development in the Colorado Front Range, anthropogenically disturbed areas will become more common. These two factors pose a challenge for managers. Strategies for protecting native diversity at high elevations in the Front range should focus on mitigating some of these influences.

At lower elevations in the Colorado Front Range, exotic species are fairly abundant. In these areas, managers should probably focus their attention on particular exotic species which threaten native diversity or other management goals (Soulé 1990, Westman 1990). For example, *Tithymalus uralensis* (leafy spurge) may be one such species. In this study it is present at one site only, but at that site it is nearly ubiquitous and is associated with low values of native species richness. Other species, such as *Anisantha tectorum* (cheatgrass), which may increase fire frequencies (D'Antonio & Vitousek 1992) or competitively exclude native species (Melgoza et. al 1990), may also be worthy of attention. In these areas, exotic species should probably be evaluated individually in order to determine whether they are likely to pose a threat in specific contexts.

Although this study presents useful information about the distribution patterns of exotic species in the Colorado Front Range, several questions remain unanswered. In particular, further investigations of the seed rain and seed banks of the study sites are required in order to determine whether seed availability is influencing occurrence patterns. In addition, experimental analyses of the interactions between native and exotic species are needed to test whether displacement is occurring.

BIBLIOGRAPHY

Allen, R. B., Peet, R. K., Baker, W. L. (1991). Gradient analysis of latitudinal variation in Southern Rocky Mountain forests. J. of Biogeography. 18:123-139.

Allen-Diaz, B. (1991) Water table and plant species relationships in Sierra Nevada meadows. Am. Midl. Nat. 126:30-43.

Axelrod, D. I. & Raven, P. H. (1985). Origin of the Cordilleran flora. J. of Biogeography. 12:21-47.

Baker, H. G. (1965). Characteristics and modes of origin of weeds. in Baker, H. G. & Stebbins, G. L. (eds.), The Genetics of Colonizing Species. Academic Press, New York.

Baker, H. G. (1986). Patterns of plant invasion in North America. in H. A. Mooney and J. A. Drake (eds.), Ecology of Biological Invasions of North America and Hawaii. Springer, New York.

Barry, R. G. (1973). A climatological transect on the east slope of the Front Range, Colorado. Arctic & Alpine Research. 5(2):89-110.

Bazzaz, F. A. (1986). Life history of colonizing plants: some demographic, genetic, and physiological features. in H. A. Mooney and J. A. Drake (eds.), Ecology of Biological Invasions of North America and Hawaii. Springer, New York.

Beatty, S. W. and Licari, D. L. (1992). Invasion of fennel *(Foeniculum vulgare)* into shrub communities on Santa Cruz Island, California. Madrono. 39(1):54-66.

Belsky, J. A. (1992). Effects of grazing , competition, disturbance and fire on species composition and diversity in grassland communities. Journal of Vegetation Science. 3:187-200.

Benedict, A. D. (1991). A Sierra Club naturalist's guide: the Southern Rockies. Sierra Club Books, San Francisco.

Benedict, N. B. (1982) Mountain meadows: stability and change. Madrono. 29(3):148-153.

Billings, W. D. (1988). Alpine vegetation. in Barbour, M. G. and Billings, D. W. (eds.). North American Terrestrial Vegetation. Cambridge University Press, Cambridge.

Billings, W. D. & Mark, A. F. (1957). Factors involved in the persistence of montane treeless balds. Ecology. 38:140-142.

Bliss, L. C. (1988). Arctic tundra and polar desert biome. in Barbour, M. G. and Billings, D. W. (eds.). North American Terrestrial Vegetation. Cambridge University Press, Cambridge.

Boulder County Parks & Open Space, #1 (no date), Betasso Preserve Management Plan.

Boulder County Parks & Open Space, #2 (no date), Bald Mountain Scenic Area Management Plan.

Brothers, T. & Spingarn, A. (1992). Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology. 6(1):91-100.

Brown, J. H. (1988). Species diversity. in Myers, A. A. & Giller, P. S. (eds.). Analytical Biogeography. Chapman & Hall, New York.

Clausen, J., Keck, D. D., Hiesey, W. M. (1940). Experimental studies on the nature of species I: effect of varied environments on western North American plants. Carnegie Inst. of Washington. Publication 520.

Clausen, J., Keck, D. D., Hiesey, W. M. (1948). Experimental studies on the nature of species III: environmental responses of climatic races of *Achillea.* Carnegie Inst. of Washington. Publication 581.

Coblentz, B. E. (1990). Exotic organisms: a dilemma for conservation biology. Conservation Biology. 4(3):261-265.

Collins, S. L. (1987). Interaction of disturbances in tallgrass prairie: A field experiment. Ecology. 68(5):1243-1250.

Crawley, M. J. (1987). What makes a community invasible? in A. J. Gray, et al (eds.) Colonization, Succession, and Stability. Blackwell, London.

D'Antonio, C. M. (1993). Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrutus edulis.* Ecology. 74(1):83-95.

