DISSERTATION

UNGULATE/VEGETATION DYNAMICS IN THE PRYOR MOUNTAIN WILD HORSE RANGE

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JAN PETERSON ENTITLED UNGULATE/VEGETATION DYNAMICS IN THE PRYOR MOUNTAIN WILD HORSE RANGE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

UNGULATE/VEGETATION DYNAMICS

IN THE PRYOR MOUNTAIN WILD HORSE RANGE

I investigated the effects of feral horses, bighorn sheep, and mule deer on structural and functional aspects of vegetation in the Pryor Mountain Wild Horse Range (PMWHR) in southern Montana and northern Wyoming, during 1992 to 1995. I monitored: 1) the biomass dynamics of graminoids, forbs and dwarf shrubs, forage utilization, and the nitrogen content of cool season grasses inside and outside grazing exclosures, 2) vegetation characteristics at the Sorenson Extension site, which had been grazed by feral horses for 10 years before their removal in fall, 1992, and 3) the nutritional dynamics of curlleaf mountain mahogany, an important food resource for wild ungulates. I also estimated protein, fiber, and dry matter digestibility in captive bighorn sheep fed diets containing 40% and 0% curlleaf mountain mahogany.

In the arid lowland communities, both live and dead graminoid biomass were greater inside exclosures than outside at two sites in the Dryhead Herd area. After 10 years of horse grazing at the lowland Sorenson Extension site, graminoid biomass was slightly greater outside than inside a fenced area, where horses had not previously grazed. In the more productive montane sites, live graminoid biomass was two to three times

greater inside than outside an exclosure on U.S. Forest Service land. Live and dead graminoid biomass were also significantly greater inside than outside the Syke's Ridge exclosure. However, there were no significant differences between graminoid biomass inside and outside the exclosure at the Penn's Cabin site in the upper elevations.

Forage utilization ranged from undetectable levels to as high as 43% of the total forb and dwarf shrub production. Although there were no consistent effects of herbivory on plant nitrogen (N) content, live graminoids from upper elevation sites had consistently higher N-concentrations than those from the lower elevations. Because both the quantity and quality of forage were always higher at the upper elevations, these areas appear to be capable of sustaining a larger number of ungulates during the fall and winter seasons.

Shrub density, which ranged from 1070 to 54,300 individuals/ha, and seedling density, which ranged from 400 to 49,000 seedlings/ha, were much higher than reported elsewhere. The site with the greatest current annual growth (CAG) production had the highest level of utilization by browsing ungulates, and browsing apparently had no effect on twig biomass or protein concentration. These results suggest that *C. ledifolius* is capable of compensating for tissue loss. Results from the digestion trial indicate that *C. ledifolius* depresses protein digestibility in bighorn sheep, but reductions in fiber and dry matter digestibility were not statistically significant.

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I. INTRODUCTION

Ungulates influence both the structure and function of grassland and shrubland ecosystems. The degree of their impact is dependent upon the density of their populations relative to the availability of the plant resources. Although ungulate densities are determined by many factors, including such things as predation, disease, and weather, perhaps the greatest influence on their numbers is the value of available plants as food for the animals (Duncan 1992).

Grazing and browsing ungulates affect their food resources in several ways. Structurally, grazing ungulates reduce the canopy height of grasses, activating tillers to produce a dense, prostrate canopy (McNaughton 1976, 1979), which McNaughton (1984) has referred to as a 'grazing lawn'. Because grazers rarely feed uniformly in space, nor continuously in time, grasslands are often a mosaic of heavily grazed short, dense patches and taller, lightly grazed areas (McNaughton 1984). Similarly, browsing ungulates alter the form of shrubs and trees by feeding on growing shoot tips, thus removing apical meristems and activating lateral meristems producing a more dense, bushy shape (McNaughton 1984, McInnes et al 1992, Molvar et al. 1993). Additionally, as palatable plants are consumed by grazers and browsers and thereby reduced in abundance, changes can occur in the composition of plant communities (Pastor et al. 1988, Jefferies et al. 1994).

In addition to influencing the physical structure of grasslands and shrublands, ungulates affect function as well, by consuming a large proportion of plant production (Duncan 1992). Whether the effects of herbivory enhance or diminish plant performance is the subject of much recent debate (McNaughton 1993, Painter and Belsky 1993). According to the grazing optimization hypothesis (McNaughton 1979, 1983), net primary production (NPP) should be maximized at moderate levels of grazing because of plant compensatory growth mechanisms. Moderate levels of herbivory have, in fact, been shown to produce increased NPP in some systems (McNaughton 1976, 1979, Cargill and Jefferies 1984, Bergstrom and Danell 1987). However, grazing was found to affect plant production only rarely in a northern mixed-grass prairie (Biondini et al. 1998). Climatic variations were apparently more important than herbivory in affecting major trends in primary production and plant species composition (Biondini et al. 1998). In addition, Milchunas and Lauenroth (1993), in their review of 236 studies, found that, in most instances, effects of grazing on production were negative.

There is also some question as to what effects herbivores have on nutrient cycling (Ritchie et al. 1998). Herbivory has been found to increase plant nitrogen concentration (Bryant 1981, Coppock et al. 1983, Danell and Huss-Danell 1985, Coughenour 1991). However, in a northern mixed-grass prairie, there was no effect of herbivory on plant nitrogen concentration in 6 out of 7 years (Biondini et al. 1998), whereas in an oak savanna, exclusion from herbivory resulted in increased nitrogen content in plants (Ritchie et al. 1998). Grazing and browsing herbivores may facilitate nutrient transfer into the soil with inputs of urinary nitrogen, which enriches soil and stimulates plant

growth (Day and Detling 1990, Jaramillo and Detling 1992), and fecal nitrogen, which boosts nitrogen mineralization (Ruess and McNaughton 1987), also leading to increased rates of plant growth (Hik and Jefferies 1990). Herbivores are also known to be drawn back to fertilized areas (Day and Detling 1990), which initiates positive feedback loops and increases the rate of nutrient cycling (Bryant and Chapin 1986). However, when populations of herbivores reach high densities, the animals may exceed the ability of their food resources to support them, thereby initiating strong negative feedbacks (Molvar et al. 1993).

For the past several years, three species of ungulates (feral horses, bighorn sheep, and mule deer) have coexisted in populations of varying densities with minimal negative impact on one another in the grasslands and shrublands of the Pryor Mountain Wild Horse Range (PMWHR) (BLM 1997). The PMWHR, which consists of approximately 18,000 ha of rangeland in southern Montana and northern Wyoming, was established in 1968 as the first officially designated wild horse range in the United States (Federal Register 1968). Upon establishment of the range, the Bureau of Land Management (BLM) was directed to manage the area for the protection and management of wild horses, wildlife, watershed, archeological, recreational, and scenic values, without impairing the productivity of the land (BLM 1984). However, 66% of the producing range has been found to be in poor condition, while only 33% is in fair to good condition (BLM 1997). In addition, the Pryor range has been nominated for designation as an Area of Critical Environmental Concern (ACEC), indicating a need for protection from further degradation (BLM 1997). Therefore, the long term management objectives of the BLM

have been to improve areas of range that are in poor condition and to promote a "thriving natural ecological balance" with viable populations of multiple floral and faunal species and mutual co-existence (BLM 1997). Increasing ungulate populations in the PMWHR, however, pose potentially serious threats to these management objectives.

In the 1970's, a small group of bighorn sheep dispersed from an earlier release site in the Bighorn Mountains and became established in the lowland communities of the PMWHR. By 1994, the sheep population had grown to an estimated 211 animals (Kissell et al. 1996). At the same time, the mule deer population had also increased to ~ 700 animals. And, although the Herd Management Area Plan (BLM 1984) established a stocking rate of 121 horses for the Pryor range, the horse population has been as high as 208 individuals (BLM 1997). There appears to be little dietary and habitat overlap between mule deer and horses (Kissell et al. 1996). However, the potential for competition between horses and bighorn sheep, both grazers, has been of concern, especially at lower elevations in the PMWHR, where much of the range is in poor condition.

Maintaining the long-term productivity and health of plant and animal populations within this ecosystem will present many challenges to the managers of the PMWHR. Making sound management decisions regarding the carrying capacity of the area for the three ungulate species which inhabit it will require information on the effects of the ungulates on the vegetation and upon one another. Recent studies have addressed habitat and dietary overlap between horses, bighorn sheep, and mule deer (Kissell et al. 1996) and the effects of ungulate herbivory on plant species composition in the Pryor

range (Fahnestock 1998). However, until my study, virtually no research had been conducted on the effects of ungulates on intraseasonal aboveground biomass dynamics of grasses, forbs and dwarf shrubs, plant nutrient concentration, the ratio of live:dead plant material, or aboveground net primary production. Additionally, there are currently no data available on the effects of ungulate browsing on *Cercocarpus ledifolius*, a key browse species in the PMWHR. And finally, there have been no studies, to date, to report the quantity of biomass and nutrients that ungulates remove from the total available to them. The purpose of the research discussed herein is to provide detailed information on these aspects of ungulate herbivory on the plants of the PMWHR. The results of this study, together with the previously mentioned studies, will provide managers with better information to use in making decisions concerning the long term health and productivity of the PMWHR.

Objectives of Research

The primary objective of my research was to evaluate the effects of feral horses, bighorn sheep, and mule deer on several structural and functional aspects of the herbaceous and woody vegetation of the Pryor Mountain Wild Horse Range. Specifically, I sought to understand how vegetation responded to short and long term exclusion from these large herbivores in the arid lowland and more mesic upland communities of the PMWHR. I also wanted to determine how herbivory affected *Cercocarpus ledifolius*, an evergreen shrub that is important in the diets of both bighorn

sheep and mule deer, and in turn, what effect *C. ledifolius* had on digestibility in bighorn sheep.

In my first study, I estimated the quantity of forage removed seasonally from grasslands by ungulates in the PMWHR by harvesting vegetation inside and outside moveable exclosures at the end of the growing season. Using permanent exclosures, I also evaluated the effects of exclusion from herbivory on: 1) the standing crop and intraseasonal aboveground biomass dynamics of grasses, forb and dwarf shrubs, 2) the ratio of live to dead plant material, 3) the nitrogen concentration of the forage, and 4) aboveground net primary production (ANPP). Two previously erected exclosures (ca. 1950 and 1963) were used in the montane grassland communities to evaluate the long term effects of exclusion from grazing, and three newly erected (1992) exclosures were used in the mid-elevation and lowland grassland communities to evaluate the short term effects. I also made vegetation measurements at two sites in the Sorenson Extension, an area which had been grazed by feral horses for the previous 10 years and then released from horse grazing pressure in the fall of 1992. This study is described more thoroughly in Chapter 2.

The overall goals of my second study were to: 1) ascertain the condition, distribution, and abundance of *C. ledifolius* in the PMWHR, 2) determine to what extent plants were being browsed, 3) examine the effects of ungulate browsing on the nutritional quality of these shrubs, and 4) determine the nutrient digestibility of *C. ledifolius* in bighorn sheep. More specifically, I estimated the density and production, as well as the utilization by ungulates, of *C. ledifolius* at twelve sites in the PMWHR. At

these same sites, I evaluated the differences in protein concentration and twig biomass between large and small shrubs. I also compared protein concentration, fiber concentration, lignin:nitrogen ratios, cell solubles:cell wall ratios, and twig biomass in shrubs that had been excluded from browsing for ~ 25 years at the Sykes Coulee exclosure and in shrubs at two river sites that had not been browsed by large ungulates to browsed shrubs at the other sites. Finally, I conducted a digestion trial with captive bighorn sheep to determine the effects of *C. ledifolius* on dry matter, protein, and fiber digestibility.

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II. RESPONSE OF VEGETATION TO EXCLUSION OF UNGULATES IN THE PRYOR MOUNTAIN WILD HORSE RANGE

ABSTRACT

From May, 1992 through August, 1994, I evaluated the effects of excluding feral horses, bighorn sheep, and mule deer from grazing on vegetation at several exclosures in the Pryor Mountain Wild Horse Range. My experimental methods involved analyzing plant material inside and outside of both previously existing and newly constructed grazing exclosures. I monitored the biomass of grasses, forbs and dwarf shrubs, and the nitrogen content of cool season grasses, which are important components of ungulate diets. I also estimated forage utilization by these three species of ungulates. I conducted research at seven sites, two of which were located in the upper elevations and built ca. 25 years ago, the Penn's Cabin and Forest Service sites. Three additional exclosures were erected in 1992, one at mid elevation, the Syke's Ridge site and two in the lowlands, the North and South Dryhead sites. I collected data from two additional lowland sites in the Sorenson Extension Area, which had been grazed by feral horses for the previous 10 years, and then released from grazing pressure in the fall of 1992.

At the North and South Dryhead sites, grass biomass was greater inside than outside both grazing exclosures. At the Sorenson Extension site, horse grazing for the

10 years preceding this study apparently resulted in a slight, but statistically significant increase in grass biomass outside the fenced area, where the horses had grazed previously. At a more productive upper elevation site on U. S. Forest Service land, live grass biomass (averaged across the growing season) was two to three times greater inside the exclosure than outside. Although there were no significant differences in total grass biomass inside and outside the Penn's Cabin exclosure, forb and dwarf shrub biomass was significantly greater outside the exclosure than inside. And at the Syke's Ridge site, there was significantly less total grass biomass outside the exclosure than inside. Live:dead grass ratios were significantly higher outside than inside all exclosures.

Forage utilization ranged from being undetectable at five sites in both upper and lower elevations in 1993, to levels as high as 43% of the total forb/dwarf shrub production at the Penn's Cabin site in 1994. Although there were no clear trends to describe the effect of herbivory on grass nitrogen content, C_3 live graminoids from upper elevation sites had consistently higher concentrations of nitrogen, both inside and outside exclosures, than those from the lower elevations.

INTRODUCTION

Herds of feral horses (*Equus caballus*), Rocky Mountain bighorn sheep (*Ovis canadensis*), and mule deer (*Odocoileus hemionus*) depend on vegetation in the Pryor Mountain Wild Horse Range (PMWHR) for their food resources and habitat requirements. The distribution, abundance, and quality of their forage has effects not

only on the health of individual animals, but also on the densities and distributions of their populations. Large herbivores such as these, in turn, play significant roles in ecosystems that go far beyond their immediate needs for food or habitat (Naiman 1988).

By grazing or browsing, herbivores physically alter their environment, affecting plant community composition, vertical and horizontal structure, and, ultimately, the biogeochemical cycling of nutrients (Holland and Detling 1990, McNaughton et al. 1997). These changes in ecosystem structure and function can have either positive or negative influences on the plant community. Some alterations may benefit the forage base, resulting in increased plant productivity (McNaughton 1979, 1985), whereas other changes may be detrimental, causing lower production rates and reducing the abundance of key forage species (Bazely and Jefferies 1986, Naiman 1988, Milchunas and Lauenroth 1993).

Herbivory also affects nutrient uptake by plants, and alters patterns of nutrient distribution within plants (Ruess 1984, Day and Detling 1990, Holland and Detling 1990, Milchunas and Lauenroth 1993). Forage quality is directly linked to the concentration of nutrients in plants, particularly nitrogen, a critical component of protein (Robbins 1993, Van Soest 1994). The value of vegetation as food, however, depends not only on its quality, but also on the quantity available. Both quantity and quality can vary greatly throughout the year in areas where plant growth is seasonal (Duncan 1992), as it is in the PMWHR.

The Pryor Mountain Wild Horse Range was designated as a refuge for feral horses in 1968 by the Secretary of the Interior (BLM 1984). Kissell et al. (1996)

estimated that the feral horse population in the PMWHR ranged from 144 individuals, in 1993, to 177 individuals in 1994. During the same time period, the mule deer population in the PMWHR ranged in size from 573 to 780 individuals (Kissell et al. 1996). In 1975, a small group of Rocky Mountain bighorn sheep dispersed from an earlier transplanted herd in the northern Bighorn Mountains and became established in the PMWHR. By spring, 1989, the bighorn sheep population in the PMWHR was estimated to be between 75 and 80 animals (Coates and Schemnitz 1989), and by 1994 had grown to an estimated size of 211 individuals (Kissell et al. 1996).

Populations of all three species have since decreased dramatically in size. In 1996, the number of sheep dropped to 125, and the population of mule deer also fell to 143 individuals. The feral horse population, after a 1994 culling effort by the Bureau of Land Management, was estimated to be approximately 126 animals (Kissell et al. 1996). Even though their numbers have recently declined, it is probable that populations of these three ungulate species will again expand in the future, creating the potential for increased competition for both habitat and available forage, a situation which may, ultimately, have detrimental effects on their forage base. Until this study, virtually no research had investigated the effects of these animals on the vegetation in the PMWHR. The overall objective of my research was to evaluate the effects of feral horses, mule deer, and bighorn sheep on a variety of structural and functional aspects of the vegetation of the Pryor Mountain Wild Horse Range.

I addressed the following specific objectives and null hypotheses (H_o) in my research:

1. Estimate the quantity of forage removed seasonally from grasslands by wild ungulates.
2. Evaluate the effects of exclusion from herbivory by wild horses, bighorn sheep, and mule deer on:
    a. the standing crop and intraseasonal aboveground biomass of grasses, forbs and dwarf shrubs.

    H_o: There are no significant differences in plant biomass inside and outside permanent exclosures.

    b. the ratio of live:dead plant material; and

    H_o: There are no significant differences in live:dead ratios inside and outside permanent exclosures.

    c. the nitrogen concentration of the forage.

    H_o: There are no significant differences in N concentration of forage inside and outside permanent exclosures.
3. Determine the effects of exclusion from herbivory by these ungulates upon aboveground net primary production (ANPP).

    H_o: There are no significant differences in aboveground net primary production inside and outside the Forest Service site exclosure.

STUDY AREA

My research was conducted from May, 1992 through August, 1994 in the Pryor Mountain Wild Horse Range (Fig. 2.1). The PMWHR covers approximately 18,000 ha, characterized by steep, rocky canyons, subalpine meadows, and desert shrublands in northern Wyoming and southern Montana. Elevations within the horse range vary from 1190 m to 2400 m, and average annual precipitation ranges from 130 mm in the lower elevations to over 500 mm in the upper elevations (BLM 1984). The majority of annual precipitation occurs during high intensity summer storms and winter snow runoff (BLM 1984). The climate in the PMWHR has been referred to as cool temperate and semi-arid (Knight et al.1987). The average growing season is between 100 and 130 days (BLM 1984).

Upper and lower elevation sites where this study was conducted are vastly different, not only in climate and topography, but also in the characteristic vegetation that they support. Upper elevations are characterized by coniferous woodlands interspersed with relatively lush, grassy plateaus and subalpine meadows. The coniferous woodlands are a mix of subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), limber pine (*Pinus flexilis*), and Engelmann spruce (*picea engelmannii*) (Knight et al. 1987). Upper areas support a wide variety of other plant species as well, including many small perennial forbs and sedges, and common grasses, including Idaho fescue (*Festuca idahoensis*), alpine timothy (*Phleum commutatum*), and alpine bluegrass (*Poa alpina*) (BLM 1984). Vegetation at low elevations, composed mainly of shrubs and grasses, is generally sparse

with large amounts of bare soil. Juniper (*Juniperus scopulorum*) and curlleaf mountain mahogany (*Cercocarpus ledifolius*) are common shrubs at the lower elevations, along with rubber rabbitbrush (*Crysothamnus nauseosus*), big sagebrush (*Artemesia tridentata*), shadscale (*Atriplex confertifolia.*), and broom snakeweed (*Gutierrezia sarothrae*) (Knight et al. 1987). Grasslands in the lower elevations are dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*), blue grama (*Bouteloua gracilis*), and needle-and-thread grass (*Stipa comata*) (Fahnestock, 1998).

METHODS

I examined the response of vegetation to exclusion from herbivory by comparing plant characteristics inside and outside of grazing exclosures. Where possible, previously erected exclosures were used to evaluate the effects of long term exclusion from grazing. At the upper elevation sites, two permanent exclosures, one constructed near Penn's Cabin in 1963, and the other erected at the Forest Service site ca. 1950, were utilized (Fig 2.1). Two 50 X 50 m plots were used to measure vegetation inside and outside an exclosure (approximately 75 X 75 m) at the Penn's Cabin site. At the Forest Service site, vegetation inside the fenced area (approximately 45 X 45 m) was compared to vegetation outside the fence in a 50 X 50 m plot. In the lowland Sorenson Extension sites (see Fig. 2.1) which were grazed by wild horses from 1982-1992, vegetation was measured inside and outside a fenced area on the north side of the Layout Creek Ranger Station, using two 50 x 50 m plots inside the fence, and two 50 x 50 m plots outside the

fence. Unfenced plots at the Sorenson Extension site were released from horse grazing pressure during fall, 1992, although mule deer and bighorn sheep still had free access to the entire area. In contrast, new 50 x 50 m exclosures were constructed at the North and South Dryhead sites and at the Syke's Ridge site in late June, 1992 (Fig. 2.1). Vegetation was sampled at these sites in May and early June of 1992, before exclosure construction, to provide data on how similar the treatment and control plots were. Also in 1992, at each of the seven unfenced plots located outside the permanent exclosures, vegetation was sampled inside twelve small (1 m x 1 m x 0.75 m high) moveable exclosures on each monthly sample date to estimate forage utilization and aboveground net primary production (ANPP). Moveable exclosures were constructed entirely of steel wire mesh (approximately 1 cm X 1 cm) and were covered to prevent ungulates from consuming vegetation within the exclosure.