D'Antonio, C. M. & Mahall, B. E. (1991). Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. Am. J. of Botany. 78(7):885-894.

D'Antonio, C. M., Odion, D. C., Tyler, C. M. (1993). Invasion of maritime chaparral by the introduced succulent *Carpobrutus edulis*: The roles of fire and herbivory. Oecologia. 95:14-21.

D'Antonio, C. M. & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Syst. 23:63-87.

Daubenmire, R. (1968) Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. Ecology. 49(3):431-438.

DeFerrari, C. M. & Naiman, R. J. (1994). A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. J. of Vegetation Science. 5:247-258.

Drake, J. A., et al (1989). Biological Invasions: A Global Perspective. Wiley, New York.

Forcella, F. & Harvey, S. J. (1983). Eurasian weed infestation in western Montana in relation to vegetation and disturbance. Madrono. 30(2):102-109.

Frankel, R. E. (1977) Ruderal Vegetation Along Some California roadsides. Univ. of California Publications in Geography. 20:1-163.

Goldblum, D. (1990). Fire history of a ponderosa pine/douglas-fir forest in the Colorado Front Range. Master's thesis, University of Colorado, Boulder.

Groves, R. H. & Burdon, J. J. (1986). Ecology of Biological Invasions. Cambridge Univ. Press, Cambridge.

Harper, J. L. (1965). Establishment, aggression and cohabitation in weedy species. in H. G. Baker and G. L. Stebbins (eds.) The Genetics of Colonizing Species. Academic Press, London.

Harrington, H. D. (1954). Manual of the plants of Colorado. Sage Books, Denver.

Hill, M. O. (1979) DECORANA: a Fortran program for detrended correspondence analysis and reciprocal averaging.

Hill, M. O. & Gauch. H. G., Jr. (1980). Detrended correspondence analysis: an improved ordination technique. Vegetatio. 42:47-58.

Hobbs, R. J. (1989). The nature and effects of disturbance relative to invasions. in Drake et. al (eds) Biological Invasions: A Global Perspective. Wiley, New York.

Hobbs, R. J. & Mooney, H. A. (1991). Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. Ecology. 72(1):59-68.

Hobbs, R. J., Huenneke, L. F. (1992). Disturbance, diversity, and invasion: implications for conservation. Conservation Biology. 6(3):324-337.

Howe, H. F. (1994). Response of early and late-flowering plants to fire season in experimental prairies. Ecological Applications. 4(1):121-133.

Huenneke, L. F., Hamburg, S. P., Koide, R., Mooney, H. A., Vitousek, P. M. (1990). Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology. 71(2):478-491.

Huenneke, L. F. & Thomson, J. K. (1995). Potential interference between a threatened endemic thistle and an invasive nonnative plant. Conservation Biology. 9(2):416-425.

Kent, M. & Coker, P. (1992). Vegetation Description and Analysis. CRC Press. Ann Arbor, Michigan.

Kooiman, M. & Linhart, Y. B. (1986) Structure and change in herbaceous communities of four ecosystems in the Front Range, Colorado, USA Arctic and Alpine Research. 18(1):97-110.

Levin, D. A. (1986) Breeding structure and genetic variation. in Crawley, M. J. (ed.) Plant Ecology. Blackwell Scientific Publications, London.

Link, S. O. , Gee, G. W., Downs, J. L. (1990) The effect of water stress on phenological and ecophysiological characteristics of cheatgrass and Sandberg's bluegrass. Journal of Range Management. 43(6):506-513.

MacArthur, R. H. (1972). Geographical Ecology. Princeton University Press, Princeton.

MacArthur, R. H. & Wilson, E. O. (1967). The Theory of Island Biogeography. Princeton University Press, Princeton.

Macdonald, I. A. W., Kruger, F. J., Ferrar, A. A. (1986). The Ecology of Biological Invasions in Southern Africa. Oxford Univ. Press, Cape Town.

Mack, R. N. & Thompson, J. N. (1982). Evolution in steppe with few large, hooved animals. American Naturalist. 119(6):757-773.

Mack, R. N. (1986). Alien plant invasion into the Intermountain West: A case history. *in* H. A. Mooney and J. A. Drake (eds.), Ecology of Biological Invasions of North America and Hawaii. Springer, New York.

Mack, R. N. (1989). Temperate grasslands vulnerable to plant invasions: characteristics and consequences. *in* Drake, J. A., et al (eds.) Biological Invasions: A Global Perspective. Wiley, New York.

Marr, J. W. (1967). Ecosystems of the east slope of the Front Range in Colorado. University of Colorado Studies, Series in Biology, No. 8. University of Colorado Press, Boulder.

Melgoza, G., Nowak, R. S., Tausch, R. J. (1990). Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. Oecologia. 83:7-13.

Melgoza, G. & Nowak, R. S. (1991) Competition between cheatgrass and two native species after fire: Implications from observations and measurements of root distribution. Journal of Range Management. 4491):27-33.

McCoy, E. D. & Mushinsky, H. R. (1994) Effects of fragmentation on the richness of vertebrates in the Florida scrub habitat. Ecology. 75(2):446-457.

McIntyre, S. & Lavorel, S. (1994a). Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. Conservation Biology. 8(2):521-531.

McIntyre, S. & Lavorel, S. (1994b). How environmental and disturbance factors influence species composition in temperate Australian grasslands. Journal of Vegetation Science. 5:373-384.

McLendon, T. & Redente, E. F. (1992) Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. Oecologia. 91:312-317.

Milchunas, D. G., Lauenroth, W. K., Chapman, P. L. (1992). Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. Oecologia. 92:520-531.

Milchunas, D. G. & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs. 63(4):327-366.

Mooney, H. A., Hamburg, S. P., Drake, J. A. (1986). The invasions of plants and animals into California. in H. A. Mooney & J. A. Drake (eds.), Ecology of Biological Invasions of North America and Hawaii. Springer, New York.

Mutel, C. D. F. (1973). An ecological study of the plant communities of certain montane meadows in the Front Range of Colorado. Master's thesis, University of Colorado, Boulder.

Newsome, A. E. & Noble, I. R. (1986). Ecological and physiological characters of invading species. in Groves, R. H. & Burdon, J. J. (eds), Ecology of Biological Invasions. Cambridge Univ. Press, Cambridge.

Palmer, M. W. (1993). Putting things in even better order: the advantages of Canonical Correspondence Analysis. Ecology. 74(8):2215-2230.

Peet, R. K. (1978) Forest Vegetation of the Colorado Front Range: patterns of species diversity. Vegetatio. 37(2):65-78.

Peet, R. K. (1981) Forest vegetation of the Colorado Front Range. Vegetatio. 45:3-75.

Peet, R. K. (1988) Forests of the Rocky Mountains. in Barbour, M. G. and Billings, D. W. (eds.). North American Terrestrial Vegetation. Cambridge University Press, Cambridge.

Pierson, E. A. & Mack, R. N. (1990). The population biology of *Bromus tectorum* in forests: distinguishing the opportunity for dispersal from environmental restriction. Oecologia. 84:519-525.

Ramaley, F. (1909). European plants growing without cultivation in Colorado. Annales du Jardin Botanique de Buitenzorg. 2 Serie Suppl. III.

Ramaley, F. (1919). Xerophytic grasslands at different altitudes in Colorado. Bull. Torr. Bot. Club. 46:37-52.

Ramaley, F. & Elder, M. E. (1912). The grass-flora of Tolland, Colorado, and vicinity. University of Colorado Studies. 9:121-141.

Ramaley, F. (1927). Colorado Plant Life. University of Colorado Press, Boulder.

Reed, E. L. (1917). Meadow vegetation in the montane region of northern Colorado. Bull. Torr. Bot. Club. 44:97-109.

Rejmanek, M & Randall, J. M. (1994). Invasive alien plants in California: 1993 summary and comparison with other areas in North America. Madrono. 41(3):161-177.

Ricklefs, R. E. (1990). Ecology. W. H. Freeman, New York.

Rice, K. J. & Mack, R. N. (1991). Ecological genetics of *Bromus tectorum* II. Intraspecific variation in phenotypic plasticity. Oecologia. 88:84-90.

Root, R. A. & Habeck, J. R. (1972). A study of high elevational grassland communities in western Montana. American Midland Naturalist. 87(1):109-121.

Rosenzweig, M. L. & Abramsky, Z. (1993). How are diversity and productivity related? in Ricklefs, R. E. & Schluter, D. (eds) Species Diversity in Ecological Communities. Univ. of Chicago Press, Chicago.

Schooland, J. B. (1980). Boulder in Perspective. Johnson Publishing Co., Boulder.

Sokal, R. S. & Rohlf, F. J. (1981). Biometry. W. H. Freeman & Co., New York.

Soulé, M. E. (1990). The onslaught of alien species, and other challenges in the coming decades. Conservation Biology. 4(3):233-239.

SPSS Inc. (1990). SPSS Base System User's Guide. SPSS Inc., Chicago.

Stahelin, R. (1943). Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. Ecology. 24(1):19-30.

Tilman, D. & Pacala, S. (1993). The maintenance of species richness in plant communities. in Ricklefs, R. E. & Schluter, D. (eds) Species Diversity in Ecological Communities. Univ. of Chicago Press, Chicago.

Tyser, R. W. & Worley, C. A. (1992). Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). Conservation Biology. 6(2):253-262.

Veblen, T. T. & Lorenz, D. C. (1986). Anthropogenic disturbance and recovery patterns in montane forests, Colorado Front Range. Physical Geography. 7:1-24.

Veblen, T. T. & Lorenz, D. C. (1991). The Colorado Front Range: a century of ecological change. Univ. of Utah Press, Salt Lake City.