In 1993, five additional sites without permanent exclosures were established to obtain a more representative estimate of the quantity and quality of available forage over the horse range. At these five sites, moveable exclosures (as described above) were utilized to measure forage utilization. Forage utilization was also assessed again at the Forest Service site, for a total of six moveable exclosure cage sites in 1993. Three of the five new sites were located in the Dryhead area of PMWHR between the northern and southern permanent exclosures that were established in 1992. Two additional grassland plots were situated on BLM land close to the upper elevation sites, one in the Syke's Ridge area and the other on a hillside with deep soil across the drainage from Penn's Cabin site. Although permanent exclosures were not erected at these five additional

sites, 12 moveable cages (as described above) were randomly placed within each plot on the first sampling date in May, 1993. As with the permanent exclosure sites, vegetation was harvested outside the moveable cages at monthly intervals from May - August 1993. Vegetation from within the 12 moveable exclosures was also harvested in August to estimate season-long forage removal by grazers at these five sites.

During 1994, vegetation was again sampled from three of the six moveable exclosure sites above. Vegetation was harvested outside the cages on each sample date from two upper elevation sites (the Penn's Cabin hillside site and the Forest Service site) and from one lower elevation site (in the southern Dryhead Herd area in PMWHR).

Aboveground Plant Biomass

The procedures used were modified from sampling techniques previously used in both northern mixed grass (Coppock et al. 1983, Whicker and Detling 1988a, Cid et al. 1991) and shortgrass steppe (Lauenroth et al. 1978, Dodd and Lauenroth 1979). Throughout the duration of this study (1992-1994), 12 circular, 0.25 m^2 quadrats were clipped to ground level at each of the permanent exclosure sites on each monthly sample date, both inside and outside the exclosure. At the time of clipping in the field, plant material was separated by functional group (C_3 graminoids, $_C$ graminoids, forbs, and dwarf shrubs). After being dried to a constant mass at 45°C, vegetation was further separated into live (at time of harvest), current year's dead, and previous year's dead in the case of graminoids, and live and total dead in the case of other functional groups. At all sites, I calculated total aboveground plant biomass (g/m^2) for any one sampling date

as the sum of all functional groups (both live and dead plant material). Live:dead graminoid ratios include live and total dead graminoid biomass.

Forage Nitrogen Concentration

I determined aboveground nitrogen concentration of live C_3 graminoids using the Kjeldahl technique (AOAC 1965) and a Leco 1000 CHN analyzer. Live graminoid samples from each site were composited into four larger group samples by combining three individual samples. Composited samples were ground in a Wiley mill through a 1 mm screen and then subsampled and analyzed for each date and site. I converted nitrogen concentration to crude protein concentration by multiplying by 6.25.

Forage Utilization

In 1993, forage utilization was estimated at six sites by harvesting vegetation on the last sample date inside and outside moveable exclosures. Clipped quadrats outside the cages were paired with clipped quadrats within the cages. Outside paired plots were established within one to four meters of the caged plot in a random direction. I calculated offtake as the difference between the aboveground biomass inside and outside moveable exclosures on the last sampling date of the season. The same methodology was used in 1994 to estimate offtake at three sites. Offtake, as used here, actually is the sum of consumption by herbivores plus wastage (e.g., biomass trampled into litter).

Aboveground Net Primary Production (ANPP)

Mean peak standing crop inside permanent exclosures was used as an estimate of ANPP for the 1992, 1993, and 1994 growing seasons at all exclosure sites. To determine the effects of long-term exclusion from herbivory on ANPP at the Forest Service site,

mean peak standing crop inside the permanent exclosure was compared to mean peak standing crop within the moveable cages outside the permanent exclosure.

Statistical Analysis

Because the 3 new permanent exclosures were not constructed until after the second sampling date in June, 1992, and vegetation was not sampled at upper elevation sites until the middle of the growing season during that year, data for the 3 new exclosure sites and the 2 upper elevation sites in 1992 are incomplete. Thus, I have included only complete data sets from 1993 and 1994 for these 5 exclosure sites in my statistical analyses to achieve a balanced statistical design. I have summarized available data for 1992 (Appendices A2.1 and A2.2), and will discuss them where applicable. Vegetation was sampled at the Sorenson Extension sites during each sampling date in 1992 and 1993, and because plots at this site were set up to investigate vegetation changes following removal of horses, I analyzed data from these sites separately.

I analyzed all herbaceous plant biomass data, including nitrogen concentration of C_3 grasses, and live:dead ratios of grasses, by site using three-way Analyses of Variance (ANOVA), with treatment (permanent exclosure vs unexclosed), year (1993 vs 1994), and month (May, June, July, and August) as factors. I expected the month factor to always be significant, as vegetation characteristics change over the growing season, and this was generally true for all variables. I also found very few significant treatment by month interactions. Thus, for the sake of clarity, I do not include the effects of month in the results or discussion section. Data were analyzed for each site separately. At the Sorenson Extension site, where there were two exclosed and two unexclosed plots within

100 m of one another, I analyzed data using four-way ANOVAs with site as an added factor to the three factors discussed previously.

Live:dead graminoid biomass data were transformed log normally for ANOVA analyses. Comparisons between ANPP inside the Forest Service permanent exclosure and outside were made across 2 years using a one-way ANOVA. I used paired Student's t-tests to determine any significant forage offtake during two years at upper and lower elevation sites (Ott 1988). All analyses were performed using the SAS statistical program, version 6.11 (SAS Institute 1989, Cody and Smith 1991). Although there were a considerable number of statistical comparisons analyzed in this data set, no correction was made for the increased chance of a Type I error, and differences are considered significant at $p \leq 0.05$ (Peters 1991).

Although the forbs plus dwarf shrubs were sorted into live and dead components and the data are presented that way in the appendices, dead material was of such small proportion (<6% in most cases), that I included it together with the live material in the forb and dwarf shrub category in my statistical analyses. In addition, because $_{C.}$ grasses were common only at the South Dryhead site and were completely absent at upper elevation sites, I combined C_3 and $_{C.}$ graminoids together into a 'total grass' category, and analyzed them as such .

RESULTS

Sampling at the new exclosure sites on the first two sample dates of 1992 (before the exclosures were built) provided data on how similar the treatment and control plots were. Although I conducted no statistical analyses on differences in biomass for 1992, fenced and unfenced plots at Syke's Ridge (Appendix A2.1) and the North Dryhead site (Appendix A2.2) were similar in total graminoid (live plus dead) biomass. All unfenced plots were situated immediately adjacent to the exclosures with the exception of the South Dryhead site, where the control plot was situated across a ravine approximately 125 m from the treatment plot. Although statistical analyses were not conducted on 1992 data, these two plots initially appeared to be similar in plant biomass. However, I determined from the first sampling date that total graminoid biomass (live plus dead material) was about 50% higher on the unfenced plot (Appendix A2.2). During May, 1992, values for mean total grass biomass on the fenced and unfenced plots at the South Dryhead site were 28.5 ± 5 g/m^2 and 42.9 ± 2 g/m^2, respectively. During June of that same year, values were 39.4 ± 9 g/m^2 on the fenced plot, and 57.3 ± 9 g/m^2 on the unfenced plot. Thus, results for this site should be interpreted with caution.

Aboveground plant biomass.

Overall, at most of the permanent exclosure sites within the PMWHR, I found significantly greater aboveground biomass inside exclosures than outside (Table 2.1) and these findings occurred for most categories, including live grass, dead grass, total grass, and total plant biomass. Forb and dwarf shrub biomass, however, was not consistently

higher inside than outside exclosures. Live:dead graminoid ratios were significantly higher outside exclosures than inside (Table 2.1).

Significant interactions between treatment (exclosed vs unexclosed) and year occurred at four out of six sites (Table 2.1). The interaction was highly significant for nitrogen concentration in C_3 live graminoids at Penn's Cabin, Forest Service, and the North and South Dryhead sites (Table 2.1). There were also significant interactions between treatment and year at the Forest service site for the dead and total grass categories. At the South Dryhead site, treatment by year interactions were also significant for live grass, dead grass, total grass, and total biomass. No significant interactions occurred at the Sykes Ridge site or the Sorenson Extension site (Table 2.1).

Upper Elevation Long Term Exclosures - Forest Service and Penn's Cabin Sites

Overall, there were highly significant differences ($p < 0.01$) in plant biomass inside and outside the Forest Service exclosure during the 1993 and 1994 growing seasons for all categories except forbs and dwarf shrubs (Table 2.1, Appendix A2.1).Aboveground biomass of live graminoids was higher at the Forest Service site than any of the other exclosure sites during the 1993 and 1994 growing seasons, and was consistently higher inside the exclosure than outside during both years (Fig. 2.1a). Seasonal mean live graminoid biomass was almost twice as high inside the exclosure (46 ± 9 g/m^2) as outside (26 ± 5 g/m^2) during 1993, and was nearly three times as high inside (53 ± 11 g/m^2 vs. 19 ± 3 g/m^2) during the 1994 growing season (treatment effect, $p < 0.001$). Differences in live graminoid biomass were not significant between 1993 and 1994 ($p = 0.936$). Seasonal mean dead grass and total grass biomass were both

higher inside than outside the exclosure ($p < 0.001$ for both variables), although the effect was larger in 1994 than in 1993 (treatment by year interaction, dead grass $p = 0.005$, total grass $p = 0.004$). Mean dead grass and total grass were higher in 1994 than in 1993 ($p < 0.001$ and $p = 0.015$, respectively). Seasonal mean live:dead grass ratios were lower inside than outside the exclosure in 1993 and 1994 ($p < 0.001$, Fig. 2.1 b, Appendix A.2.2). Live:dead ratios were higher in 1993 ($p < 0.001$) and the interaction between treatment and year was not significant ($p = 0.130$).

In contrast, seasonal mean biomass of forbs and dwarf shrubs (live plus dead material) was not significantly different inside and outside the exclosure during 1993 and 1994 ($p = 0.132$), nor was there a significant difference between years ($p = 0.941$). Outside the exclosure, forb and dwarf shrub biomass averaged 80 $\pm$ 8 g/m2 during 1993, and 81 $\pm$ 7 g/m2 during the 1994 growing season. Inside the exclosure it was 70 $\pm$ 16 g/m2 during 1993 and 68 $\pm$ 7 g/m2 during 1994.

I detected no significant differences in live, dead, or total graminoid biomass inside and outside the permanent exclosure at the Penn's Cabin site ($p = 0.845$, $p = 0.226$, or $p = 0.409$, respectively; Table 2.1 and Appendix A2.3). However, in 1993 and 1994, the mean biomass of forbs and dwarf shrubs was higher outside the exclosure than inside ($p < 0.001$). Seasonal mean biomass of forbs and dwarf shrubs outside the exclosure for 1993 and 1994 was 88 $\pm$ 19 g/m^2 and 82 $\pm$ 13 g/m^2, respectively, while within the exclosure, it was 64 $\pm$ 13 g/m^2 during 1993, and 44 $\pm$ 4 g/m^2 during 1994. Because graminoid biomass did not differ inside and outside the exclosure, the significant differences in total plant biomass (treatment, $p = 0.003$, year $p = 0.024$) likely

resulted from the large differences in forb plus dwarf shrub biomass. The interaction between treatment and year was not significant for total plant biomass ($p = 0.435$).

Although the seasonal mean live:dead graminoid ratio inside the Penn's Cabin exclosure was significantly lower than it was outside in 1993, the following year there were no significant differences inside and outside the exclosure (treatment $p = 0.006$), and there was a large interaction between treatment and month (Fig. 2.3). The difference between years was highly significant ($p < 0.001$), as was the treatment by year interaction ($p = 0.001$).

Mid-Elevation Short-Term Exclosure - Syke's Ridge Site

During the 1993 and 1994 growing seasons, only the forb and dwarf shrub (live plus dead biomass) component was not significantly different inside and outside this exclosure (Table 2.1, Appendix A2.4). Differences in seasonal mean live grass biomass, however, were not evident until 1994 (Fig. 2.4). In 1993, seasonal mean live grass biomass inside the exclosure was 18 ± 3 g/m^2, whereas outside the exclosure it was 17 ± 5 g/m^2. The fence height was raised at the end of the 1993 growing season, and significant differences in live graminoid biomass appeared in 1994 ($p = 0.001$, Fig. 2.4). In 1994, there was 13 ± 3 g/m^2 inside the exclosure and 9 ± 2 g/m^2 outside.

Although seasonal means for dead grass biomass (Appendix A2.4) were approximately equal in 1993 and 1994 ($p = 0.224$), they were significantly higher inside the exclosure, 25 ± 7 g/m^2 and 28 ± 2 g/m^2 for 1993 and 1994, respectively, than outside, where they were 15 ± 1 g/m^2 and 17 ± 2 g/m^2 ($p < 0.001$).

Seasonal mean live:dead grass ratios (Appendix A2.3) were significantly higher outside this exclosure during both the 1993 and 1994 growing seasons ($p < 0.001$). In 1993, the mean ratio was 1.01 ± 0.20 inside and 1.51 ± 0.38 outside the exclosure. The mean ratio dropped to 0.54 ± 0.11 inside the exclosure and 0.74 ± 0.14 outside in 1994. Mean live:dead ratios were also significantly higher in 1993 than in 1994 ($p < 0.001$).

Although no statistical difference showed up between treatments ($p = 0.119$), possibly because of the relatively high variance associated with the data, a trend was apparent in live forb plus dwarf shrub biomass. Seasonal means were consistently higher inside the exclosure than outside: 49 ± 33 g/m^2 and 65 ± 28 g/m^2 inside the exclosure in 1993 and 1994, respectively, and 32 ± 21 g/m^2 and 55 ± 19 g/m^2 outside. Means were significantly higher in 1994 than in 1993 ($p = 0.048$).

Lower Elevation Short-Term Exclosures - North and South Dryhead Herd Area Sites

Again, except for the forb/dwarf shrub category, plant biomass was significantly greater inside these two short-term exclosures than outside during the 1993 and 1994 growing seasons (Table 2.1). At the less productive North Dryhead site, differences in live and dead grass biomass inside and outside the exclosure were especially noticeable (Figs. 2.5a and 2.5b and Appendix A2.5). During the 1993 growing season, the seasonal mean biomass of live grass inside the north exclosure was 11 ± 2 g/m^2, whereas outside it was 8 ± 1 g/m^2. In 1994, mean live grass biomass was about half of what it was during 1993; 6 ± 1 g/m^2 inside and 3 ± 1 g/m^2 outside the exclosure (treatment effect, $p < 0.001$ and year effect, $p < 0.001$). Similarly, there was more dead grass inside the exclosure than outside during both years ($p < 0.001$), but there was no significant difference

between years ($p = 0.073$). Inside the exclosure during 1993, the seasonal mean dead grass biomass was 16 ± 3 g/m^2, whereas outside it was 6 ± 1 g/m^2. In 1994, the seasonal mean for dead grass was 21 ± 3 g/m^2 inside, and 4 ± 1 g/m^2 outside the exclosure.

Seasonal mean live:dead graminoid biomass ratios at the North Dryhead site (Fig. 2.6) were significantly higher outside than inside the exclosure (treatment effect, $p < 0.001$, see Table 2.1 and Appendix A2.6). In 1993, seasonal mean live:dead ratios were 1.32 ± 0.16 outside and 0.58 ± 0.03 inside the exclosure. During 1994, those ratios dropped to 0.84 ± 0.16 outside and 0.35 ± 0.04 inside (year effect, $p < 0.001$).

At the South Dryhead site, differences in seasonal mean live grass biomass between treatments were significant ($p = 0.011$). However, the treatment by year interaction was also significant (Table 2.1). Inside the exclosure the mean was 20 ± 2 g/m^2 during the 1993 growing season, and was 19 ± 1 g/m^2 outside. . Mean live grass biomass in 1994 was 12 ± 2 g/m^2 inside the exclosure, and 5 ± 1 g/m^2 outside the exclosure. In 1994 live grass biomass was lower than it was in 1993 ($p < 0.001$), as it was at most other sites (Appendix A2.7).

Seasonal mean graminoid biomass live:dead ratios at the South Dryhead site (Fig. 2.7, Appendix A2.6) were significantly higher outside the fenced plot than inside ($p < 0.001$). In 1993, ratios were 1.14 ± 0.09 outside and 0.91 ± 0.10 inside the exclosure. During the 1994 growing season, live:dead grass ratios were 1.14 ± 0.09 outside and 0.48 ± 0.05 inside the fenced plot. Live:dead ratios were significantly higher in 1993 than they were in 1994 ($p < 0.001$) Mean forb/dwarf shrub biomass was slightly greater outside than inside the exclosure at the South Dryhead site ($p = 0.053$). This

difference was more evident during 1994, although there was no significant interaction between treatment and year (Table 2.1). In 1993, seasonal mean forb/dwarf shrub biomass inside the exclosure was 33 ± 4 g/m^2, and outside it was 37 ± 5 g/m^2. Seasonal mean forb/dwarf shrub biomass was significantly lower during the 1994 growing season than it was in 1993 at the south site ($p = 0.006$): 19 ± 3 g/m^2 inside and 29 ± 6 g/m^2 outside the exclosure. There were no such trends at the North Dryhead site.

Lower Elevation - Sorenson Extension Site

I found unexpected differences in live graminoid biomass inside and outside this fenced area (Appendices A2.8 and A2.9). Seasonal mean live grass biomass was slightly, yet significantly, greater outside the fence than inside during the two year sampling period ($p = 0.015$), although there were also significant differences between the east and west plots ($p < 0.001$). The seasonal mean for live grass biomass averaged across the two adjacent sites (east and west) and four sampling dates in 1992 (just prior to the permanent removal of the wild horses) was 18 ± 2 g/m^2 inside the exclosure and 20 ± 2 g/m^2 outside. During 1993, after the horses were removed, mean live grass biomass was 12 ± 1 g/m^2 inside and 15 ± 1 g/m^2 outside the exclosure. Live grass biomass was significantly higher in 1992 ($p < 0.001$).

Dead grass biomass was significantly greater inside the exclosure ($p < 0.001$) during both years of sampling (Table 2.1, Appendices A2.8 and A2.9). In 1992, mean seasonal dead grass biomass inside the exclosure was 16 ± 2 g/m^2, whereas, outside it was 12 ± 2 g/m^2. Inside the exclosure in 1993, the mean seasonal biomass was 24 ± 2

g/m^2 and outside it was 20 ± 1 g/m^2. Dead grass biomass was significantly greater in 1993 than in 1992 ($p < 0.001$).

Seasonal mean live:dead grass ratios, averaged across east and west sites, (Fig. 2.8) were significantly greater outside than inside the exclosure (treatment; $p < 0.001$). In 1992, they averaged 1.35 ± 0.19 inside the exclosure and 2.10 ± 0.34 outside. In 1993, the ratios dropped to 0.69 ± 0.11 inside and 0.81 ± 0.03 outside the exclosure (Appendix A2.10). Differences in live:dead ratios between years were also significant ($p < 0.001$).

The biomass of forbs/dwarf shrubs was also greater outside the Sorenson exclosure during both years (treatment effect, $p < 0.001$), and was also greater during the 1993 than 1992 growing season ($p = 0.002$, see Appendices A2.8 and A2.9). The mean seasonal forb/dwarf shrub biomass inside the exclosure during 1992 was 24 ± 2 g/m^2 and was 35 ± 2 g/m^2 outside the exclosure. In 1993, the mean was 31 ± 3 g/m^2 inside, and 42 ± 3 g/m^2 outside.

Forage Nitrogen Content

During this investigation, no clear pattern emerged to describe the effects of herbivory on forage nitrogen content. I found no significant differences in nitrogen concentration of live C_3 graminoids inside and outside exclosures at the Penn's Cabin site ($p = 0.084$) and the North Dryhead site ($p = 0.488$) during the 1993 and 1994 growing seasons (Tables 2.1, and 2.2 and Appendix A2.11). Significant differences in nitrogen concentration between years did not exist at the Penn's Cabin site ($p = 0.546$), although these differences did occur at the North Dryhead site ($p = 0.027$). There also appears to

be little difference in N concentration of C_3 graminoids inside and outside the exclosures during the 1992 growing season at these sites. (Appendix A2.16). I detected no difference inside and outside the exclosure at the Sorenson Extension site during the 1992 and 1993 growing seasons ($p = 0.143$, Appendix A2.12). However, there was a significant difference between years at this site ($p = 0.006$).

Nitrogen concentration in C_3 graminoids was significantly higher outside than inside exclosures at two sites, Syke's Ridge ($p < 0.001$) and the South Dryhead site ($p = 0.003$, see Appendix A2.11). Differences between years did not show up at either Syke's Ridge ($p = 0.941$) or the South Dryhead ($p = 0.057$), although the treatment effect was significantly greater in 1994 than 1993 at South Dryhead (treatment by year interaction effect $p < 0.001$).