Weaver, T., Lichthart, J., Gustafson, D. (1990). Exotic invasion of timberline vegetation, Northern Rocky Mountains, USA Proceedings -- Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High Mountain Resource. USDA Gen Tech Report INT-270.

Weber, W. A. (1965). Plant geography of the Southern Rocky Mountains. in Wright, H. E. Jr. & Frey, D. G. (eds.), The Quaternary of the United States. Princeton University Press, Princeton.

Weber, W. A. (1990). Colorado Flora: eastern slope. University Press of Colorado, Niwot.

Westman, W. E. (1990). Park management of exotic plant species: problems and issues. Conservation Biology. 4(3):251-260.

Whitson, T D, et. al (1992). Weeds of the West. Western Society of Weed Science. Newark, California.

Whittaker, R. H. (1965). Dominance and diversity in land plant communities. Science. 147:250-260.

Whittaker, R. H. (1975). Communities and Ecosystems. Macmillan, New York.

Williams, D. G., Mack, R. N., Black, R. A. (1995). Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. Ecology. 76(5):1569-1580.

Wilson, H. C. (1969). Ecology and successional patterns of wet meadows, Rocky Mountain National Park, Colorado. Dissertation, University of Utah.

Appendix A. Species List. Notation is as follows: E = exotic species, N = native species, X = present in meadow.

		Subalpine			Montane			L. Montane		
Species		1	2	3	1	2	3	1	2	3
Acetosella vulgaris (Koch) Fourreau	E						X			
Achillea lanulosa Nuttall	N	X	X	X	X	X	X			X
Aconitum columbianum Nuttall	N	X	X							
Adenolinum lewisii (Pursh) Love & Love	N								X	
Agoseris glauca (Pursh) Rafinesque	N				X	X				
Agoserus aurantiaca (Hooker) Greene	N			X						
Agrostis gigantea Roth	E						X			
Agrostis scabra Willdenow	N						X			
Allium geyeri (Watson)	N				X	X	X			
Alyssum minus (L.) Rothmaler	E									X
Ambrosia psilostachya de Candolle	N							X	X	X
Amerosedum lanceolatum (Torrey) Lve & Lve	N		X	X		X				
Andropogon gerardii Vitman	N								X	
Anisantha tectorum (L.) Nevski	E							X	X	
Antennaria spp	N		X	X		X	X	X	X	
Anticlea elegans (Pursh) Rydberg	N						X			
Apiaceae spp	–						X			
Aristida purpurea Nuttall	N							X		
Arnica chamissonis Lessing	N		X							
Arnica fulgens Pursh	N									X
Artemisia frigida Wildenow	N		X			X		X	X	
Artemisia ludoviciana Nuttall	N		X			X	X	X	X	X
Aster porteri Gray	N					X		X		X
Astragalus flexuosus (Hooker) G. Don	N			X				X	X	X
Astragalus miser Douglas	N			X		X				
Astragalus spp S-3	–			X						
Bistorta bistortoides (Pursh) Small	N		X				X			
Bistorta vivipara (L.) S. Gray	N	X								
Boechera drummondii (Gray) Love & Love	N			X		X	X			
Bromopsis inermis (Leysser) Holub	E				X		X			
Bromus japonicus Thunberg	E								X	X
Camelina microcarpa Andrzejowski	E								X	X
Campanula rotundifolia L.	N		X	X		X				
Carex aquatilis Wahlenberg	N	X								
Carex brevior (Dewey) Mackenzie	N									X
Carex festivella Mackenzie	N					X				
Carex foenea Willdenow	N		X	X						
Carex microptera Mackenzie	N	X	X		X					
Carex obtusata Liljebad	N					X				
Carex pennsylvanica	N		X					X	X	
Cerastium strictum L. emend. Haenke	N	X	X			X	X	X	X	
Chenopodium spp S-3	–			X						
Cirsium coloradense (Rydberg) Cockerell	N					X				
Cirsium spp (S-3)	–			X						
Clementsia rhodantha (Gray) Rose	N	X								
Convolvulus arvensis L.	E									X
Coryphantha spp	N								X	
Danthonia parryi Scribner	N				X		X			
Deschampsia cespitosa (L.) P. Beauvois	N	X	X		X		X			

Appendix A. Species list (continued).