In contrast, N concentration was significantly higher in C_3 graminoids inside the exclosure than outside ($p = 0.004$) at the Forest Service site (Table 2.2, Appendix A2.11), but here too, there were no significant differences between years ($p = 0.340$). At the Forest Service site, the treatment effect was greater in 1993 than in 1994 (treatment by year interaction, $p = 0.031$). At all sites, nitrogen concentration in C_3 live graminoids was highest in May, and then decreased over the growing season (Fig. 2.9). Nitrogen concentration was also consistently higher in C_3 live graminoids at upper elevation sites than at lower elevation sites (Fig. 2.9).

Monthly mean nitrogen standing crop (g/m^2) of C_3 live graminoids for both upper and lower elevation sites during the study are presented in Appendix A2.17. At the Forest Service site, values appeared higher inside the exclosure than outside. In addition,

monthly mean nitrogen standing crop of C_3 graminoids (averaged across inside and outside plots for two upland and two lowland sites) was from two-to-five times higher at the upper sites than at lower sites (Fig.2.10).

Forage Utilization

Forage utilization was difficult to estimate because of the large variance associated with the samples. I was unable to detect any utilization (i.e., a significant difference in biomass inside and outside of the moveable exclosures) during the 1992 growing season. During 1993, however, there was significantly less graminoid biomass outside cages than inside at the Southeast Dryhead site, and in 1994 I detected significant grass utilization at the Northeast Dryhead and Forest Service sites (Table 2.3). In 1993, 12.1 ± 5.2 g/m^2 (or 44% of the total live + dead grass biomass) was removed at the lower elevation Southeast Dryhead site. In the 1994 growing season, animals apparently consumed 15.9 ± 7.0 g/m^2 of grass at the upper elevation Forest Service site (or 33% of the total grass biomass), and 2.9 ± 1.2 g/m^2 at the lower elevation Northeast Dryhead site (or 43% of the total grass biomass). Also in 1994, 48 ± 16.7 g/m^2 of forbs and dwarf shrubs were apparently consumed at the upper elevation site on the hillside opposite the Penn's Cabin exclosure. This figure represents 40% of the total forb and dwarf shrub biomass for that year.

Aboveground Net Primary Production

Throughout this three year study, total aboveground net primary production (ANPP) inside the exclosures was highest at the two upper elevation sites, Forest Service, where ANPP averaged across three years was 161 g/m^2 and Penn's Cabin, where mean

ANPP was 99 g/m^2 (Appendix A2.13). In the lowlands, ANPP averaged 50 g/m^2 at the North Dryhead site and 58 g/m^2 in the South Dryhead during the same period.

To determine whether productivity was higher inside the permanent exclosures than outside, I compared current year's aboveground plant biomass harvested in August (for 1993 and 1994) inside the Forest Service permanent exclosure to that harvested inside the moveable cages (outside the permanent exclosure) on the same date (Table 2.4). Production of current year's grass was significantly higher inside the permanent exclosure ($p < 0.01$), whereas there were no significant differences between fenced and unfenced plots in forbs/dwarf shrubs ($p = 0.243$) or total production ($p = 0.924$).

DISCUSSION

Aboveground Plant Biomass Dynamics

As an apparent result of grazing by ungulates in the PMWHR, total aboveground plant biomass was lower outside the permanent exclosures at all sites during the 1993-94 growing seasons, with the exception of an upper elevation site, Penn's Cabin, where total biomass was significantly higher outside the exclosure than inside. Biomass inside the fenced exclosure at Penn's Cabin site was 78% of the aboveground biomass on the adjacent plot outside. Data from the Penn's Cabin site suggest that ungulates did not graze much, if at all, on the adjacent control plot. In fact, we more often saw horses grazing across the ravine (at the more productive moveable exclosure site) than at the

permanent exclosure site itself. Aboveground plant biomass outside the other four permanent exclosures was generally maintained at 67 to 80% of the plant biomass found within the exclosures.

Total graminoid biomass was typically a higher percentage of aboveground biomass inside exclosures than outside, ranging from 41 to 61% of total biomass inside the two long-term exclosures in the upper elevation montane sites, and 30 to 32% outside those same exclosures. At the short-term exclosure sites in the Dryhead area, graminoid biomass comprised generally 45 to 54% of total biomass inside the fenced areas, as compared to 24 to 42% of plant biomass outside the fence. The decline in standing crop of live and dead grasses outside exclosures was likely the result of consumption by horses and sheep (Kissell et al. 1996, Duncan 1992, Reiner and Urness 1982). Graminoids were the major dietary component (79%) of horse diets in the summer (Kissell et al. 1996), although results from my offtake calculations suggest they also consumed significant quantities of forbs at the Penn's Cabin moveable exclosure site. Grasses also represented 41% of the summer diet of bighorn sheep (Kissell et al. 1996). A reduction in standing dead material will decrease litter accumulation, ultimately affecting microclimate and nutrient cycling (Coughenour 1991).

Live to dead ratios of grass biomass were as much as two to three times higher outside exclosures than inside, probably as a result of a reduction in the accumulation of live biomass, which could subsequently become standing dead biomass. Animals are also likely to feed more heavily on dead grass over the winter months. The diet of zebras in Ethiopia, during the dry season, reportedly consisted of from 84-89% dry grass

(current year's dead), and only 11-16% live, green grass (Abaturov et al. 1995). Ungulates also undoubtedly trample some dead grass material and litter into the soil. Higher live to dead ratios likely enhanced the overall nutritional quality of grass forage by increasing the availability of live tissue (Willms et al. 1980, 1981).

Forage Utilization

During the 1993 and 1994 growing seasons, grazing ungulates removed up to 26% of the herbaceous standing crop on unfenced plots in the PMWHR. Feral horses in other parts of the world have been reported to ingest anywhere from 3 to 20% of annual production (Duncan 1992, Keiper 1981, Welsh 1973, Table 2.5). In the grasslands of South Dakota, bison (*Bison bison*) consumed 1 - 16% of annual production (Coppock et al. 1983). In contrast, ungulates in the Serengeti reportedly removed 17 - 95% of annual production (McNaughton 1985) and geese removed 80% of annual production in marshes on Hudson Bay (Cargill and Jefferies 1984). Lacey and Van Poollen (1981) assumed a moderate level of grazing by livestock in western U. S. rangelands to be from 40 - 60% removal of current year's growth. Detling (1987) and Whicker and Detling (1988b) reported that on a world-wide basis, cattle and native large mammalian herbivores consume an average of 30-40% of aboveground net primary production. In comparison to these values, grazing intensity at the PMWHR would appear to have been light to moderate.

At three of the four sites where significant utilization was detected, graminoids were the primary functional group consumed. In 1994, however, ungulates apparently consumed almost 44% of the current year's production of forbs and dwarf shrubs on a

hillside across the ravine from the permanent exclosure site at the upper elevation Penn's Cabin moveable exclosure site, and at this site there was no detectable grass offtake. These findings were somewhat surprising, as horses, which were often observed feeding in this area, typically select grass species over other forage classes. Duncan (1992) reported that monocotyledons comprised more than 90% of the summer diet of feral horses in the Camargue, France. Zebras in Ethiopia consumed a 100% grass diet (Abaturov et al. 1995). Horses in Utah, however, utilized as much as 20% of forb production under conditions of heavy grazing pressure, but never consumed shrubs even under a heavy stocking regime (Reiner and Urness 1982). From 1992 to 1994, Kissell et al. (1996) reported that graminoids made up from 61 to 90% of the diet of feral horses in the Pryor Mountain Wild Horse Range, but they consumed a diet that was at times composed of up to 15% forbs, and up to 24% shrubs.

Although statistically significant utilization of herbaceous plant material was detected at four sites over the course of the study, I was unable to detect biomass removal at other sites. This may simply be the result of low grazing pressure at those sites or, alternatively, it may be a function of the spatial patchiness of plant biomass in the environment. Using the variance associated with the sampling technique at each site, I calculated sample sizes (see equation Appendix A2.19) that would have been necessary to detect 30% and 50% utilization at these sites (Appendices A2.19 and A2.20). The sampling effort would have had to have been increased by as much as ten times, at some sites, to detect a 30% utilization of grasses or forbs/dwarf shrubs. However, to detect utilization of 50% of production, the sample size used during this study would have been

sufficient to detect it at at least three sites. Thus, even though there was difficulty in detecting utilization of less than 30% of production, the sampling technique used during the study would have allowed me to measure utilization greater than 50% at least 44% of the time for graminoids, and 22% of the time for forbs and shrubs. Sample size undoubtedly should have been larger in this study for better estimates of utilization.

Aboveground Net Primary Production (ANPP)

I detected no effects of grazing on total aboveground plant production or on forb/dwarf shrub production at the upper elevation long-term Forest Service site,. Grazing appeared to have a negative effect on the production of grasses, however, even though grass offtake was fairly moderate (38% of grass production). Coughenour et al. (1985) found that the aboveground yield of a perennial grass was unaffected by defoliation, and Hobbs et al. (1996) and Coughenour (1991) found no effect of elk winter-grazing on herbaceous primary production.

McNaughton (1979, 1983) has argued that grazing can actually stimulate productivity of grasslands in the Serengeti up to twice the levels in ungrazed control plots because the compensatory growth response in plants can alleviate the deleterious effects of herbivores. Grazing stimulates the relative growth rate of defoliated plants so that the tissue lost to herbivory may be partially, fully, or overcompensated (Belsky 1986, Oesterheld and McNaughton 1991). Whether grazing has a beneficial or detrimental effect on plant growth is dependent on several factors, among them, the intensity and frequency of herbivory (Oesterheld 1992). High densities of herbivores can have negative effects on aboveground primary productivity because of high levels of

consumption and trampling (McNaughton et al. 1988). The level of stress at which plants grow and the length of time for recovery can also have effects on the compensatory response of plants (Oesterheld and McNaughton 1991). Plants exhibit lower compensatory responses at low levels of nutrient availability (McNaughton and Chapin 1985, Chapin and McNaughton 1989), and with a shorter recovery time, relative growth rates in plants were decreased (Oesterheld and McNaughton 1991). Semmartin and Oesterheld (1996) reported that patch size could also influence the outcome of the compensatory response in defoliated plants. The negative effects of herbivory on grass production at the Forest Service site were likely not due to a high grazing intensity, since grass offtake was undetectable in 1993 and was only moderate (44% of grass production) in 1994. Frequency of grazing, rather than intensity, may have instead decreased recovery time for plants, or there may have been low levels of nutrient availability at this site.

Researchers have long been arguing over the idea that herbivory can actually increase production in certain situations (Belsky 1986, McNaughton 1986, Hobbs and Swift 1988). However, Milchunas and Lauenroth (1993) reviewed 236 studies and found that most effects of grazing on ANPP were negative. In only 17% of the studies did grazing have a positive effect on productivity, and these were generally in cases of low grazing intensity and few years of treatment. Even though grazing intensity at the Forest Service site in 1993-94 was fairly low, the length of treatment there was relatively long, with at least 30 years of grazing by feral horses. Additionally, grazing levels in the past may have been more intense than those observed during this study.

Forage Nitrogen Concentration

Mean nitrogen concentration in C_3 live graminoids was consistently higher at the two upper elevation montane sites than it was at the two lower elevation Dryhead Area sites (Fig. 2.9). This difference may be the result of different grass species at upper and lower sites. For instance, *Pseudoroegneria spicata* (bluebunch wheatgrass) appeared to be the most abundant C_3 grass in the lowland Dryhead Herd Area, whereas, *Elymus lanceolatus*, *Festuca idahoensis*, and *Koeleria macrantha* were the abundant grasses at the upper montane sites (Fahnestock 1998). Differences in soils, temperatures, and precipitation between upper and lower elevation sites may also have played a role in levels of nitrogen concentration in plants, although these relationships were not investigated in this study.

The rate of food intake by herbivorous mammals depends not only on the nutrient requirements and digestion rates of the animal, but also on nutrient concentrations in, and the quantity of, available forage. Lactating ungulates typically require twice as much forage as those not lactating (Duncan 1992, Robbins 1993). Domestic horses require dietary protein levels above 12% for growth and lactation (NRC 1978), whereas deer and other ruminants require levels from 13% to 20% for maximum growth, and levels > 5% for maintenance (Robbins 1993, Holter et al. 1979, NRC 1978, NRC 1984, Smith et al. 1975, Ullrey et al. 1967). At lower elevation Dryhead sites, peak levels of protein in C_3 live grasses averaged 10.8% in May and then steadily declined over the growing season to 5.5% in August. At the two upper montane sites, however, protein levels in C_3 grasses averaged 15.8% in May, declining to an average of 9.0% in August. During this study,

the quality and quantity of grasses were always higher at the upper elevations, which may mean that these areas are capable of sustaining a greater number of ungulates during the summer and fall seasons. During the winter months, however, temperatures and snowfall accumulations at upper elevations likely increase the energy expenditures of animals there beyond those at the lower elevations. Kissell et al. (1996) reported that all horses used the lower elevations in winter, but that many migrated to higher elevations in the PMWHR during the summer months, presumably in response to seasonal changes in vegetation.

Grazing had mixed effects on nitrogen concentration of live C_3 graminoid tissue. Nitrogen concentration of C_3 grasses was higher on grazed plots at two sites, both of them short-term exclosures: one at mid-elevation (Syke's Ridge) and the other at the lower elevation South Dryhead site. Although I was unable to detect utilization at either of these sites, live grass biomass was significantly lower on unfenced plots at both sites, particularly in 1994. Several authors have documented increases in plant protein (or nitrogen) concentration as a result of grazing (Jameson 1963, Coppock et al. 1983, McNaughton 1985, Coughenour 1991). Milchunas et al. (1995) found that both nitrogen concentration and digestibility increased with defoliation in lightly, but not in heavily grazed treatments. Increases in nitrogen concentration may be a consequence of enhanced nitrogen uptake by defoliated plants (Ruess 1984), an increase in nitrogen availability which can result from input from dung and urine (Ruess and McNaughton 1987, Day and Detling 1990, Archer and Smeins 1991, Jaramillo and Detling 1992), or increased nitrogen mineralization (Holland and Detling 1990, McNaughton et al.1997).

In this study, there were no effects of grazing on C_3 graminoid nitrogen concentration at three sites (Penn's Cabin, Sorenson Extension, or North Dryhead), but at the Forest Service site, nitrogen concentration was significantly higher in ungrazed C_3 grasses inside the exclosure. The concentration of nitrogen in graminoids inside the Forest Service exclosure may have been influenced by the presence of pocket gophers. Gopher mounds with evidence of recent activity were prevalent inside the exclosure throughout this study, and gopher mound soil has been reported to be higher in nitrogen availability (Huntly and Inouye 1988).

Vegetation in the PMWHR exhibited different levels of responses to herbivory. Plant response likely depended on such factors as: 1) plant species consumed, 2) elevation, 3) soil type, 4) precipitation, 5) temperature, 6) length of exclosure from ungulate herbivory, 7) frequency, timing, and intensity of grazing, 8) presence or absence of fossorial mammals, and 8) placement of exclosure. Differences in plant responses between upper and lower elevation sites were undoubtedly due to factors one through seven above. Differences in response between the two upper elevation sites, however, could have resulted from exclosure placement or location. The Forest Service site was situated in a grassy meadow that was quite homogeneous in appearance, where horses were frequently observed feeding. Penn's Cabin site, on the other hand, was located along a rocky drainage with heterogeneous, patchy vegetation, and apparent differences in soil types inside and outside the fence. Horses were more often observed here feeding across the drainage on a grassy hillside.

Results from this study lead me to agree with Hjalten et al. (1993), who concluded that we should expect a continuum of plant responses to herbivory. Perhaps, instead of always asking whether herbivory has positive or negative effects on the plants that are consumed, we should, as they suggest (Hjalten et al. 1993), place more emphasis on identifying the conditions under which we would expect different responses.

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Table 2.1. Effects of fenced exclosure on biomass and shoot N-concentration in vegetation during the 1993 and 1994 growing seasons (1992 and 1993 for Sorenson Extension site) at six sites in the Pryor Mountain Wild Horse Range.

Site	Factor	Live Grass Biomass	Dead Grass Biomass	Total Grass Biomass	Live:Dead Grass Biomass	Forb & Dwarf Shrub Biomass	Total Biomass	Nitrogen Conc.
Penn's Cabin	Exclosure	NS	NS	NS	**	**	**	NS
	Year	**	NS	NS	**	*	*	NS
	Interaction	NS	NS	NS	**	NS	NS	**
Forest Service	Exclosure	**	**	**	**	NS	**	**
	Year	NS	**	*	**	NS	NS	NS
	Interaction	NS	**	**	NS	NS	NS	**
Syke's Ridge	Exclosure	**	**	**	**	NS	**	**
	Year	**	NS	NS	**	*	NS	NS
	Interaction	NS	NS	NS	NS	NS	NS	NS
North Dryhead	Exclosure	**	**	**	**	NS	**	NS
	Year	**	NS	**	**	NS	NS	*
	Interaction	NS	NS	NS	NS	NS	NS	**
South Dryhead	Exclosure	*	**	**	**	NS	*	**
	Year	**	NS	NS	**	**	**	NS
	Interaction	*	**	**	**	NS	*	**

Table 2.1 continued on next page.

Table 2.1 continued.

Sorenson Extension	Exclosure	*	**	NS	**	**	**	NS
(1992 - 1993)	Year	**	**	NS	**	**	**	**
	Interaction	NS	NS	NS	NS	NS	NS	NS

*0.01 < p ≤ 0.05, **p < 0.01, NS - No significant difference

Table 2.2 Seasonal mean nitrogen concentration (± SE) of C_3 live graminoids inside and outside permanent exclosure sites in the Pryor Mountain Wild Horse Range.

Site	Year	Exclosure	Outside
Upper Elevation			
Forest Service	1993	2.09 ± 0.3	1.73 ± 0.3
	1994	2.01 ± 0.5	1.95 ± 0.4
Penn's Cabin	1993	1.88 ± 0.2	1.64 ± 0.1
	1994	1.77 ± 0.4	1.82 ± 0.3
Syke's Ridge	1993	1.50 ± 0.1	1.66 ± 0.2
	1994	1.48 ± 0.2	1.67 ± 0.3
Lower Elevation			
North Dryhead	1993	1.19 ± 0.2	1.12 ± 0.2
	1994	1.17 ± 0.2	1.28 ± 0.2
South Dryhead	1993	1.20 ± 0.1	1.17 ± 0.1
	1994	1.14 ± 0.2	1.34 ± 0.2
Sorenson East	1992	1.08 ± 0.2	1.01 ± 0.1
	1993	1.19 ± 0.1	1.05 ± 0.1
Sorenson West	1992	1.00 ± 0.2	1.03 ± 0.2
	1993	1.12 ± 0.1	1.10 ± 0.1

Table 2.3. Estimated forage utilization ($g/m^2 \pm SE$) at upper and lower elevation sites in the Pryor Mountain Wild Horse Range. Values were calculated using data from moveable exclosures for August 1993-94.

Year	Elevation	Site	Grass Utilization	P-Value	Forb/Shrub Utilization	P-Value
1993	Lower	NE Dryhead	1.9 ± 4.1	0.643	-9.5 ± 7.5	0.232
		SE Dryhead	12.1 ± 5.2	0.041	-1.7 ± 5.6	0.770
		SW Dryhead	1.4 ± 3.2	0.683	-20.0 ± 6.8	0.014
	Upper	Forest Service	5.9 ± 8.1	0.479	55.1 ± 35.3	0.157
		Penn's Cabin	-14.6 ± 21.2	0.508	41.9 ± 24.2	0.111
		Syke's Ridge	7.4 ± 8.6	0.408	48.1 ± 59.4	0.435
1994	Lower	NE Dryhead	2.9 ± 1.2	0.033	0.1 ± 2.1	0.986
	Upper	Forest Service	15.9 ± 7.0	0.045	8.7 ± 18.7	0.651
		Penn's Cabin	17.2 ± 19.7	0.401	48.0 ± 16.7	0.015

Table 2.4. Estimated aboveground plant production ($g/m^2 \pm SE$) inside and outside (within the moveable cages) the permanent exclosure at the Forest Service Site during the 1993 and 1994 growing seasons.

Plant Material	Year	Inside Exclosure	Outside Exclosure
Live + Recent Dead Grass	1993	67.5 ± 6.5	29.6 ± 3.5
	1994	63.3 ± 12.5	38.4 ± 3.2
Forbs & Dwarf Shrubs	1993	61.2 ± 8.0	135.4 ± 32.5
	1994	88.6 ± 33.3	72.5 ± 13.2
Total Production	1993	128.8 ± 17.5	164.9 ± 33.3
	1994	151.9 ± 33.7	110.9 ± 13.3

Table 2.5. Utilization removed by grazers and browsers as a percentage of current year's production.