		Subalpine			Montane			L. Montane		
Species		1	2	3	1	2	3	1	2	3
Dodecatheon pulchellum (Rafinesque) M.	N	X			X					
Eleocharis eliptica Kunth	N									
Eleocharis quinquflora (F. X. Hartman)S.	N	X					X			
Elymus longifolius (Smith) Gould	N					X			X	
Elymus scribneri (Vassey) Jones	N			X						
Elymus trachycaulus (Link) Gould	N		X	X						X
Elytrigia repens (L.) Nevski	E				X					
Epilobium brachycarpum Presl.	N						X			
Epilobium spp S-1	–	X								
Eremogone fendleri (Gray) Ikonnikov	N		X	X						
Erigeron colo-mexicanus Nelson	N							X		
Erigeron compositus Pursh	N			X						
Erigeron flagellaris Gray	N									X
Erigeron glabellus Nutall	N		X	X	X	X	X	X	X	
Erigeron speciosus (Lindley) de Candolle	N		X							
Eriogonum spp	N							X	X	
Eriogonum umbellatum Torrey	N				X	X	X	X	X	
Festuca brachyphylla S. subsp.*coloradensis* F.	N			X						
Festuca rubra L.	N		X							
Festuca saximontana Rydberg	N					X				
Festuca thurberi Vasey	N		X							
Fragaria virginiana Miller	N					X				
Frasera speciosa Douglas	N			X		X				
Gaillardia aristata Pursh	N									
Galium septentrionale Roemer & Schultes	N		X			X	X			
Gayophytum diffusum Torrey & Gray	N			X						
Geranium spp	N					X			X	
Gutierrezia sarothrae (Pursh) Britt. & Rusby	N									X
Harbouria trachypleura (Gray) Coult. & Rose	N					X				
Helianthus pumilus Nuttall	N							X	X	
Heterotheca spp (S-2)	N		X	X						
Heterotheca villosa (Pursh) Shinners	N					X	X	X	X	
Hieracium aurantiacum L.	E						X			
Iris missouriensis Nuttall	N				X	X	X			
Juncus arcticus Willdenow	N	X			X	X	X			X
Juncus parryi Engelmann	N	X								
Juncus spp S-2	–		X							
Juniperus communis L. subsp. *alpina* (Smith) C	N			X						
Koeleria macrantha (Ledebour) Schultes	N		X			X	X		X	
Lappula redowskii (Hornemann) Greene	N								X	
Liatris punctata Hooker	N							X	X	X
Linaria vulgaris Miller	E						X			
Lupinus argenteus Pursh	N			X						
Lupinus spp	N					X				
Machaeranthera pattersonii (Gray) Greene	N			X						
Medicago lupulina L.	E									X
Mertensia lanceolata (Pursh) de Candolle	N			X		X				
Neolepia campestris (L.) W. A. Weber	E									X
Oligosporous campestris (L.) Cassini	N			X				X		
Opuntia spp	N							X	X	X

Appendix A. Species list (continued)

		Subalpine			Montane			L. Montane		
Species		1	2	3	1	2	3	1	2	3
Orthocarpus luteus Nutall	N					X				
Oxalis dillenii Jacquin	N									X
Oxytropis lambertii Pursh	N					X			X	
Oxytropis parryi Gray	N			X						
Oxytropis sericea Nuttall	N		X							
Oxytropis splendens Douglas	N		X							
Oxytropis spp M-2	–					X				
Oxytropis spp S-3	–									
Pentaphylloides floribunda (Pursh) Love	N	X	X				X			
Phleum commutatum Gaudin	N	X								
Phleum pratense L.	E		X		X	X	X			X
Pinus ponderosa Douglas	N					X				X
Plantago lanceolata L.	E				X					X
Pneumonanthe parryi (Englelmann) Greene	N					X				
Poa alpina L.	N	X								
Poa compressa L.	E		X	X	X	X	X	X	X	X
Poa fendleriana (Steudel) Vasey	N			X			X			
Poa glauca Vahl.	N			X						
Poa nemoralis L. subsp. *interior* (Ryd) B. & A.	N		X							
Poa pratensis L.	E					X		X	X	X
Potentilla diversifolia Lehmann	N		X							
Potentilla effusa Douglas	N				X					
Potentilla hippiana Lehmann	N		X			X	X			
Potentilla pulcherrima Lehmann	N		X		X		X			
Potentilla pulcherrima x hippiana	N					X				
Potentilla recta L.	E									X
Potentilla subjuga Rydberg	N			X						
Potentilla sp (S-1)	N	X								
Potentilla sp (S-1)	N	X								
Potentilla sp (S-2)	N		X							
Prunella vulgaris L.	N									X
Psilochenia runcinata (James) Love & Love	N	X								
Psoralidium tenuiflorum (Pursh) Rydberg	N									X
Psychrophila leptosepala (de Cand.) Weber	N	X								
Pulsatilla patens (L.) M. subs *hirsutissima* Z.	N		X	X		X				
Ranunculus cardiophyllus Hooker	N	X			X	X	X			
Ratibida columnifera (Nuttall) W. & S.	N									X
Rhus aromatica A. subs *trilobata* (Nut.) W.	N									X
Rosa woodsii Lindley	N							X	X	X
Schizachyrium scoparium (Michaux) Nash	N							X	X	
Silene antirrhina L.	E							X	X	X
Solidago nana Nuttall	N					X				
Sporobolus spp	N							X		
Stipa comata Trinius & Ruprecht	N							X	X	X
Symphoricarpos occidentalis Hooker	N									X
Taraxacum officinale G. H. Weber	E	X	X	X	X	X	X			X
Tetraneuris brevifolia Greene	N			X						
Thermopsis spp	N		X	X		X	X			
Tithymalus uralensis (Fischer)Prokhanov	E				X					
Tradescantia occidentalis (Britton) Smyth	N				X					

Appendix A. Species list (continued).