Location	Herbivore	Plant Material Removed	% Production Removed	Reference
France	Feral horses	herbaceous	3 - 20	Duncan 1992
Virginia	Feral ponies	herbaceous	11	Keiper 1981
Nova Scotia	Feral horses	herbaceous	13	Welsh 1975
Montana	Feral horses and bighorn sheep	herbaceous	0 - 26	This study
South Dakota	Bison	herbaceous	1 - 16	Coppock et al. 1983
Serengeti	Ungulates	herbaceous	17 - 95	McNaughton 1985
Manitoba	Geese	herbaceous	80	Cargill and Jefferies 1984
Isle Royale	Moose	woody	0 - 3	McInnes et al. 1992
Montana	Bighorn sheep and mule deer	woody	0 - 4	This study, Chapter 2

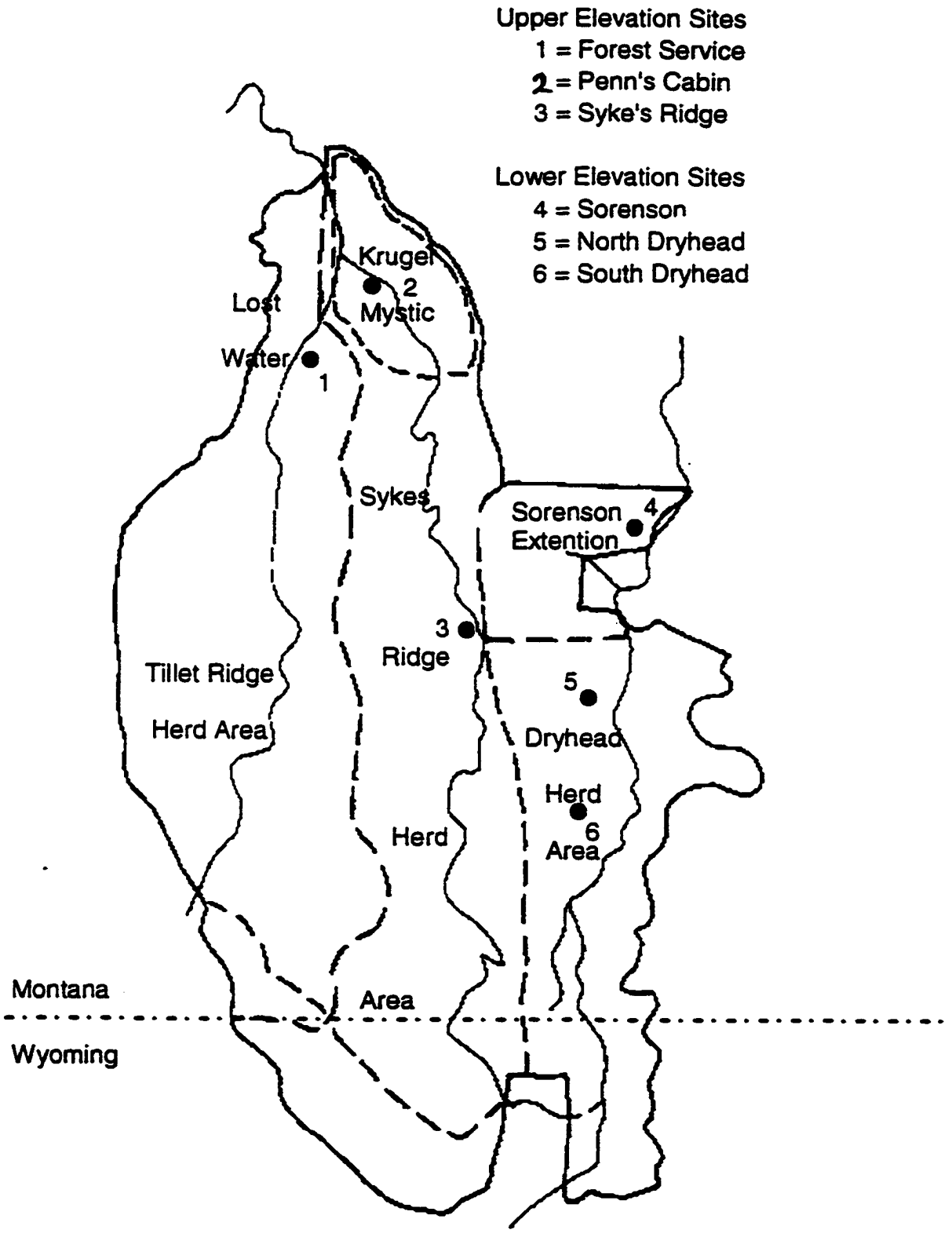

Figure 2.1 Map of upper and lower elevation exclosure sites in the Pryor Mountain Wild Horse Range.

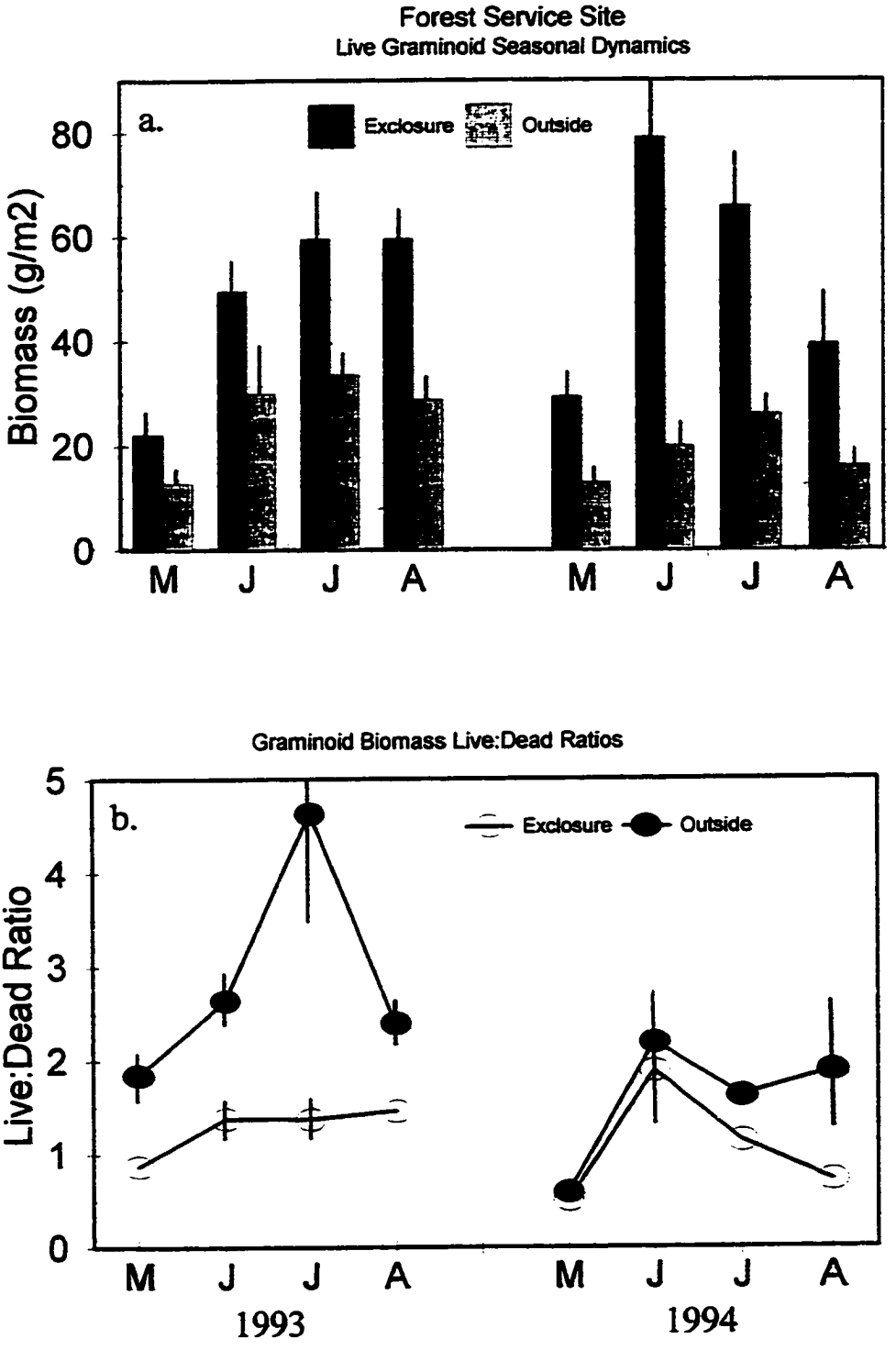

Figure 2.2. Monthly mean live graminoid biomass (a.) and live:dead graminoid biomass ratios (b.) inside and outside the Forest Service exclosure (± SE) from May, 1993 to August, 1994 in the Pryor Mountain Wild Horse Range.

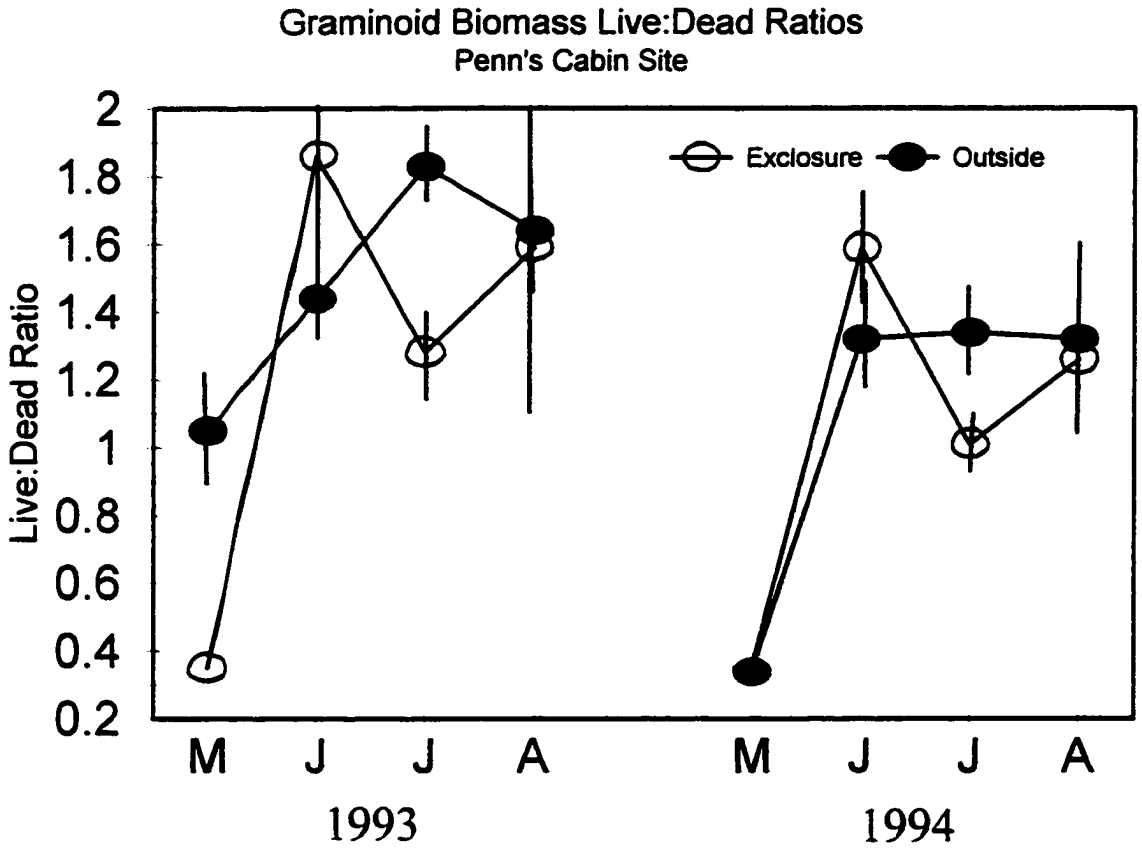

Figure 2.3. Monthly mean graminoid biomass live:dead ratios (± SE) inside and outside the Penn's Cabin exclosure from May, 1993 through August, 1994 in the Pryor Mountain Wild Horse Range.

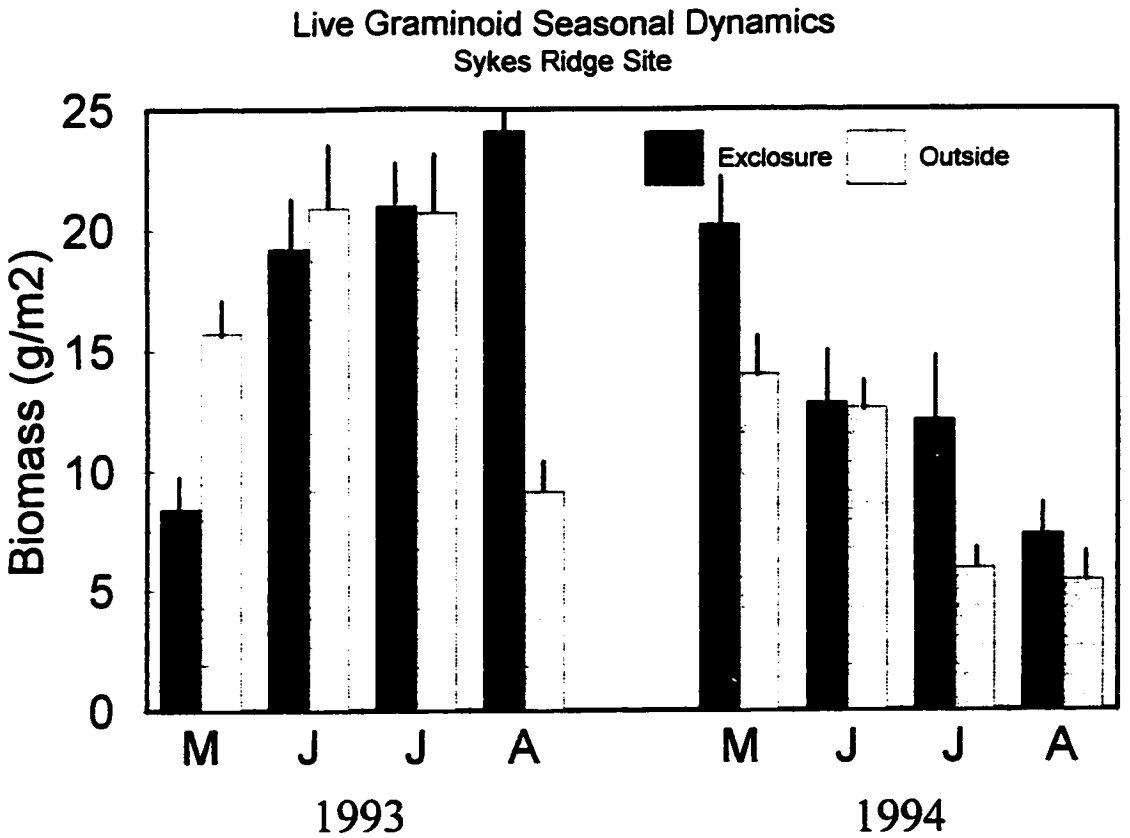

Figure 2.4. Monthly mean live graminoid biomass (± SE) inside and outside the Syke's Ridge exclosure from May, 1993 through August, 1994 in the Pryor Mountain Wild Horse Range.

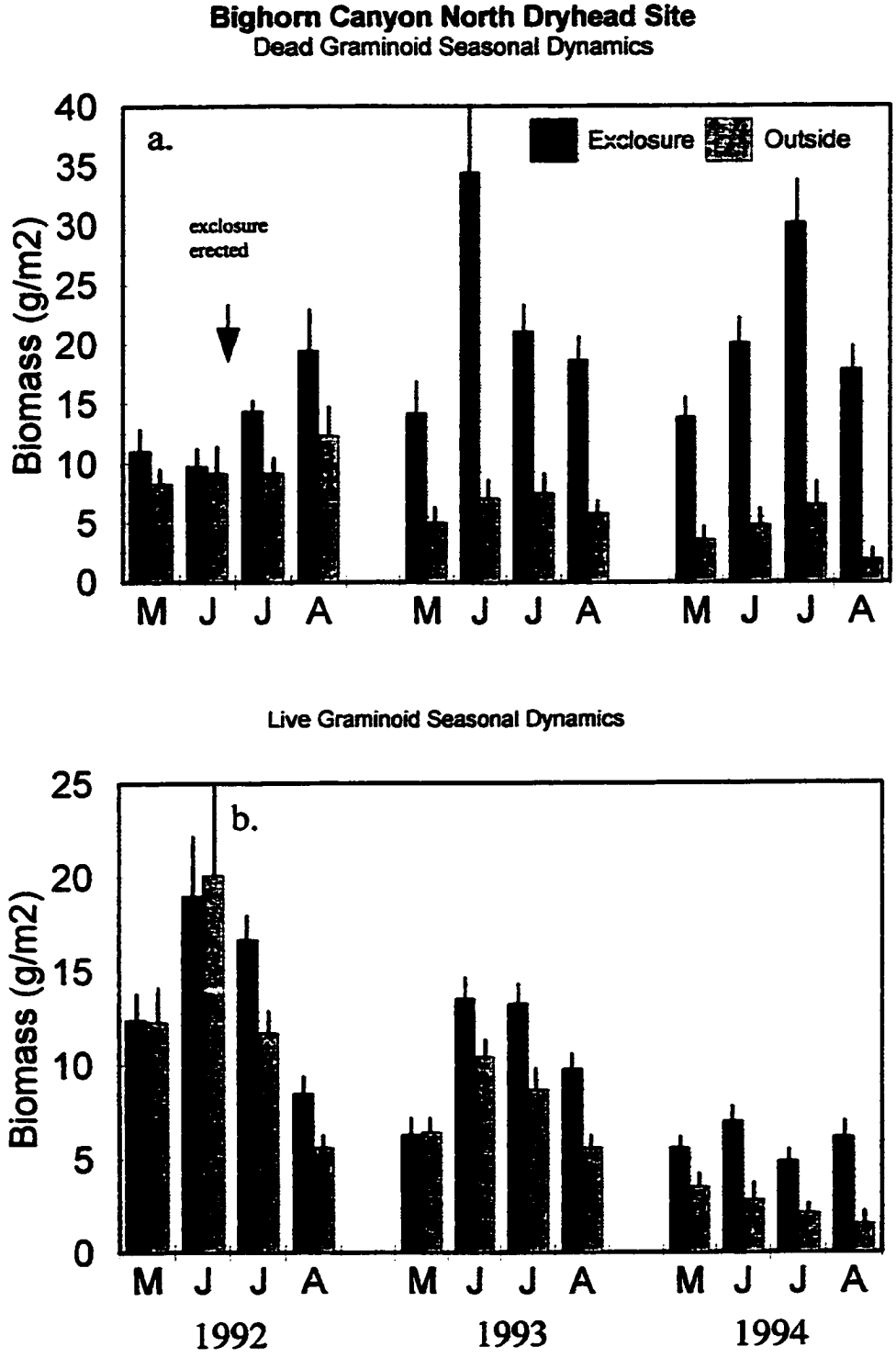

Figure 2.5. Mean monthly dead graminoid (a.) and live graminoid (b.) biomass (±SE) inside and outside the North Dryhead exclosure from June, 1992 to August, 1994 in the Pryor Mountain Wild Horse Range.

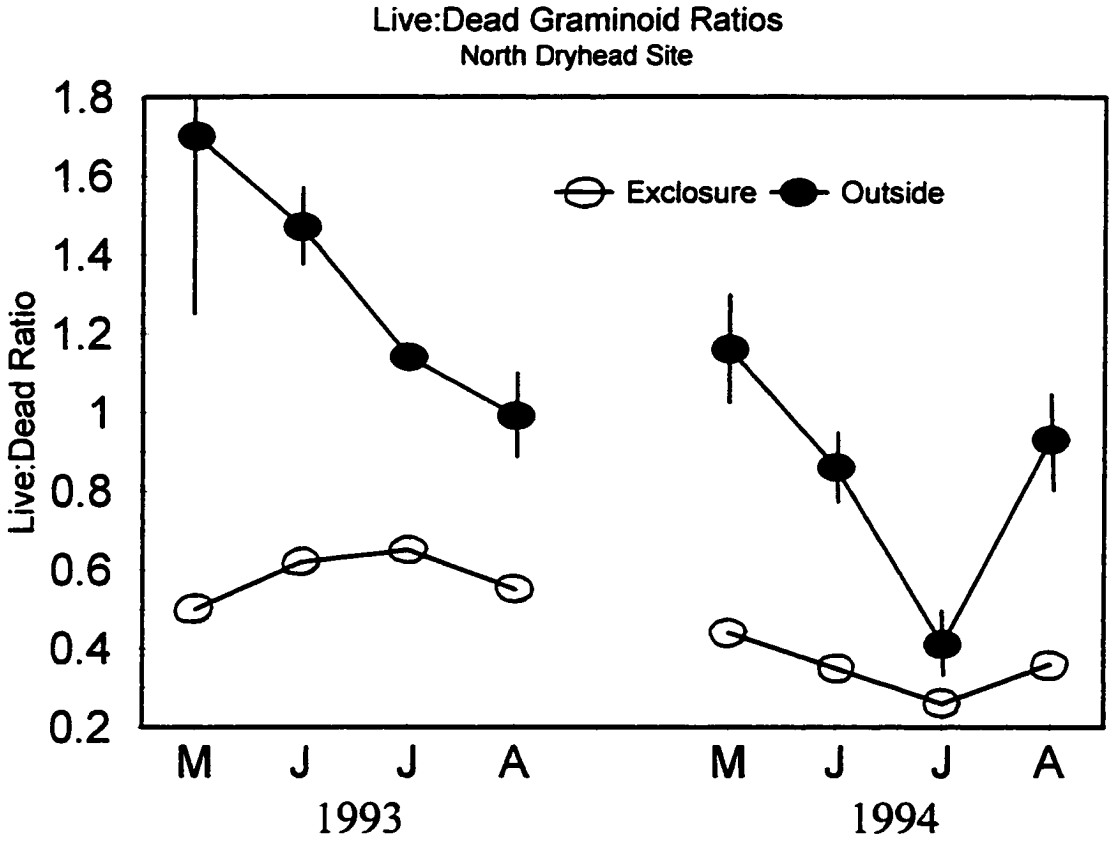

Figure 2.6. Monthly mean graminoid biomass live:dead ratios (±SE) inside and outside the North Dryhead exclosure from May, 1993 to August, 1994 in the Pryor Mountain Wild Horse Range.