		Subalpine			Montane			L. Montane		
Species		1	2	3	1	2	3	1	2	3
Tragopogon dubius Scopoli	E						X	X	X	X
Trifolium spp	E				X					
Trisetum spicatum (L.) Richter	N			X						
Valeriana edulis Nuttall	N		X		X		X			
Virgulaster ascendens	N		X				X			
Virgulus falcatus (Lindley) Reveal & Keener	N							X	X	X

Appendix B: Species List by family.

Alliaceae
Allium geyeri (Watson)

Alsinaceae
Cerastium strictum L. emend. Haenke
Eremogone fendleri (Gray) Ikonnikov

Anacardaceae
Rhus aromatica Aiton subsp *trilobata*

Apiaceae
Apiaceae spp
Harbouria trachypleura (Gray) Coulter & Rose

Asteraceae
Achillea lanulosa Nuttall
Agoseris glauca (Pursh) Rafinesque
Agoserus aurantiaca (Hooker) Greene
Ambrosia psilostachya de Candolle
Antennaria spp
Arnica chamissonis Lessing
Arnica fulgens Pursh
Artemisia frigida Wildenow
Artemisia ludoviciana Nuttall
Aster porteri Gray
Cirsium coloradense (Rydberg) Cockerell
Cirsium spp
Erigeron colo-mexicanus Nelson
Erigeron compositus Pursh
Erigeron flagellaris Gray
Erigeron glabellus Nutall
Erigeron speciosus (Lindley) de Candolle
Gaillardia aristata Pursh
Gutierrezia sarothrae (Pursh) Britton & Rusby
Helianthus pumilus Nuttall
Heterotheca spp.
Heterotheca villosa (Pursh) Shinners
Hieracium aurantiacum L.
Liatris punctata Hooker
Machaeranthera pattersonii (Gray) Greene
Oligosporous campestris (L.) Cassini
Psilochenia runcinata (James) Love
Ratibida columnifera (Nuttall) Wooton & Standley
Solidago nana Nuttall
Taraxacum officinale G. H. Weber
Tetraneuris brevifolia Greene
Tragopogon dubius Scopoli
Virgulaster ascendens
Virgulus falcatus (Lindley) Reveal

Boraginacae
Lappula redowskii (Hornemann) Greene
Mertensia lanceolata (Pursh) de Candolle

Appendix B: Species List by family (continued).

Brassicaceae
Alyssum minus (L.) Rothmaler
Boechera drummondii (Gray) Love & Love
Camelina microcarpa Andrzejowski
Neolepia campestris (L.) W. A. Weber

Cactaceae
Coryphantha spp
Opuntia spp

Campanulaceae
Campanula rotundifolia L.

Caprifoliaceae
Symphoricarpos occidentalis Hooker

Caryophyllaceae
Silene antirrhina L.

Chenopodiaceae
Chenopodium spp

Commelinaceae
Tradescantia occidentalis (Britton) Smyth

Convolvulaceae
Convolvulus arvensis L.

Crassulaceae
Amerosedum lanceolatum (Torrey) Love & Love
Clementsia rhodantha (Gray) Rose

Cupressaceae
Juniperus communis L. subsp. *alpina* (Smith) Celakovsky

Cyperaceae
Carex aquatilis Wahlenberg
Carex brevior (Dewey) Mackenzie
Carex festivella Mackenzie
Carex foenea Willdenow
Carex microptera Mackenzie
Carex obtusata Liljebad
Carex pennsylvanica Lamarck ssp. *heliophila* (Mackenzie) Weber
Eleocharis eliptica Kunth
Eleocharis quinquflora (F. X. Hartman) Schwartz

Euphorbiaceae
Tithymalus uralensis (Fischer)Prokhanov

Fabaceae
Astragalus flexuosus (Hooker) G. Don
Astragalus miser Douglas
Astragalus spp.
Lupinus argenteus Pursh
Lupinus spp.

Appendix B: Species List by family (continued).

Fabaceae (continued)
Medicago lupulina L.
Oxytropis lambertii Pursh
Oxytropis parryi Gray
Oxytropis sericea Nuttall
Oxytropis splendens Douglas
Oxytropis spp.
Psoralidium tenuiflorum (Pursh) Rydberg
Thermopsis spp.
Trifolium spp.

Gentianaceae
Frasera speciosa Douglas
Pneumonanthe parryi (Engelmann) Greene

Geraniaceae
Geranium spp

Helleboraceae
Aconitum columbianum Nuttall
Psychrophila leptosepala (de Candolle) Weber

Iridaceae
Iris missouriensis Nuttall

Juncacae
Juncus arcticus Willdenow
Juncus parryi Engelmann
Juncus spp.

Lamiaceae
Prunella vulgaris L.

Linaceae
Adenolinum lewisii (Pursh) Love & Love

Melanthiaceae
Anticlea elegans (Pursh) Rydberg

Onagraceae
Epilobium brachycarpum Presl.
Epilobium spp.
Gayophytum diffusum Torrey & Gray

Oxalidaceae
Oxalis dillenii Jacquin

Pinaceae
Pinus ponderosa Douglas

Plantaginacae
Plantago lanceolata L.

Appendix B: Species List by family (continued).

Poacae

Agrostis gigantea Roth
Agrostis scabra Willdenow
Andropogon gerardii Vitman
Anisantha tectorum (L.) Nevski
Aristida purpurea Nuttall
Bromopsis inermis (Leysser) Holub
Bromus japonicus Thunberg
Danthonia parryi Scribner
Deschampsia cespitosa (L.) P. Beauvois
Elymus longifolius (Smith) Gould
Elymus scribneri (Vassey) Jones
Elymus trachycaulus (Link) Gould
Elytrigia repens (L.) Nevski
Festuca brachyphylla Schultes subsp
Festuca rubra L.
Festuca saximontana Rydberg
Festuca thurberi Vasey
Koeleria macrantha (Ledebour) Schultes
Phleum commutatum Gaudin
Phleum pratense L.
Poa alpina L.
Poa compressa L.
Poa fendleriana (Steudel) Vasey
Poa glauca Vahl.
Poa nemoralis L. subsp. *interior* (Rydberg)
Poa pratensis L.
Schizachyrium scoparium (Michaux) Nash
Sporobolus spp
Stipa comata Trinius & Ruprecht
Trisetum spicatum (L.) Richter

Polygonacae

Acetosella vulgaris (Koch) Fourreau
Bistorta bistortoides (Pursh) Small
Bistorta vivipara (L.) S. Gray
Eriogonum spp
Eriogonum umbellatum Torrey

Primulaceae

Dodecatheon pulchellum (Rafinesque)

Ranunculacae

Pulsatilla patens (L.) Miller subsp. *hirsutissima* Zamels
Ranunculus cardiophyllus Hooker

Rosacae

Fragaria virginiana Miller
Pentaphylloides floribunda (Pursh)
Potentilla diversifolia Lehmann
Potentilla effusa Douglas
Potentilla hippiana Lehmann
Potentilla pulcherrima Lehmann
Potentilla pulcherrima x *hippiana*
Potentilla recta L.

Appendix B: Species list by family (continued).

Rosacae (continued)
Potentilla subjuga Rydberg
Rosa woodsii Lindley
Potentilla spp. (S-1, S-2)

Rubiaceae
Galium septentrionale Roemer & Schultes

Scrophulariaceae
Linaria vulgaris Miller
Orthocarpus luteus Nutall

Valerianaceae
Valeriana edulis Nuttall

Appendix C. Frequencies of native species occurrences in each meadow. Frequency was determined from presence in the 150 sampled meters in each meadow (maximum frequency = 150). A frequency of 30 = 20%. The species are organized into groups of common elevational range. Note that the subalpine sites are on the left, the montane sites in the middle, and the lower montane sites on the right. See Table 5.1 for a comparable listing of exotic species.

	Meadow:								
	Subalpine			Montane			L. Montane		
Name of species:	S1	S2	S3	M1	M2	M3	L1	L2	L3
Species found at all three elevations:									
Achillea lanulosa	12	65	65	97	90	53	0	0	71
Antennaria spp	0	7	15	0	24	3	4	4	0
Artemisia frigida	0	39	0	0	3	0	2	3	0
Artemisia ludoviciana	0	1	0	0	9	3	4	10	4
Cerastium strictum	1	4	0	0	10	9	3	32	0
Erigeron glabellus	0	1	1	21	42	24	2	1	0
Koeleria macrantha	0	8	0	0	31	23	0	34	0
Juncus arcticus	91	0	0	73	2	82	0	0	31
Species of the subalpine & montane zones:									
Amerosedum lanceolatum	0	7	82	0	10	0			
Astragalus miser	0	0	1	0	2	0			
Bistorta bistortoides	0	17	0	0	0	7			
Boechera drummondii	0	0	2	0	3	1			
Campanula rotundifolia.	0	22	24	0	10	0			
Carex microptera	79	17	0	5	0	0			
Deschampsia cespitosa	80	33	0	5	0	19			
Dodecatheon pulchellum	34	0	0	1	0	0			
Frasera speciosa	0	0	8	0	20	0			
Galium septentrionale	0	24	0	0	1	9			
Mertensia lanceolata	0	0	1	0	2	0			
Pentaphylloides floribunda	1	32	0	0	0	14			
Poa fendleriana	0	0	36	0	0	15			
Potentilla hippiana	0	1	0	0	104	2			
Potentilla pulcherrima	0	4	0	28	0	65			
Pulsatilla patens subsp*hirsutissima*	0	2	63	0	1	0			
Ranunculus cardiophyllus	31	0	0	3	3	18			
Thermopsis spp	0	49	39	0	65	13			
Valeriana edulis	0	19	0	24	0	93			
Virgulaster ascendens	0	2	0	0	0	1			
Species of the montane & lower montane zones:									
Aster porteri				0	12	0	10	0	29
Eriogonum umbellatum				1	7	5	2	3	0
Elymus longifolius				0	3	0	0	4	0
Geranium spp				0	1	0	0	6	0
Heterotheca villosa				0	25	3	118	120	0
Oxytropis lambertii				0	33	0	0	3	0
Pinus ponderosa				0	1	0	0	0	2
Species of the subalpine and lower montane zones:									
Astragalus flexuosus	0	0	1				3	5	15
Carex pennsylvanica	0	1	0				2	96	0
Elymus trachycaulus	0	112	4				0	0	1
Oligosporous campestris	0	0	55				2	0	0