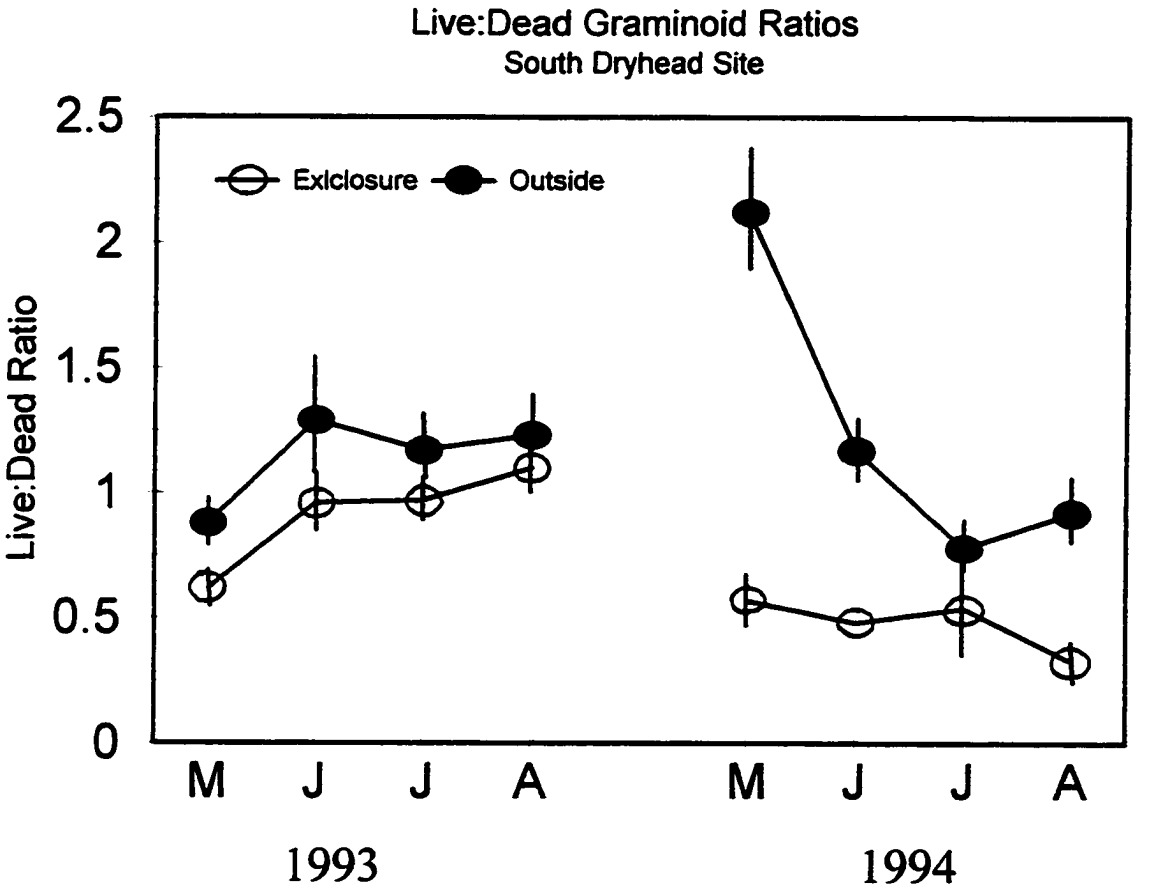

Figure 2.7. Monthly mean graminoid biomass live:dead ratios (± SE) inside and outside the South Dryhead exclosure from May, 1993 to August, 1994 in the Pryor Mountain Wild Horse Range.

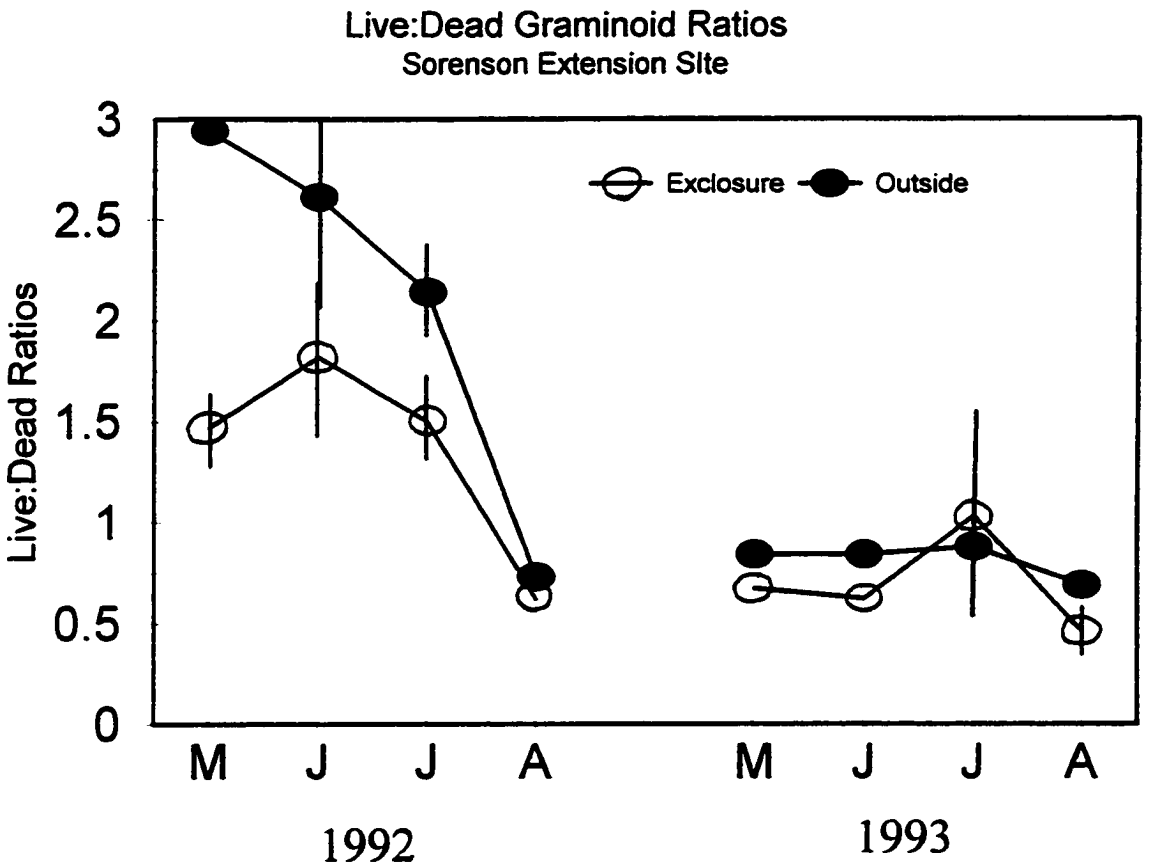

Figure 2.8. Monthly mean graminoid biomass live:dead ratios (± SE) outside and inside the Sorenson Extension exclosure from May, 1992 to August, 1994 in the Pryor Mountain Wild Horse Range. Live:dead ratios are averaged across the east and west sites for each month.

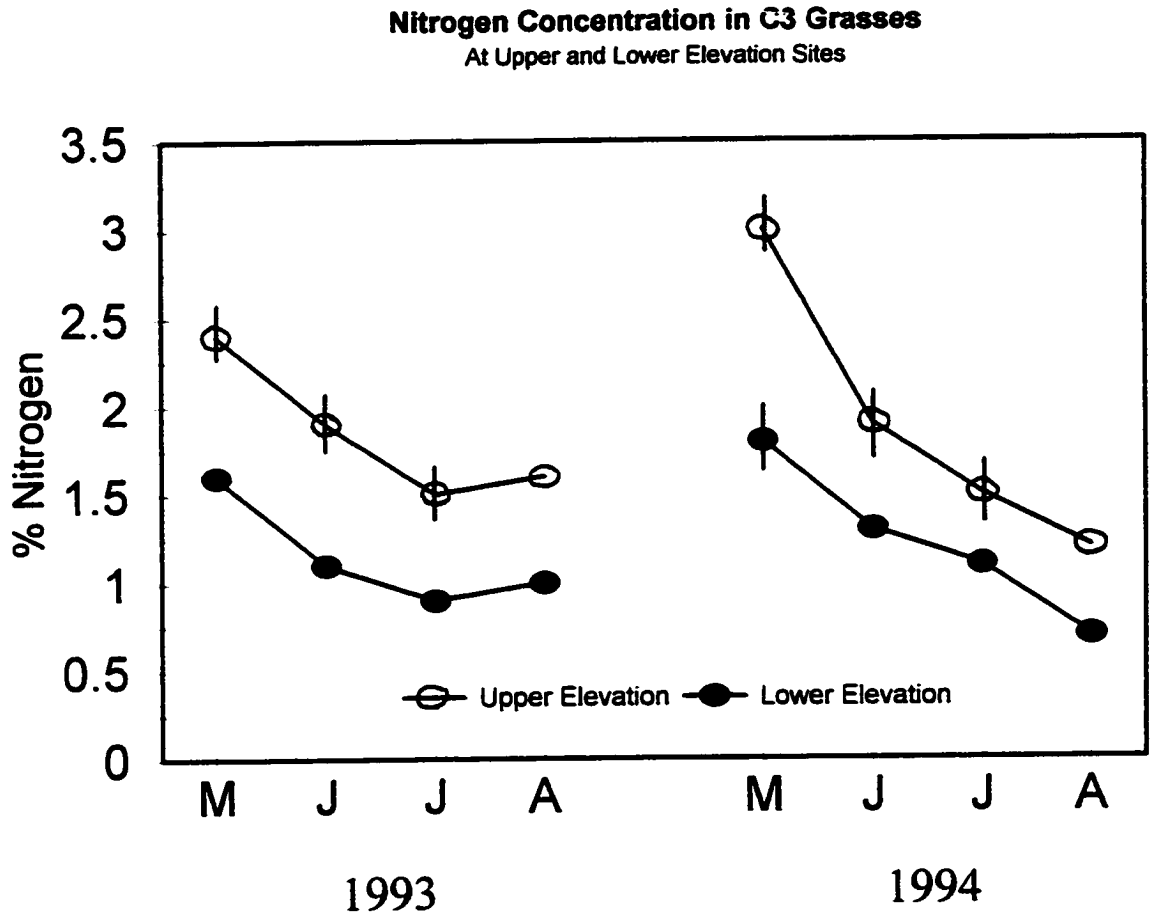

Figure 2.9. Mean nitrogen concentration (± SE) in C_3 live graminoids averaged across 2 upper elevation sites (Forest Service and Penn's Cabin) and 2 lower elevation sites (North and South Dryhead) for the months of May, June, July, and August during 1993 and 1994 in the Pryor Mountain Wild Horse Range. Values are averaged across plots inside and outside exclosures.

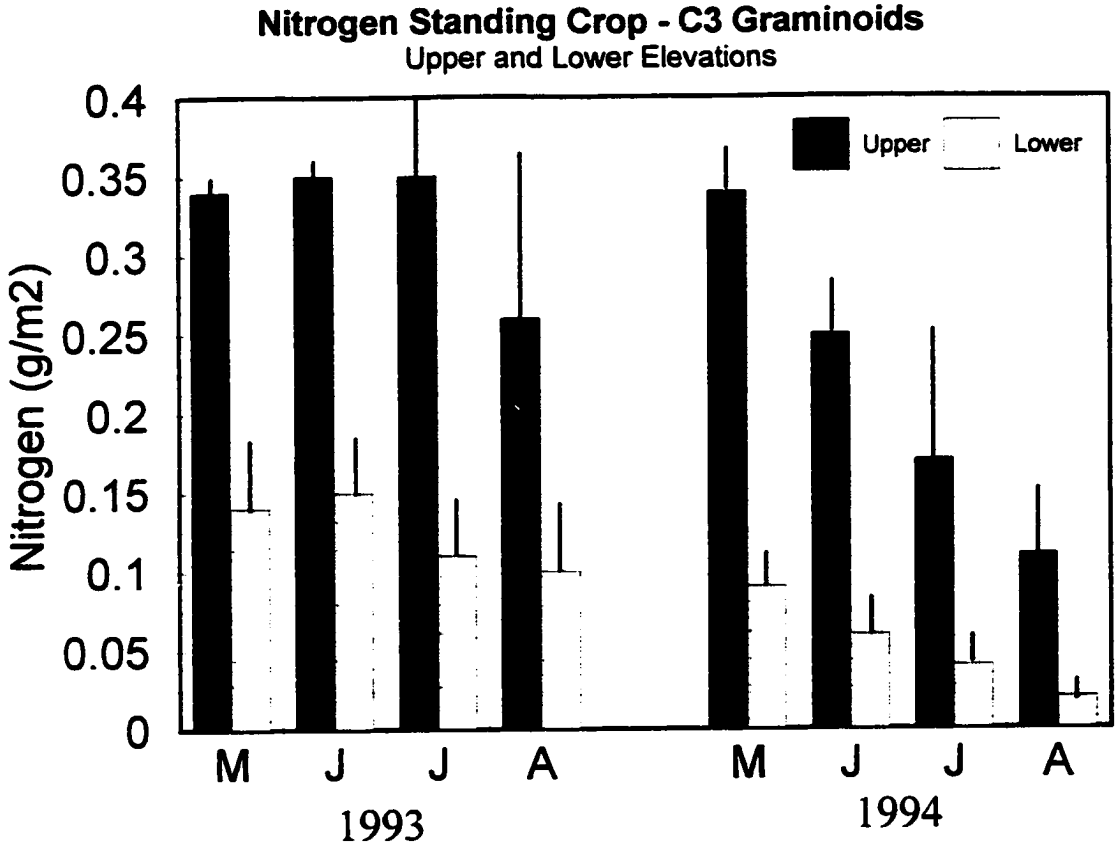

Figure 2.10. Monthly mean nitrogen standing crop ($g/m^2 \pm SE$) of C_3 graminoids averaged across 2 upper elevation (Forest Service and Penn's Cabin) and 2 lower elevation sites (North and South Dryhead) for 1993 and 1994 in the Pryor Mountain Wild Horse Range.

APPENDIX 2.1

Table A2.1. Mean plant biomass ($g/m^2 \pm SE$) at the Forest Service site during the 1993 and 1994 growing seasons in the Pryor Mountain Wild Horse Range.

Plot	Date	Live Graminoids	Total Dead Graminoids	Live Forbs & Shrubs	Dead Forbs & Shrubs	Total Biomass
Exclosure	5/93	22.1 ± 1.8	29.8 ± 4.4	38.8 ± 4.6	7.8 ± 3.8	98.5 ± 8.2
Outside		12.7 ± 1.4	8.9 ± 1.4	51.8 ± 5.6	5.7 ± 2.7	79.1 ± 8.3
Exclosure	6/93	49.6 ± 5.9	37.3 ± 5.4	47.9 ± 4.3	6.3 ± 1.3	136.1 ± 9.9
Outside		29.9 ± 8.0	13.1 ± 3.8	78.6 ± 11.4	9.2 ± 1.8	130.8 ± 18.8
Exclosure	7/93	59.5 ± 8.1	52.9 ± 12.0	95.4 ± 12.4	23.2 ± 5.4	231.0 ± 18.3
Outside		33.5 ± 2.4	13.4 ± 2.7	89.9 ± 15.2	5.8 ± 1.9	142.5 ± 17.4
Exclosure	8/93	59.6 ± 5.3	44.2 ± 5.2	50.1 ± 5.9	11.1 ± 3.7	165.0 ± 14.1
Outside		28.7 ± 3.3	13.1 ± 1.9	65.1 ± 5.9	15.1 ± 3.9	122.1 ± 9.0
Exclosure	5/94	29.3 ± 4.0	82.2 ± 13.1	46.6 ± 9.4	16.6 ± 5.1	174.7 ± 22.2
Outside		12.9 ± 1.4	24.6 ± 3.7	54.0 ± 9.8	23.7 ± 8.0	115.1 ± 15.9
Exclosure	6/94	79.1 ± 23.3	64.2 ± 16.2	45.1 ± 10.4	9.7 ± 3.6	198.1 ± 33.0
Outside		19.8 ± 3.6	10.8 ± 1.9	87.7 ± 13.9	11.8 ± 4.1	130.1 ± 20.5
Exclosure	7/94	65.8 ± 9.0	63.8 ± 10.9	48.2 ± 8.0	17.2 ± 4.3	194.9 ± 22.4
Outside		25.9 ± 2.7	16.3 ± 1.5	63.1 ± 15.8	20.7 ± 4.3	126.1 ± 18.2
Exclosure	8/94	39.4 ± 8.5	61.8 ± 11.8	60.6 ± 22.8	28.0 ± 12.0	189.8 ± 36.8
Outside		15.9 ± 2.3	16.1 ± 3.6	55.4 ± 23.7	8.5 ± 1.5	95.9 ± 22.4

Table A2.2. Live:dead graminoid ratios for three upper elevation exclosures in the Pryor Mountain Wild Horse Range.

Date	Plot	Penn's Cabin	Forest Service	Syke's Ridge
5/92	Exclosure	NA	NA	NA
	Outside	NA	NA	NA
6/92	Exclosure	NA	8.35 ± 3.14	3.11 ±0.27
	Outside	NA	12.09 ± 3.48	3.45 ± 0.41
7/92	Exclosure	2.06 ± 0.25	2.89 ± 0.45	1.30 ± 0.25
	Outside	2.81 ± 0.79	2.70 ± 0.61	1.65 ± 0.14
8/92	Exclosure	0.81 ± 0.07	1.04 ± 0.12	0.77 ± 0.12
	Outside	1.16 ± 0.22	1.49 ± 0.67	1.34 ± 0.13
5/93	Exclosure	0.35 ± 0.04	0.87 ± 0.11	1.13 ± 0.11
	Outside	1.05 ± 0.16	1.84 ± 0.32	1.09 ± 0.07
6/93	Exclosure	1.86 ± 0.50	1.38 ± 0.16	1.50 ± 0.13
	Outside	1.44 ± 0.14	2.64 ± 0.34	2.28 ± 0.27
7/93	Exclosure	1.28 ± 0.14	1.37 ± 0.19	0.91 ± 0.05
	Outside	1.83 ± 0.13	4.63 ± 1.25	2.00 ± 0.49
8/93	Exclosure	1.59 ± 0.55	1.46 ± 0.13	0.53 ± 0.06
	Outside	1.64 ± 0.18	2.40 ± 0.19	0.67 ± 0.05
5/94	Exclosure	0.35 ± 0.05	0.50 ± 0.11	0.82 ± 0.10
	Outside	0.34 ± 0.04	0.59 ± 0.07	0.97 ± 0.10
6/94	Exclosure	1.59 ± 0.19	1.89 ± 0.85	0.63 ± 0.05
	Outside	1.32 ± 0.18	2.19 ± 0.31	0.93 ± 0.08
7/94	Exclosure	1.01 ± 0.09	1.14 ± 0.13	0.38 ± 0.03
	Outside	1.34 ± 0.17	1.62 ± 0.10	0.38 ± 0.04
8/94	Exclosure	1.26 ± 0.13	0.72 ± 0.08	0.34 ± 0.18
	Outside	1.32 ± 0.28	1.89 ± 0.78	0.68 ± 0.14

Table A2.3. Mean plant biomass ($g/m^2 \pm SE$) at the Penn's Cabin site during the 1993 and 1994 growing seasons in the Pryor Mountain Wild Horse Range.