	Subalpine			Montane			L. Montane		
Name of species:	S1	S2	S3	M1	M2	M3	L1	L2	L3
Species of the subalpine zone only:									
Aconitum columbianum	2	1	0						
Agoserus aurantiaca	0	0	9						
Arnica chamissonis	0	5	0						
Bistorta vivipara	19	0	0						
Carex aquatilis	18	0	0						
Carex foenea	0	72	127						
Clementsia rhodantha	12	0	0						
Eleocharis quinquflora	41	0	0						
Elymus scribneri	0	0	59						
Eremogone fendleri	0	25	31						
Erigeron compositus	0	0	42						
Erigeron speciosus	0	10	0						
Festuca brachyphylla subsp*colradensis*	0	0	43						
Festuca rubra	0	3	0						
Festuca thurberi	0	5	0						
Gayophytum diffusum	0	0	3						
Juncus parryi	54	0	0						
Juncus spp S-2	0	37	0						
Juniperus communis subsp.*alpina*	0	0	2						
Lupinus argenteus	0	0	30						
Machaeranthera pattersonii	0	0	10						
Oxytropis parryi	0	0	40						
Oxytropis sericea	0	13	0						
Oxytropis splendens	0	2	0						
Phleum commutatum	27	0	0						
Poa alpina	4	0	0						
Poa glauca	0	0	17						
Poa nemoralis subsp. *interior*	0	25	0						
Potentilla diversifolia	0	2	0						
Potentilla subjuga	0	0	49						
Potentilla sp (S-1)	12	0	0						
Potentilla sp (S-1)	6	0	0						
Potentilla sp (S-2)	0	3	0						
Psilochenia runcinata	5	0	0						
Psychrophila leptosepala	125	0	0						
Tetraneuris brevifolia	0	0	11						
Trisetum spicatum	0	0	13						
Species of the montane zone only:									
Agrostis scabra				0	0	1			
Allium geyeri				65	3	50			
Agoseris glauca				20	1	0			
Anticlea elegans				0	0	11			
Carex festivella				0	2	0			
Carex obtusata				0	3	0			
Cirsium coloradense				0	3	0			
Danthonia parryi				4	0	20			
Epilobium brachycarpum				0	0	2			

	Subalpine			Montane			L. Montane		
Name of species:	S1	S2	S3	M1	M2	M3	L1	L2	L3
Species of the montane zone only continued:									
Festuca saximontana				0	11	0			
Fragaria virginiana				0	1	0			
Harbouria trachypleura				0	4	0			
Iris missouriensis				1	2	36			
Lupinus spp				0	5	0			
Orthocarpus luteus				0	6	0			
Pneumonanthe parryi				0	2	0			
Potentilla effusa				4	0	0			
Potentilla pulcherrima x hippiana				0	130	0			
Solidago nana				0	8	0			
Tradescantia occidentalis				2	0	0			
Species of the lower montane zone only:									
Ambrosia psilostachya							46	30	53
Adenolinum lewisii							0	4	0
Andropogon gerardii							0	23	0
Aristida purpurea							4	0	0
Arnica fulgens							0	0	49
Carex brevior							0	0	3
Coryphantha spp							0	2	0
Erigeron colo-mexicanus							2	0	0
Erigeron flagellaris							0	0	26
Eriogonum spp							1	3	0
Gutierrezia sarothrae							0	0	7
Helianthus pumilus							1	5	0
Lappula redowskii							0	1	0
Liatris punctata							7	18	6
Opuntia spp							1	9	1
Oxalis dillenii							0	0	10
Prunella vulgaris							0	0	2
Psoralidium tenuiflorum							0	0	38
Ratibida columnifera.							0	0	6
Rhus aromatica subsp *trilobata*							0	0	1
Rosa woodsii							8	3	6
Schizachyrium scoparium							1	10	0
Sporobolus spp							25	0	0
Stipa comata							5	94	4
Symphoricarpos occidentalis							0	0	2
Virgulus falcatus							13	10	64