Plot	Date	Live Grass	Total Dead Grass	Live Forbs & Shrubs	Dead Forbs & Shrubs	Total (L+D) Biomass
Exclosure	5/93	8.4 ± 1.4	24.1 ± 2.9	21.4 ± 5.8	7.7 ± 4.2	61.6 ± 12.9
Outside		18.2 ± 3.8	19.7 ± 4.4	35.5 ± 3.3	5.8 ± 2.9	79.3 ± 10.8
Exclosure	6/93	19.7 ± 3.0	16.4 ± 3.3	57.1 ± 9.9	8.1 ± 2.6	101.3 ± 12.5
Outside		23.5 ± 3.7	19.0 ± 4.0	81.9 ± 12.9	9.2 ± 2.9	133.6 ± 19.6
Exclosure	7/93	32.2 ± 6.8	29.0 ± 6.3	69.3 ± 9.5	13.0 ± 3.6	143.5 ± 22.7
Outside		24.2 ± 4.1	15.1 ± 3.3	116.0 ± 14.7	17.9 ± 5.3	173.2 ± 23.2
Exclosure	8/93	24.6 ± 5.5	22.0 ± 5.0	75.5 ± 14.2	7.8 ± 2.6	129.8 ± 18.1
Outside		24.5 ± 3.9	17.7 ± 4.3	73.6 ± 13.7	13.1 ± 2.9	128.8 ± 16.4
Exclosure	5/94	7.1 ± 1.6	27.8 ± 10.6	26.5 ± 4.6	5.1 ± 1.6	66.5 ± 11.5
Outside		10.9 ± 1.9	34.2 ± 5.6	51.8 ± 10.5	45.0 ± 11.8	142.0 ± 19.5
Exclosure	6/94	16.9 ± 2.7	13.6 ± 3.7	44.2 ± 5.6	5.5 ± 2.1	80.3 ± 8.9
Outside		15.9 ± 2.4	15.2 ± 3.1	90.5 ± 14.6	6.6 ± 1.4	128.2 ± 16.6
Exclosure	7/94	29.1 ± 11.8	33.6 ± 15.5	45.9 ± 7.4	4.1 ± 1.1	112.7 ± 31.0
Outside		17.9 ± 3.8	14.3 ± 2.4	79.0 ± 13.9	10.8 ± 4.5	122.0 ± 21.1
Exclosure	8/94	13.2 ± 2.3	10.9 ± 1.9	42.4 ± 5.3	3.8 ± 1.2	70.3 ± 7.6
Outside		12.3 ± 2.5	13.3 ± 3.2	37.5 ± 4.7	7.3 ± 3.0	70.4 ± 8.6

Table A2.4. Mean plant biomass ($g/m^2 \pm SE$) at the Syke's Ridge site during the 1993 and 1994 growing seasons in the Pryor Mountain Wild Horse Range.

Plot	Date	Live Graminoids	Total Dead Graminoids	Live Forbs & Shrubs	Dead Forbs & Shrubs	Total (L+D) Biomass
Exclosure	5/93	8.4 ± 1.4	24.1 ± 2.9	21.4 ± 5.8	7.7 ± 4.2	61.6 ± 12.9
Outside		15.7 ± 1.1	14.7 ± 1.1	10.5 ± 3.6	tr.	41.0 ± 4.1
Exclosure	6/93	19.2 ± 2.4	9.3 ± 2.1	7.8 ± 2.8	0.2 ± 0.1	37.2 ± 4.4
Outside		20.9 ± 2.4	16.2 ± 2.8	3.7 ± 1.2	tr.	40.8 ± 4.7
Exclosure	7/93	21.0 ± 1.5	24.0 ± 2.2	17.4 ± 5.6	0.4 ± 0.3	62.9 ± 6.5
Outside		20.7 ± 2.4	16.9 ± 3.5	17.8 ± 4.6	1.5 ± 0.5	56.9 ± 7.9
Exclosure	8/93	24.1 ± 8.0	43.7 ± 9.5	149.5 ± 30.2	34.1 ± 9.8	251.5 ± 51.7
Outside		9.1 ± 1.2	13.8 ± 1.5	95.1 ± 32.5	4.4 ± 4.2	122.4 ± 34.7
Exclosure	5/94	20.2 ± 2.2	30.1 ± 6.2	111.3 ± 27.1	14.4 ± 13.2	176.1 ± 34.2
Outside		14.0 ± 1.6	15.8 ± 2.2	88.3 ± 24.9	1.3 ± 0.6	119.5 ± 27.1
Exclosure	6/94	12.8 ± 2.6	29.3 ± 3.9	116.0 ± 34.2	9.3 ± 6.4	172.4 ± 35.0
Outside		12.6 ± 1.8	12.4 ± 2.2	87.9 ± 23.9	6.1 ± 2.4	121.1 ± 25.4
Exclosure	7/94	12.1 ± 3.1	30.2 ± 5.7	27.1 ± 9.4	1.6 ± 0.7	71.0 ± 15.0
Outside		5.9 ± 0.7	19.7 ± 4.0	34.3 ± 8.4	3.2 ± 1.4	63.1 ± 12.2
Exclosure	8/94	7.3 ± 1.1	20.8 ± 1.9	5.8 ± 1.6	tr.	33.9 ± 3.1
Outside		5.4 ± 0.9	21.3 ± 13.6	10.8 ± 2.8	tr.	37.5 ± 13.2

Table A2.5. Mean plant biomass ($g/m^2 \pm$ SE) at the North Dryhead site during the 1993 and 1994 growing seasons in the Pryor Mountain Wild Horse Refuge.

Plot	Date	C_3 Live Grass	Total C_3 Dead	C_4 Live Grass	Total C_4 Dead	Live Forbs & Shrubs	Dead Forbs & Shrubs	Total(L+D) Biomass
Exclosure	5/93	6.3 ± 1.1	14.2 ± 2.8	0	0	22.2 ± 4.4	0.3 ± 0.3	43.0 ± 6.4
Outside		6.4 ± 0.7	5.0 ± 0.6	0	0	30.4 ± 4.7	0.3 ± 0.2	42.1 ± 4.2
Exclosure	6/93	13.4 ± 1.6	21.4 ± 2.5	0.1 ± 0.1	0.1 ± 0.1	39.4 ± 9.4	0.4 ± 0.3	74.9 ± 11.2
Outside		10.3 ± 1.5	6.8 ± 0.9	0.2 ± 0.1	0.3 ± 0.2	25.2 ± 5.7	0.1 ± 0.1	42.8 ± 7.4
Exclosure	7/93	13.3 ± 1.3	21.1 ± 2.4	0	0	32.5 ± 7.6	3.4 ± 1.8	70.3 ± 9.7
Outside		8.7 ± 1.3	7.5 ± 1.0	0	0	37.7 ± 5.4	0	54.0 ± 5.8
Exclosure	8/93	9.8 ± 1.0	18.7 ± 2.5	0	0	32.3 ± 9.5	1.5 ± 0.6	62.3 ± 10.9
Outside		5.6 ± 0.9	5.8 ± 0.8	0	0	37.7 ± 5.0	1.6 ± 0.8	50.7 ± 5.5
Exclosure	5/94	5.6 ± 0.9	13.9 ± 2.4	0	0	36.4 ± 8.1	1.4 ± 0.7	57.3 ± 7.2
Outside		3.5 ± 0.6	3.1 ± 0.5	0.2 ± 0.1	0.5 ± 0.4	20.9 ± 5.6	1.1 ± 0.6	29.3 ± 5.9
Exclosure	6/94	7.0 ± 0.9	20.1 ± 2.0	0	0	32.4 ± 6.3	5.1 ± 1.2	64.6 ± 7.3
Outside		2.8 ± 0.5	3.9 ± 1.1	0.4 ± 0.3	0.7 ± 0.6	37.3 ± 7.3	1.5 ± 0.5	46.6 ± 7.5
Exclosure	7/94	4.9 ± 0.6	30.2 ± 4.1	0	0	38.4 ± 5.8	9.2 ± 2.8	73.6 ± 9.3
Outside		1.9 ± 0.4	3.7 ± 0.6	0.2 ± 0.2	0.7 ± 0.7	21.9 ± 2.8	6.4 ± 2.2	34.8 ± 4.5
Exclosure	8/94	6.1 ± 0.9	17.7 ± 2.6	0.1 ± 0.1	0.1 ± 0.1	29.6 ± 7.3	0	53.7 ± 9.0
Outside		1.5 ± 0.3	1.9 ± 0.5	0	0	33.0 ± 4.5	0	36.5 ± 4.9

Table A2.6. Live:dead grass ratios for two lower elevation sites, the North and South Dryhead, in the Pryor Mountain Wild Horse Range.

Date	Plot	North Dryhead	South Dryhead
5/92	Exclosure	1.23 ± 0.40	3.92 ± 0.69
	Outside	1.58 ± 0.14	2.62 ± 0.23
6/92	Exclosure	1.95 ± 0.32	2.27 ± 0.35
	Outside	3.32 ± 1.09	2.60 ± 1.09
7/92	Exclosure	1.18 ± 0.08	1.52 ± 0.21
	Outside	1.37 ± 0.21	1.36 ± 0.11
8/92	Exclosure	0.49 ± 0.05	0.86 ± 0.10
	Outside	0.49 ± 0.04	0.59 ± 0.14
5/93	Exclosure	0.50 ± 0.04	0.62 ± 0.06
	Outside	1.70 ± 0.47	0.88 ± 0.08
6/93	Exclosure	0.62 ± 0.03	0.96 ± 0.12
	Outside	1.47 ± 0.12	1.29 ± 0.25
7/93	Exclosure	0.65 ± 0.04	0.97 ± 0.08
	Outside	1.14 ± 0.06	1.17 ± 0.12
8/93	Exclosure	0.55 ± 0.03	1.10 ± 0.16
	Outside	0.99 ± 0.13	1.23 ± 0.18
5/94	Exclosure	0.44 ±0.04	0.57 ± 0.08
	Outside	1.16 ± 0.18	2.12 ± 0.26
6/94	Exclosure	0.35 ± 0.03	0.48 ± 0.04
	Outside	0.86 ± 0.10	1.17 ±0.12
7/94	Exclosure	0.26 ± 0.03	0.54 ± 0.23
	Outside	0.41 ± 0.08	0.78 ± 0.09
8/94	Exclosure	0.36 ± 0.03	0.33 ± 0.06
	Outside	0.93 ± 0.15	0.92 ± 0.15

Table A2.7. Mean plant biomass ($g/m^2 \pm SE$) at the South Dryhead site during the 1993 and 1994 growing seasons in the Pryor Mountain Wild Horse Range.

Plot	Date	C_3 Live Grass	Total C_3 Dead	C_4 Live Grass	Total C_4 Dead	Live Forbs & Shrubs	Dead Forbs & Shrubs	Total (L+D) Biomass
Exclosure	5/93	11.0 ± 2.2	18.3 ± 4.1	6.8 ± 2.9	12.7 ± 5.2	20.9 ± 4.4	1.2 ± 0.9	70.9 ± 6.5
Outside		11.2 ± 1.9	13.0 ± 2.7	4.7 ± 2.4	6.8 ± 3.7	28.1 ± 9.9	0.1 ± 0.1	63.8 ± 9.2
Exclosure	6/93	12.9 ± 2.6	14.4 ± 2.8	3.6 ± 1.5	3.7 ± 1.1	39.3 ± 7.5	0.9 ± 0.5	74.8 ± 6.1
Outside		18.1 ± 2.3	16.7 ± 2.9	3.4 ± 1.4	4.1 ± 1.9	50.2 ± 15.5	2.0 ± 1.6	94.5 ± 18.0
Exclosure	7/93	13.4 ± 2.0	17.7 ± 3.9	6.9 ± 3.6	4.9 ± 2.5	32.5 ± 5.3	1.8 ± 0.8	77.3 ± 7.1
Outside		15.2 ± 2.1	14.8 ± 3.0	2.3 ± 1.7	2.9 ± 2.0	33.6 ± 9.4	0.1 ± 0.1	68.9 ± 8.9
Exclosure	8/93	9.7 ± 1.4	13.2 ± 2.4	14.7 ± 6.0	0.4 ± 0.2	29.7 ± 7.2	4.2 ± 1.2	80.5 ± 10.4
Outside		13.7 ± 2.0	13.7 ± 2.3	7.4 ± 3.7	5.6 ± 2.9	31.2 ± 7.8	1.3 ± 0.8	72.9 ± 7.4
Exclosure	5/94	9.4 ± 1.9	13.8 ± 3.0	3.7 ± 1.7	6.3 ± 3.2	16.2 ± 2.6	1.8 ± 0.8	55.9 ± 8.7
Outside		5.8 ± 0.9	2.5 ± 0.5	0.7 ± 0.3	1.4 ± 0.9	13.8 ± 3.3	0.3 ± 0.1	24.6 ± 3.1
Exclosure	6/94	11.4 ± 1.3	22.6 ± 2.6	1.1 ± 0.6	5.9 ± 3.7	11.8 ± 2.3	1.1 ± 0.4	53.9 ± 7.2
Outside		4.8 ± 0.5	4.2 ± 0.4	0.3 ± 0.2	0.6 ± 0.4	36.6 ± 6.5	5.2 ± 1.2	51.8 ± 6.5
Exclosure	7/94	14.4 ± 6.6	23.0 ± 4.4	1.7 ± 1.2	7.1 ± 4.7	20.9 ± 5.3	4.7 ± 1.1	101.8 ± 35.1
Outside		5.2 ± 0.8	6.5 ± 1.5	0.5 ± 0.4	1.9 ± 1.2	32.7 ± 6.0	4.2 ± 1.1	51.0 ± 7.6
Exclosure	8/94	6.5 ± 1.5	20.4 ± 2.4	0.2 ± 0.2	1.7 ± 1.2	17.8 ± 3.2	0	66.6 ± 19.6

Table A2.8. Mean plant biomass ($g/m^2 \pm SE$) at the west Sorenson Extension Site during the 1992 and 1993 growing seasons in the Pryor Mountain Wild Horse Refuge.

Plot	Date	Live Grass	Total Dead Grass	Live Forbs & Shrubs	Dead Forbs & Shrubs	Total (L+D) Biomass
Exclosure	5/92	21.0 ± 2.6	14.4 ± 2.2	19.2 ± 3.1	0	54.6 ± 4.0
Outside		20.5 ± 2.4	7.7 ± 1.2	36.0 ± 10.5	0.4 ± 0.4	64.6 ± 8.6
Exclosure	6/92	24.9 ± 4.1	19.5 ± 3.8	14.3 ± 4.5	0.5 ± 0.5	59.2 ± 6.5
Outside		25.2 ± 6.0	8.4 ± 1.4	36.9 ± 7.1	tr.	70.6 ± 7.5
Exclosure	7/92	27.8 ± 2.6	22.1 ± 2.5	22.9 ± 4.2	0.4 ± 0.4	73.2 ± 6.3
Outside		27.6 ± 3.4	13.7 ± 2.0	28.3 ± 5.3	0	69.6 ± 6.9
Exclosure	8/92	12.8 ± 2.7	24.5 ± 5.4	25.3 ± 4.8	0.2 ± 0.2	62.7 ± 8.6
Outside		14.6 ± 2.0	20.6 ± 3.7	45.2 ± 6.9	0.2 ± 0.2	80.7 ± 6.1
Exclosure	5/93	10.3 ± 1.8	16.4 ± 2.9	24.5 ± 5.6	1.1 ± 0.7	52.3 ± 7.5
Outside		14.0 ± 1.9	17.7 ± 2.4	40.8 ± 6.3	1.1 ± 0.8	73.7 ± 5.6
Exclosure	6/93	15.8 ± 1.8	26.8 ± 3.2	25.0 ± 3.4	0.1 ± 0.1	67.7 ± 4.9
Outside		16.0 ± 2.7	21.2 ± 3.1	45.9 ± 7.3	0	83.1 ± 6.5
Exclosure	7/93	15.1 ± 1.8	27.9 ± 5.5	19.1 ± 3.5	1.1 ± 0.6	63.2 ± 7.8
Outside		19.5 ± 1.6	22.8 ± 3.4	45.2 ± 5.8	2.8 ± 1.5	90.4 ± 6.1
Exclosure	8/93	11.7 ± 1.1	24.1 ± 3.5	36.6 ± 9.2	4.2 ± 1.9	76.6 ± 12.5
Outside		16.9 ± 2.6	23.7 ± 3.3	49.4 ± 9.9	1.1 ± 0.5	91.2 ± 9.5

Table A2.9. Mean plant biomass ($g/m^2 \pm SE$) at the east Sorenson Extension Site during the 1992 and 1993 growing seasons in the Pryor Mountain Wild Horse Range.

Plot	Date	Live Grass	Total Dead Grass	Live Forbs & Shrubs	Dead Forbs & Shrubs	Total(L+D) Biomass
Exclosure	5/92	17.6 ± 2.4	15.8 ± 3.9	21.2 ± 4.1	0.2 ± 0.1	54.8 ± 4.5
Outside		20.8 ± 2.6	7.8 ± 1.4	26.2 ± 6.6	0.1 ± 0.1	54.9 ± 8.0
Exclosure	6/92	18.1 ± 2.2	11.4 ± 2.1	23.6 ± 4.6	0.5 ± 0.5	53.6 ± 7.1
Outside		19.4 ± 2.3	9.9 ± 1.0	40.0 ± 4.8	0	69.2 ± 3.8
Exclosure	7/92	14.6 ± 2.6	11.4 ± 2.5	34.0 ±5.2	0	60.1 ± 4.32
Outside		19.3 ± 2.4	10.8 ± 1.8	30.5 ± 5.0	0	60.6 ± 6.3
Exclosure	8/92	11.5 ± 1.1	22.2 ± 2.3	31.5 ± 3.8	0	65.2 ± 4.8
Outside		10.7 ± 1.6	16.7 ± 2.6	34.9 ± 6.7	0.4 ± 0.4	62.7 ± 6.0
Exclosure	5/93	7.4 ± 1.1	13.2 ± 2.7	35.1 ± 6.5	0.1 ± 0.1	55.7 ± 5.4
Outside		13.3 ± 1.9	16.6 ± 2.6	25.0 ± 5.4	0.6 ± 0.3	55.4 ± 6.7
Exclosure	6/93	13.6 ± 2.4	24.4 ± 5.2	43.1 ± 8.0	0.6 ± 0.3	81.8 ± 5.7
Outside		15.4 ± 2.1	20.0 ± 3.3	31.8 ± 5.2	0	67.2 ± 8.3
Exclosure	7/93	17.3 ± 2.0	32.1 ± 6.2	22.2 ± 4.4	0.6 ± 0.3	72.2 ± 9.5
Outside		14.8 ± 1.8	20.0 ± 3.1	47.1 ± 8.13	0.5 ± 0.4	82.4 ± 9.2
Exclosure	8/93	7.9 ± 1.1	24.2 ± 5.5	36.6 ± 6.1	1.6 ± 0.9	70.3 ± 9.2
Outside		13.1 ± 1.5	21.6 ± 2.4	41.0 ± 5.7	0.8 ± 0.7	76.5 ± 8.4

Table A2.10. Live:dead graminoid ratios during the 1992 and 1993 growing seasons at the Sorenson Extension sites in the Pryor Mountain Wild Horse Range.

Date	Plot	East Site	West Site
5/92	Exclosure	1.32 ± 0.12	1.62 ± 0.18
	Outside	2.99 ± 0.36	2.89 ± 0.20
6/92	Exclosure	2.21 ± 0.46	1.43 ± 0.14
	Outside	2.01 ± 0.19	3.21 ± 0.49
7/92	Exclosure	1.67 ± 0.27	1.33 ± 0.09
	Outside	1.89 ± 0.12	2.39 ± 0.40
8/92	Exclosure	0.56 ± 0.05	0.68 ± 0.14
	Outside	0.66 ± 0.04	0.79 ± 0.08
5/93	Exclosure	0.70 ± 0.12	0.64 ± 0.02
	Outside	0.83 ± 0.04	0.84 ± 0.10
6/93	Exclosure	0.64 ± 0.06	0.60 ± 0.03
	Outside	0.84 ± 0.08	0.83 ± 0.09
7/93	Exclosure	1.45 ± 0.86	0.60 ± 0.04
	Outside	0.83 ± 0.08	0.92 ± 0.07
8/93	Exclosure	0.38 ± 0.04	0.54 ± 0.05
	Outside	0.63 ± 0.06	0.75 ± 0.07

Table A2.11. Mean nitrogen concentration (% N ± SE) in C_3 live graminoids at five permanent exclosure sites during the 1993 and 1994 growing seasons in the Pryor Mountain Wild Horse Range.

Site	Plot	Year	May	June	July	August
Upper Elevation Sites						
Forest Service	Excl	1993	2.87 ± 0.2	2.21 ± 0.1	1.65 ± 0.1	1.64 ± 0.1
	Out		2.39 ± 0.4	1.90 ± 0.2	1.03 ± 0.2	1.60 ± 0.1
	Excl	1994	3.36 ± 0.1	1.99 ± 0.1	1.54 ± 0	1.15 ± 0
	Out		3.04 ± 0	1.96 ± 0.1	1.47 ± 0.1	1.34 ± 0.1
Penn's Cabin	Excl	1993	2.38 ± 0	2.17 ± 0	1.47 ± 0.2	1.51 ± 0
	Out		1.91 ± 0.2	1.50 ± 0.2	1.68 ± 0	1.50 ± 0.1
	Excl	1994	2.68 ± 0.1	1.99 ± 0	1.49 ± 0	0.94 ± 0.1
	Out		2.81 ± 0.1	1.73 ± 0.1	1.45 ± 0.1	1.32 ± 0
Syke's Ridge	Excl	1993	1.88 ± 0.1	1.51 ± 0.1	1.25 ± 0	1.36 ± 0.1
	Out		2.13 ± 0	1.61 ± 0.1	1.41 ± 0	1.50 ± 0.1
	Excl	1994	2.16 ± 0.1	1.50 ± 0	1.17 ± 0.1	1.09 ± 0
	Out		2.58 ± 0	1.74 ± 0.1	1.39 ± 0.1	0.98 ± 0
Lower Elevation Sites						
North Dryhead	Excl	1993	1.79 ± 0.1	1.13 ± 0.1	0.86 ± 0.1	0.97 ± 0.
	Out		1.59 ± 0.1	1.14 ± 0.1	0.86 ± 0.1	0.89 ± 0.1
	Excl	1994	1.82 ± 0	1.26 ± 0	0.98 ± 0	0.61 ± 0
	Out		1.71 ± 0.1	1.37 ± 0	1.29 ± 0	0.75 ± 0
South Dryhead	Excl	1993	1.64 ± 0.1	1.06 ± 0	1.01 ± 0.1	1.11 ± 0.1
	Out		1.61 ± 0.1	1.02 ± 0.1	0.97 ± 0	1.10 ± 0
	Excl	1994	1.61 ± 0	1.16 ± 0.1	1.11 ± 0.1	0.70 ± 0.1
	Out		2.01 ± 0	1.37 ± 0	1.19 ± 0.1	0.78 ± 0

Table A2.12. Mean nitrogen concentration (% N + SE) in C3 live graminoids at the east and west Sorenson Extension sites during the 1992 and 1993 growing seasons.

Site	Plot	Year	May	June	July	August
East	Excl	1992	1.47 ± 0.1	1.25 ± 0	0.96 ± 0	0.66 ± 0.1
	Out		1.44 ± 0.1	0.98 ± 0.1	0.95 ± 0.1	0.69 ± 0.1
	Excl	1993	1.59 ± 0	1.24 ± 0	0.93 ± 0	1.00 ± 0
	Out		1.19 ± 0.3	1.17 ± 0.1	0.90 ± 0	0.95 ± 0
West	Excl	1992	1.44 ± 0.1	1.04 ± 0	0.91 ± 0.1	0.61 ± 0.1
	Out		1.54 ± 0.1	1.11 ± 0.1	0.80 ± 0.1	0.69 ± 0
	Excl	1993	1.31 ± 0.2	1.16 ± 0.1	1.04 ± 0.1	0.97 ± 0
	Out		1.52 ± 0.1	1.00 ± 0.1	0.92 ± 0	0.99 ± 0

Table A2.13. Biomass data for upper elevation sites ($g/m^2 \pm SE$) during the 1992 growing season at the Pryor Mountain Wild Horse Range, Montana.

Plot	Date	Live Grass	Total Dead Grass	Live Forbs & Shrubs	Dead Forbs & Shrubs	Total (L + D) Biomass
Penn's Cabin						
Exclosure	5/92	NA*	NA	NA	NA	NA
Outside		NA	NA	NA	NA	NA
Exclosure	6/92	NA	NA	NA	NA	NA
Outside		NA	NA	NA	NA	NA
Exclosure	7/92	21.5 ± 2.5	13.2 ± 2.3	49.8 ± 13.2	18.9 ± 12.7	103.3 ± 26.5
Outside		22.2 ± 4.2	16.5 ± 5.4	46.2 ± 4.2	16.4 ± 5.1	101.4 ± 11.2
Exclosure	8/92	15.2 ± 2.7	18.7 ± 3.3	31.5 ± 7.2	1.2 ± 0.5	66.6 ± 9.7
Outside		15.4 ± 2.8	16.1 ± 3.5	31.0 ± 5.2	1.6 ± 0.7	64.1 ± 8.5
Sykes Ridge						
Exclosure	5/92	NA	NA	NA	NA	NA
Outside		NA	NA	NA	NA	NA
Exclosure	6/92	24.7 ± 1.7	8.7 ± 1.0	18.9 ±5.3	0.2 ± 0.2	52.6 ± 6.1
Outside		23.7 ± 4.4	6.6 ± 1.9	72.3 ± 21.8	0.8 ± 0.8	103.5 ± 25.0

Table A2.13 continued on next page.

Table A2.13 continued.

Exclosure	7/92	14.4 ± 1.0	14.6 ± 2.4	16.7 ± 8.6	tr.	45.8 ± 7.5
Outside		19.7 ± 2.9	12.1 ± 1.6	19.3 ± 5.3	tr.	51.2 ± 7.8
Exclosure	8/92	11.5 ± 1.6	15.5 ± 1.9	4.7 ± 2.7	0.1 ± 0.1	31.8 ± 3.6
Outside		15.4 ± 2.8	16.1 ± 3.5	31.0 ± 5.2	1.6 ± 0.7	64.1 ± 8.5
Forest Service						
Exclosure	5/92	NA	NA	NA	NA	NA
Outside		NA	NA	NA	NA	NA
Exclosure	6/92	69.3 ± 10.2	16.3 ± 4.1	59.4 ± 6.6	3.3 ± 1.0	148.2 ± 13.0
Outside		31.8 ± 3.0	3.4 ± 0.6	71.0 ± 8.3	3.9 ± 2.0	110.1 ± 10.1
Exclosure	7/92	78.1 ± 7.2	38.7 ± 8.9	44.9 ± 8.2	5.1 ± 1.2	166.9 ± 12.5
Outside		39.6 ± 7.7	16.3 ± 2.8	89.1 ± 11.7	12.3 ± 4.2	157.3 ± 13.9
Exclosure	8/92	45.1 ± 4.8	49.2 ± 5.6	46.6 ± 7.6	8.1 ± 2.9	148.9 ± 14.7
Outside		24.5 ± 3.1	18.5 ± 2.6	53.9 ± 6.1	0.6 ± 0.2	97.5 ± 6.7

*NA - no sample available for this date

Table A2.14. Biomass data for two lower elevation sites ($g/m^2 \pm SE$) during 1992 at the Pryor Mountain Wild Horse Range, Montana.

Plot	Date	C_3 Live Grass	Total C_3 Dead Grass	C_4 Live Grass	Total C_4 Dead Grass	Live Forbs & Shrubs	Dead Forbs & Shrubs	Total (L+D) Biomass
North								
Outside		12.3 ± 2.4	8.3 ± 1.5	0	0	26.4 ± 4.4	0.5 ± 0.4	47.5 ± 6.0
Exclosure	6/92	19.0 ± 3.4	9.8 ± 1.9	0	0	19.9 ± 4.3	0.1 ± 0.1	47.0 ± 7.6
Outside		20.1 ± 5.1	9.2 ± 2.5	0	0	29.6 ± 8.1	0.1 ± 0.1	58.9 ± 10.8
Exclosure	7/92	16.7 ± 1.7	14.4 ± 1.4	0	0	20.6 ± 5.6	0.5 ± 0.5	52.2 ± 5.7
Outside		11.7 ± 1.5	9.2 ± 0.9	0	0	50.7 ± 21.8	0.6 ± 0.4	72.2 ± 23.2
Exclosure	8/92	8.5 ± 1.3	19.5 ± 3.7	0	0	36.3 ± 11.6	trace	64.4 ± 14.0
Outside		5.6 ± 1.0	12.3 ± 2.8	0	0	20.8 ± 3.9	0.6 ± 0.4	39.3 ± 4.3
South								
Exclosure	5/92	19.0 ± 2.8	5.8 ± 1.1	2.9 ± 1.3	0.8 ± 0.4	22.9 ± 6.8	1.1 ± 0.5	52.4 ± 7.1
Outside		27.1 ± 2.3	10.3 ± 1.6	3.4 ± 1.9	2.1 ± 1.2	20.6 ± 4.5	1.4 ± 0.5	64.9 ± 4.5
Exclosure	6/92	13.5 ± 2.7	11.3 ± 1.7	13.7 ± 6.6	0.9 ± 0.5	23.6 ± 6.1	0.1 ± 0.1	63.0 ± 8.5
Outside		28.3 ± 8.0	18.9 ± 3.2	7.4 ± 3.3	2.7 ± 1.4	23.5 ± 8.2	0	80.9 ± 8.6
Exclosure	7/92	18.1 ± 3.2	17.6 ± 3.5	11.3 ± 3.5	5.5 ± 2.1	29.2 ± 6.9	0.3 ± 0.2	81.9 ± 6.9
Outside		17.6 ± 3.0	15.0 ± 2.0	3.4 ± 2.1	1.5 ± 0.9	28.3 ± 5.7	1.5 ± 1.0	67.2 ± 6.2
Exclosure	8/92	7.8 ± 1.5	11.2 ± 1.5	3.8 ± 2.2	3.6 ± 2.1	35.2 ± 12.8	0.2 ± 0.2	61.7 ± 13.1
Outside		7.9 ± 1.6	17.1 ± 3.0	1.1 ± 1.1	2.1 ± 2.1	51.1 ± 11.4	0.2 ± 0.2	79.4 ± 7.8

Table A2.15. Estimated total aboveground net primary production (g/m^2) for 3 growing seasons inside permanent exclosures. Values represent peak standing biomass of current year's production.

Year	Site	Live + Recent Dead Grass	Total Forbs + Dwarf Shrubs	Total Live + Recent Dead Biomass
Upper Elevation				
1992	Forest Service	106.3 ± 11.2	50.1 ± 8.6	156.4 ± 12.3
	Penn's Cabin	28.8 ± 3.3	68.6 ± 25.4	97.4 ± 25.9
	Syke's Ridge	24.5 ± 2.1	16.8 ± 8.6	41.3 ± 7.7
1993	Forest Service	71.2 ± 9.4	118.6 ± 14.7	189.8 ± 13.3
	Penn's Cabin	36.5 ± 7.5	82.3 ± 12.6	118.8 ± 18.3
	Syke's Ridge	22.7 ± 1.6	17.8 ± 5.8	40.5 ± 6.3
1994	Forest Service	71.9 ± 9.9	65.4 ± 11.8	137.3 ± 16.1
	Penn's Cabin	32.6 ± 12.3	50.0 ± 7.9	82.6 ± 16.7
	Syke's Ridge	15.3 ± 4.3	28.7 ± 9.6	44.0 ± 12.1
Lower Elevation				
1992	North Dryhead	24.5 ± 2.3	21.1 ± 5.4	45.6 ± 5.6
	South Dryhead	40.7 ± 4.2	29.5 ± 6.9	70.2 ± 5.2
	Sorenson-East	18.9 ± 3.4	34.0 ± 5.2	52.9 ± 4.0
	Sorenson-West	35.6 ± 3.0	23.3 ± 4.3	58.9 ± 5.2
1993	North Dryhead	14.7 ± 1.6	35.9 ± 8.3	50.6 ± 8.8
	South Dryhead	23.2 ± 3.9	34.4 ± 5.5	57.5 ± 4.6
	Sorenson-East	19.4 ± 2.4	22.7 ± 4.5	42.2 ± 5.2
	Sorenson-West	18.6 ± 2.4	20.1 ± 3.9	38.7 ± 4.6
1994	North Dryhead	7.0 ± 0.8	47.6 ± 7.6	54.6 ± 7.9
	South Dryhead	19.8 ± 7.5	25.6 ± 6.3	45.4 ± 8.1

Table A2.16. Mean nitrogen concentration (% N ± SE) in C3 live grasses at five permanent exclosure sites during the 1992 growing season in the Pryor Mountain Wild Horse Range, Montana.

Site	Plot	May	June	July	August
Upper Elevation Sites					
Forest Service	Excl	N/A*	1.83 ± 0.1	1.42 ± 0.1	1.39 ± 0.1
	Out	N/A	1.99 ± 0	1.73 ± 0.1	1.54 ± 0.1
Penn's Cabin	Excl	N/A	N/A	1.84 ± 0	1.18 ± 0.2
	Out	N/A	N/A	1.85 ± 0.1	1.48 ± 0.1
Syke's Ridge	Excl	N/A	1.78 ± 0.1	1.67 ± 0	1.27 ± 0.1
	Out	N/A	1.70 ± 0.1	1.68 ± 0.1	1.10 ± 0.1
Lower Elevation Sites					
North Dryhead	Excl	1.55 ± 0.1	0.98 ± 0	0.87 ± 0.1	0.55 ± 0.1
	Out	1.47 ± 0	0.98 ± 0.1	0.84 ± 0.1	0.77 ± 0
South Dryhead	Excl	1.43 ± 0.1	1.05 ± 0.1	0.87 ± 0	0.72 ± 0
	Out	1.32 ± 0	0.95 ± 0.1	0.84 ± 0	0.61 ± 0.2

*N/A = No sample available for this date

Table A2.17. Standing crop of nitrogen (g/m^2) in C3 live graminoids at 5 sites in the Pryor Mountain Wild Horse Range, Montana.

		Site				
		Upper Elevation		Lower Elevation		
Plot	Date	Penn's	Syke's	Forest	North	South
Exclosure	5/92	NA*	NA	NA	0.19	0.27
Outside		NA	NA	NA	0.18	0.36
Exclosure	6/92	NA	0.44	1.27	0.19	0.14
Outside		NA	0.40	0.63	0.20	0.27
Exclosure	7/92	0.40	0.24	1.11	0.15	0.16
Outside		0.41	0.33	0.69	0.10	0.15
Exclosure	8/92	0.18	0.15	0.63	0.05	0.06
Outside		0.23	0.17	0.38	0.04	0.05
Exclosure	5/93	0.20	0.16	0.63	0.11	0.18
Outside		0.35	0.33	0.30	0.10	0.18
Exclosure	6/93	0.43	0.29	1.10	0.15	0.14
Outside		0.35	0.34	0.57	0.12	0.18
Exclosure	7/93	0.47	0.26	0.98	0.11	0.14
Outside		0.41	0.29	0.35	0.07	0.15
Exclosure	8/93	0.37	0.33	0.98	0.10	0.11
Outside		0.37	0.14	0.46	0.05	0.15
Exclosure	5/94	0.19	0.44	0.98	0.10	0.15
Outside		0.31	0.36	0.39	0.06	0.12
Exclosure	6/94	0.34	0.19	1.57	0.09	0.13
Outside		0.28	0.22	0.39	0.04	0.07
Exclosure	7/94	0.43	0.14	1.01	0.05	0.16
Outside		0.26	0.08	0.38	0.02	0.06
Exclosure	8/94	0.12	0.08	0.45	0.04	0.05
Outside		0.16	0.05	0.21	0.01	0.02

*NA - no sample available for this date

Table A2.18. Mean July nitrogen concentration (%nitrogen) in live forbs plus dwarf shrubs and current year's dead C_3 grasses averaged across three years (1992-1994) at upper and lower elevation sites in the Pryor Mountain Wild Horse Range, Montana.

Site	Plot	Live Forbs & Shrubs	Current Year's Dead C_3 Grass
Upper Elevation Sites			
Forest Service	Exclosure	1.58 ± 0.1	1.13 ± 0.2
	Outside	1.70 ± 0.2	1.13 ± 0.2
Penn's Cabin	Exclosure	1.89 ± 0.2	1.16 ± 0.2
	Outside	1.63 ± 0.1	1.11 ± 0.1
Syke's Ridge	Exclosure	1.47 ± 0.1	0.78 ± 0.1
	Outside	1.50 ± 0.1	0.95 ± 0.2
Lower Elevation Sites			
South Dryhead	Exclosure	1.22 ± 0.1	0.70 ± 0.1
	Outside	1.09 ± 0.1	0.72 ± 0.1
North Dryhead	Exclosure	1.07 ± 0.1	0.69 ± 0.1
	Outside	1.12 ± 0.1	0.81 ± 0.1

Table A2.19. Calculated sample sizes required to detect 30 - 50 % utilization as a proportion of current year's graminoid production during 1993 and 1994 at six sites in the Pryor Mountain Wild Horse Refuge, Montana ($\alpha = 0.05$, $\beta = 0.1$).

Site	Year	Graminoid production ($g/m^2 \pm SE$)	# samples required - 30%	# samples required - 50%
NE Dryhead	1993	12.3 ± 4.1	126*	45
SE Dryhead		27.8 ± 5.2	40	14
SW Dryhead		13.7 ± 3.2	64	23
Forest Service		47.7 ± 8.1	33	12
Penn's Cabin		101.5 ± 21.2	50	18
Syke's Ridge		43.5 ± 8.6	45	16
NE Dryhead	1994	6.8 ± 1.2	35	12
Forest Service		47.9 ± 7.0	25	9
Penn's Cabin		120.8 ± 19.7	30	11

*equation used to calculate sample size from Ott (1988):

$$n = \frac{\sigma^2(z_\alpha + z_\beta)}{\Delta^2}$$

Table A2.20. Calculated sample sizes required to detect 30 - 50 % utilization as a proportion of current year's forb/dwarf shrub production during 1993 and 1994 at six sites in the Pryor Mountain Wild Horse Refuge, Montana ($\alpha = 0.05$, $\beta = 0.1$).

Site	Year	Forb/Shrub Production ($g/m^2 \pm SE$)	# Samples required - 30%	# Samples required - 50%
NE Dryhead	1993	38.1 ± 7.5	44	16
SE Dryhead		17.8 ± 5.6	115	41
SW Dryhead		33.9 ± 6.8	46	17
Forest Service		135.3 ± 36.3	82	30
Penn's Cabin		170.5 ± 24.2	23	8
Syke's Ridge		161.8 ± 59.4	154	55
NE Dryhead	1994	32.0 ± 8.2	75	27
Forest Service		72.5 ± 18.7	76	27
Penn's Cabin		120.2 ± 16.7	22	8

III. INTERACTIONS BETWEEN BROWSING UNGULATES AND AN EVERGREEN XEROPHYTE (*CERCOCARPUS LEDIFOLIUS*) IN THE PRYOR MOUNTAIN WILD HORSE RANGE

ABSTRACT

I examined several characteristics of curlleaf mountain mahogany (*Cercocarpus ledifolius*) stands and the effects of browsing ungulates on this evergreen shrub in the Pryor Mountain Wild Horse Range from May, 1993 through August, 1995. I monitored the seasonal dynamics of protein concentration and twig biomass at twelve sites, two of which had no exposure to browsing ungulates, and I conducted research on the response of this shrub to a lack of browsing for 25 years at the Syke's Coulee exclosure in the PMWHR. I also looked at the effects of curlleaf mountain mahogany on protein, fiber, and dry matter digestibility in captive bighorn sheep.

Both shrub density, which ranged from 1066 to 54,263 individuals/ha and seedling density, which ranged from 400 to 49,000/ha, in *Cercocarpus* stands in the PMWHR were much higher than those reported elsewhere, and the relatively low, shrub-like growth form here permitted easy access by browsers. Production was highest at a site where utilization by browsers was also highest, and browsing appeared to have no

effect on twig biomass or protein concentration. These results may indicate that *Cercocarpus* is capable of compensating for tissues lost to herbivory. Results from the digestion trial with bighorn sheep suggest that curlleaf mountain mahogany may depress protein digestibility, but there were no significant reductions in fiber or dry matter digestibility.

INTRODUCTION

Recent controversy regarding plant-herbivore interactions has focused on plant compensatory growth and the grazing optimization hypothesis (McNaughton 1983, 1993, Belsky 1986, Painter and Belsky 1993, Milchunas et al. 1988). It has been suggested that herbivory, if not too severe, can actually enhance the nutritive value of vegetation by indirectly causing elevated plant growth and protein yields, as well as by increasing digestibility (Mattson 1980, McNaughton 1984). Compensatory growth reactions in plants are known to bring about redistributions of reserves and nutrients to meristematic tissues. As a result, both total biomass and protein yields can be enhanced (Mattson 1980).

Compensatory growth and other responses of grass to grazing herbivores have been widely discussed (McNaughton 1979, Detling 1987, Detling and Painter 1983, Coppock et al. 1983, Jaramillo and Detling 1988, Belsky 1986, Milchunas and Lauenroth 1993). However, shrub response to browsers has not been as thoroughly researched. McNaughton (1984) has suggested that browsing mammals alter shrub form by

activating lateral buds, thus producing a dense, bushy surface with high a foliage density, analogous to a 'grazing lawn'. He suggests that this higher concentration of biomass translates into a potentially higher food yield to herbivores per mouthful eaten. He has also asserted that grazing [browsing] can increase the digestibility of forages by raising the nutrient concentration and relative yield to herbivores in 'grazing lawns' ['browsing hedges'] (McNaughton 1984).

Plant response to browsing is varied, and apparently is species-dependent. Browsing (or simulated browsing) has been shown to increase total nitrogen concentration in the leaves of *Acacia nigrescens* (du Toit et al. 1990) and in the leaves and stems of the African dwarf shrub, *Indogofera spinosa*, which also increased total nitrogen yield (Coughenour et al. 1990). Simulated browsing resulted in a slight reduction of total biomass production in *I. spinosa* (Coughenour et al. 1990), but in an increase in current-year twig biomass in feltleaf willow (*Salix alaxensis*) (Bryant 1987) and in jojoba (*Simmondsia chinensis*) (Roundy and Ruyle 1989). Heavily browsed acacia trees maintained a net annual shoot extension that was not significantly different from that of lightly browsed trees (du Toit et al. 1990), but simulated browsing caused a reduction in plant height growth in feltleaf willow (Bryant 1987).

Two measures of nutritional quality which have not received much attention in this ongoing debate on how herbivores affect the plants they eat are plant secondary compounds and lignin. Condensed tannins have been shown to deter feeding by browsing ruminants in a South African savanna (Cooper and Owen-Smith 1985). Tannins in flowers and leaves of shrubs and trees are also known to reduce protein

availability to large herbivores (Robbins et al. 1987). Additionally, the adventitious shoots of four trees in Alaska produce exceptionally large quantities of terpenes and phenolic resins, which apparently account for low palatability of the shoots for snowshoe hares (*Lepus americanus*) (Bryant 1981).

Woody plants, especially evergreen trees and shrubs, typically have higher levels of digestibility-reducing allelochemicals, such as tannins, than herbaceous plants (Mattson 1980). Additionally, although woody plants generally contain higher levels of phosphorous, calcium, and protein than herbaceous plants, they also contain higher levels of lignin, which is one of the main factors limiting forage digestibility (Cook 1972, Van Soest 1994).

Lignin, a constituent of plant cell walls, can pose digestive difficulties for large herbivores (Hanley 1982). Browse quality is affected by lignin content in at least two ways. First, lignin is virtually indigestible; secondly, it interferes with microbial breakdown of cellulose, apparently by decreasing the availability of cellulose for bacterial action (Robbins and Moen 1975, Baker and Hobbs 1987). The cellular contents of plants, in contrast, are highly digestible, and contain nonstructural carbohydrates and proteins. Because plant cell walls can be difficult for mammalian herbivores to digest, a good indicator of nutrient availability is the ratio of plant cell solubles to cell walls.

Although browse-dominated diets are less digestible and more lignified than grass or forb-dominated diets (Baker and Hobbs 1987), diets of bighorn sheep (*Ovis canadensis*) in the PMWHR were dominated by curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt., hereafter referred to as *Cercocarpus*), during winter,

summer, and fall (Kissell et al. 1996). Mule deer (*Odocoileus hemionus*) diets in the PMWHR were also heavily dominated by *Cercocarpus* in winter and fall (Kissell et al. 1996). Overall, the nutritional quality of this evergreen shrub is considered to be good. It is one of only a very few shrubs that meet or exceed the protein requirements of wintering deer (Smith 1957, Welch 1980). Although it is a highly digestible forage for deer (Smith 1957), its digestibility for bighorn sheep has not been reported.

Cercocarpus is a long-lived, slow-growing plant that is commonly found in nutrient-deficient environments and associated with shallow soils (Davis and Brotherson 1991, Duncan 1975). One reason it may be successful in occupying infertile sites is its capacity to produce root nodules capable of fixing nitrogen (Youngberg and Hu 1972, Lepper and Fleshner 1977). Because it is so valuable as a nutritious forage for wildlife, there has recently been much concern from range and wildlife managers regarding the poor condition of *Cercocarpus* stands from southwestern Montana through southern Idaho (Davis and Brotherson 1991). *Cercocarpus* stands were also observed to be in poor condition in Utah and Nevada (Davis and Brotherson 1991, Schultz et al. 1990). The major problems observed were the failure of reproduction in *Cercocarpus* communities and the majority of edible browse being beyond the reach of browsing mammals.

In the Pryor Mountain Wild Horse Range (PMWHR), *Cercocarpus* is especially important to mule deer and bighorn sheep, whose diets include up to 84% and 68% of this shrub, respectively (Kissell et al. 1996). Thus, the overall goals of my study were: 1) to ascertain the condition, distribution, and abundance of *Cercocarpus* in the

PMWHR, 2) to determine to what extent plants were being browsed, 3) to examine the effects of ungulate browsing on the nutritional quality of these shrubs, and 4) to determine how *Cercocarpus* affects digestibility in bighorn sheep.

I addressed the following specific objectives and null hypotheses (H_o) in this research:

1. Estimate the density, production, and utilization of *Cercocarpus* by ungulates.
2. Evaluate the differences in nutritional quality between large and small *Cercocarpus* shrubs.

   H_o: There are no significant differences between nitrogen concentration in, or biomass of, current annual growth (CAG) twigs on large and small *Cercocarpus* shrubs.
3. Evaluate the effects of ungulate browsing on the nutritional quality of *Cercocarpus* shrubs.

   H_o: There are no significant differences in CAG protein concentration, fiber concentration, lignin:nitrogen ratios, cell solubles:cell wall (NDS:NDF) ratios, or biomass between browsed and unbrowsed *Cercocarpus* shrubs.
4. Evaluate the effects of *Cercocarpus* on dry matter, protein, and fiber digestibility in bighorn sheep.

   H_o: There are no significant differences between digestibility coefficients of bighorn sheep fed a 100% alfalfa/grass hay diet and those fed a 40% *Cercocarpus*: 60% alfalfa/grass hay diet.

STUDY AREA

From May, 1993 to August, 1995, I conducted research on *Cercocarpus* shrubs in the Pryor Mountain Wild Horse Range (Fig. 3.1). The Pryor Mountain Wild Horse Range (PMWHR), administered by the Bureau of Land Management, consists of 14,812 ha of designated rangeland in southern Montana and northern Wyoming (BLM 1984). Approximately one-fourth of this area lies in the Dryhead Herd Area of Bighorn Canyon National Recreation Area (BCNRA), which is bordered to the east by the Bighorn River, and to the west by BLM land. My study sites were located at lower to mid-elevations (approximately 1190 m to 1800 m) within the southern portion of the BCNRA, along the Bighorn River, and on BLM land. All sites are classified as mountain mahogany shrublands (Knight et al. 1987). These areas are associated with shallow soils and rock, and are typically characterized as being dry (Knight et al. 1987). The climate here is considered cool temperate and semi-arid; average annual precipitation at lower elevations in the south end of the BCNRA is 180 mm (Knight et al. 1987).

Plant species generally associated with these shrublands include bluebunch wheatgrass (*Pseudoroegneria spicata*), needle and thread grass (*Stipa comata*), broom snakeweed (*Gutierrezia sarothrae*), Indian ricegrass (*Oryzopsis hymenoides*), juniper (*Juniperus osteosperma*), and an occasional ponderosa pine (*Pinus ponderosa*), or limber pine (*Pinus flexilis*) (Duncan 1975, Knight et al. 1987). Taxonomic nomenclature follows Lichvar et al. (1985).

METHODS

Browse abundance, production, nitrogen content, and utilization

In May, 1993, I selected 12 sites in the PMWHR for sampling *Cercocarpus*. My objectives were to estimate the density and size class distribution of *Cercocarpus* and to evaluate the nutritional quality of small and large sized shrubs across sites. Additionally, I sought to estimate current annual production and utilization of this shrub by ungulate herbivores. Six sites were established within the BCNRA, two were located along the east side of the Bighorn River in areas which were inaccessible to bighorn sheep, horses, and mule deer (i.e., those sites were considered unbrowsed), and four sites were situated on BLM land within 1.6 km of the Syke's Coulee permanent exclosure (Fig.3.1).

At each site, three 5 x 5 m plots were established along a 50 m transect, and all *Cercocarpus* shrubs within the plots were counted and measured (height and crown diameter) to determine density and size class distribution. Additionally, 10 plants (five small, or immature, greater than 10 cm, but $\leq$ 40 cm in height, and five large, or mature > 40 cm in height) along the transects were identified with numbered aluminum tags. These plants were sampled in May, June, July, August, and November, 1993, at browsed sites and May, July and August, 1993 at unbrowsed sites for nitrogen (protein) concentration and twig biomass. During each sampling period, I clipped ten unbrowsed twigs from each tagged plant and brought them back to the laboratory, where they were dried to constant mass at 45°C, weighed and then analyzed for nitrogen concentration, using a Leco 1000 CHN analyzer. Twigs sampled in May included the previous year's

growth as well as the terminal bud. Plant material collected on all other sample dates consisted only of current annual growth (CAG) twigs.

In addition to the above measurements, in August, 1993 and 1994, I estimated browse production at four of the browsed *Cercocarpus* sites, selected at random, three in BCNRA (C1, C5 and C6) and one on BLM land (C7), using density, the total number of CAG twigs per shrub, and average dry mass per twig. In 1994, production was also estimated at the two unbrowsed river sites, C11 and C12. Production was estimated by averaging total CAG mass for each of three different size classes (seedlings, 1 - 10 cm tall; medium, 11 - 40 cm tall; and large, > 40 cm tall) and then multiplying average total CAG mass/shrub by the number of shrubs per size class at each site. During 1993, I sampled 10 shrubs, chosen randomly, at each of the four sites. Because relatively few small and medium-sized shrubs were included in the random sample, I used an across-site average for these two size classes, and a site specific average for large shrubs. In 1994, I randomly sampled ten shrubs of each size class at each site and was able to use site specific averages for all size classes.

In May, 1994 and 1995, I estimated browse utilization at the same four sites where I estimated production, using three measurements. These included the percentage of current annual growth (CAG) length removed, the percentage of CAG twigs browsed per shrub, and the number (percentage) of shrubs (out of 10 randomly selected shrubs > 10 cm) with evidence of browsing per site. The percentage of twigs browsed on each shrub was estimated by counting the number of recently browsed CAG twigs on two randomly selected branches per shrub and dividing that number by the total number of

CAG twigs (browsed and unbrowsed) on those branches. I measured the length of 20 unbrowsed CAG twigs per shrub, and the length of 20 (where possible) browsed CAG twigs to estimate the percentage of twig length removed. A site-specific regression of CAG biomass as a function of CAG length was then used in estimating total CAG biomass utilization (Appendix A3.1).

Twig Biomass and Nutrient Concentrations in *Cercocarpus* Shrubs

In August, 1993, I initiated an experiment at a previously erected exclosure (the Syke's Coulee exclosure - built in 1968) to examine the effects of browsing on protein and fiber concentration in, and biomass of, *Cercocarpus* twigs. Four transects were established inside and outside the exclosure, parallel to one another. Outside the exclosure, five *Cercocarpus* shrubs with evidence of recent browsing were tagged and paired with unbrowsed shrubs inside the exclosure within the parallel transect. Forty CAG twigs were randomly selected and clipped from each shrub in August and November, 1993, and again in May, 1994. Within the exclosure, after a shrub had been clipped once, it was considered thereafter as a 'browsed' shrub; thus, on subsequent sampling dates, new unbrowsed shrubs inside were paired with browsed shrubs outside. Additional comparisons were made within the exclosure between simulated 'browsed' shrubs (those previously clipped) and unbrowsed (previously unclipped) shrubs. "Browsed' and 'unbrowsed' shrubs were sampled in November, 1993 and in May, 1994.

All twigs were oven dried at 45 ° C to constant mass, weighed and then leaves were separated from stems. Stems and leaves were weighed separately and then ground

together through a 1 mm screen in a Wiley mill. Composited, ground twigs for each shrub (20 twigs per shrub) were then subsampled and nitrogen and carbon concentrations were determined using a Leco 1000 CHN analyzer. Fiber concentrations (neutral detergent fiber, acid detergent fiber, and lignin) in whole twigs were determined using sequential detergent analysis (Goering and Van Soest 1970).

In addition to the exclosure experiment, I compared CAG nitrogen concentration and twig biomass of shrubs, for May, July and August, 1993, at two heavily browsed sites (C1 and C5) in the BCNRA to those of unbrowsed shrubs at two sites (C11 and C12) along the Bighorn River.

Forage Digestibility

Bighorn sheep are considered to be intermediate grazers, rather than browsers (McArthur et al. 1991). As such, they typically feed more on grasses and forbs than on shrubs. However, in the BCNRA we often observed bighorn sheep feeding on *Cercocarpus*. Kissell et al. (1996) confirmed our observations and estimated that this evergreen shrub made up as much as 51% of sheep diets during July and August, 1993, and even more than that during the winter (up to 70%). Thus, I conducted an experiment to address the question of how *Cercocarpus* affects protein, dry matter, and fiber digestibility in bighorn sheep. Approximately 60 kg of *Cercocarpus* CAG twigs were collected from BCNRA in 1994 and air dried. In January, 1995, the collected forage was fed to captive bighorn sheep, maintained at the Colorado Division of Wildlife Research Facility, in a 5-day trial to determine digestibility. The study was conducted with 8 adult

female bighorn sheep (mean weight = 75.5 kg). Control animals (n = 4) were fed a grass/hay diet, and sheep receiving the treatment diet were fed a mixture of 40% *Cercocarpus* CAG twigs and 60% grass/hay. Animals were maintained in individual isolation pens and gradually acclimated to their respective diets over a period of 10 days, and then were held in individual total collection digestion cages during the trial.

Each day of the trial, all leftover food (orts), feces, and urine from each animal were collected, weighed, and frozen. I measured total dry matter intake and fecal excretion (dry mass) daily. A subsample from each animal's diet, fecal output, and orts was collected daily and dried to a constant mass at 55°C (to avoid formation of Maillard products - see Van Soest 1994) for analysis of nitrogen, fiber (NDF, ADF, and lignin), and energy. Total nitrogen was determined using the Kjeldahl method, and fiber content using sequential detergent analysis (Goering and Van Soest 1970). Energy content was measured using a bomb-calorimeter. Similar samples of forage, feces, and orts were oven-dried at 100°C and weighed for dry matter determination. Subsamples of urine were freeze-dried and analyzed for nitrogen and energy content.

Apparent digestibility coefficients were calculated for protein, dry matter, and fiber using the following equation:

$$\text{Digestibility} = \frac{\text{Amount of component ingested - Amount of component excreted}}{\text{Amount of component ingested}}$$

Statistical Analysis

Cercocarpus CAG biomass and protein concentration were compared in large versus small shrubs, with date, site, and shrub size as factors in a three-way ANOVA for ten browsed sites (n = 250), and in separate AVOVAs using the same factors for two unbrowsed sites (n = 30). A two-way ANOVA was used to compare differences in CAG biomass and protein concentration at two browsed and two unbrowsed sites, with browse history (browsed vs. unbrowsed) and date as factors (n = 60) . Differences in browsed and unbrowsed shrubs inside and outside the Syke's Coulee exclosure were compared using a split plot analysis, with treatment as the mainplot and date as the subplot (n = 24 for fiber concentration, n = 60 for all other variables). Differences in clipped and unclipped shrubs inside the exclosure were also analyzed as a spilt plot design (n = 16 for fiber concentration, n = 40 for all other variables). Arcsin square root transformations were used on protein and fiber concentration data (Ott 1988).

Digestibility coefficients for protein, dry matter, and fiber were compared for bighorn sheep maintained on two diets using a paired Student's t-test (Ott 1988). Digestibility data were analyzed after arcsin square root transformation (Ott 1988). Analyses were performed using the SAS statistical program, version 6.11 (SAS Institute 1989, Cody and Smith 1991). Differences are considered significant at $p \leq 0.05$.

RESULTS

Abundance, production, and utilization of *Cercocarpus*

Density and size class distribution of *Cercocarpus* varied widely between sites (Fig. 3.2). Density ranged from 1066 individuals/ha, at an unbrowsed site established along the Bighorn River, to 54,263 individuals/ha at a site located within BCNRA, close to the state line of Wyoming and Montana (Table 3.1). Major density differences between sites were mainly the result of an abundance, or lack thereof, of seedling plants (i.e., shrubs that measured less than 10 cm in height; Fig. 3.3). At sites C5 and C7, where I suspect heavy utilization by ungulates as evidenced by the abundance of fecal droppings and tracks (personal observation), seedling density ranged from 17,000 to 49,000 individuals/ha. In contrast, seedling density at the two river sites (C11 and C12), which were not browsed by large herbivores, ranged from about 400 to 4,800 individuals/ha (Fig. 3.3). Average plant height (not including seedlings) varied between sites, ranging from a low of 0.2 m to a high of 0.6 m (Table 3.1). Site differences were even more apparent for mean shrub crown volume (for plants > 10 cm tall), ranging from a low of 0.18 m^3 at site C5 to a high of 13.26 m^3 at site C12 (Table 3.1). Seedling density was highest at the site where mean crown volume was lowest, and conversely, density of seedlings was lowest where the mean crown volume of shrubs was highest (Table 3.1).

Cercocarpus CAG production was estimated at four browsed sites in August 1993 and 1994. Production values at the browsed sites ranged from 68 to 413 kg of current annual growth twigs (CAG)/ha in 1993, and 38 to 163 kg CAG/ha in 1994 (Table 3.2). Production was also estimated at the two unbrowsed sites, C11 and C12, in 1994, where

it was 46 and 10 kg/ha, respectively. Utilization of *Cercocarpus* by ungulates was estimated at the same four sites in May 1994 and 1995. Site utilization varied from 20% of shrubs browsed per site to 100%, with a mean of 60 % (Table 3.2). The percentage of CAG twigs browsed per shrub at each site averaged 27.1 ± 3 % in 1994 and 21.4 ± 1.9 % in 1995 (Table 3.2). Utilization as a percentage of CAG production ranged from 0.3 % to 3.6 %, with a mean of 2.4 %. Average utilization as a percentage of CAG production was higher in 1995 (3.1 ± 0.2%) than in 1994 (1.7 ± 0.7%). The mean length of unbrowsed CAG twigs appeared to be greatest at site C1 (Fig.3. 4), and the mean percentage of CAG length removed by browsers appeared to be less in 1994 (37.7 ± 2.8%), than in 1995 (57.6 ± 1.4%, Fig. 3.4).

Twig Biomass and Nutrient Concentrations in *Cercocarpus* Shrubs

Large vs. Small Shrubs at Browsed Sites

Overall, mean protein concentration in CAG twigs (averaged across site and size class) differed significantly between sampling dates ($p < 0.001$), being highest during June (10.2 ± 0.9%) and lowest in May (8.3 ± 0.16 %, Fig. 3.5). Differences between sites were also significant ($p < 0.001$); mean protein concentration in CAG twigs (averaged across date and size class) was highest at site C6 (10.5% ± 0.36) and lowest at site C9 (8.5 ± 0.16 %, Appendix A3.2). A significant interaction occurred, however, between site and date ($p < 0.001$). Differences in mean protein concentration between large and small shrubs (averaged across site and date) approached significance (9.1 ± 0.10 and 9.4 ± 0.10 %, respectively, $p = 0.053$).

Mean CAG twig biomass at browsed sites (averaged across site and size class) was greatest in May, 1993, (twigs collected in May were previous year's growth with current year's buds) and least in June, 1993 (0.285 ± 0.01 and 0.090 ± 0.00 g, respectively, $p < 0.001$, Fig. 3.6). Site differences were also significant (Appendix A3.2), mean CAG twig biomass (averaged across date and size class) being greatest at site C1 and least at site C8 (0.21 ± 0.02 g and 0.12 ± 0.01 g, respectively, $p < 0.001$). There was, however, a significant interaction between date and site ($p < 0.001$). Small shrubs had significantly heavier CAG twigs ($p = 0.025$) than large shrubs (0.165 ± 0.01 g and 0.155 ± 0.00 g, respectively), although there also was a significant interaction between size and site ($p < 0.001$) and date and site ($p < 0.001$).

Large vs. Small Shrubs at Unbrowsed Sites

At the two unbrowsed river sites (C11 and C12), mean protein concentration was highest in August (10.3 ± 0.15%) and lowest in July (9.5 ± 0.15%, $p = 0.003$). Large shrubs had a higher mean protein concentration (10.1 ± 0.15%) than small shrubs (9.7 ± 0.12%, $p = 0.008$), although there was a significant interaction between site, date, and size class ($p = 0.007$). Mean twig biomass (averaged across site and size class) was greatest in May (0.41 ± 0.04) and least in July (0.16 ± 0.01, $p < 0.001$) at the two unbrowsed sites, and there were no significant differences in mean CAG twig biomass between large and small shrubs ($p = 0.541$).

Shrubs From Browsed Sites vs. Shrubs From Unbrowsed Sites

Comparisons were made between CAG twigs clipped from shrubs in May, July, and August, 1993 at two unbrowsed sites (C11 and C12) along the Bighorn River and

from two browsed sites (C1 and C5) within the BCNRA. Mean seasonal CAG twig biomass of shrubs at the unbrowsed locations was significantly heavier ($p = 0.003$) than that of shrubs in browsed areas (mean twig biomass = 0.26 ± 0.07 and 0.20 ± 0.05 g, respectively, Fig. 3.7). Twigs collected from the unbrowsed river sites also differed significantly in protein concentration ($p = 0.013$) from those at browsed sites (seasonal means = $9.4 \pm 0.9\%$ and $9.9 \pm 0.2\%$, respectively), although there was a highly significant interaction ($p < 0.001$) between the date of sampling and browsing history of the shrubs (Fig.3.8). The significant difference in protein concentration between twigs collected at browsed and unbrowsed sites resulted from the large difference evident in May values (Fig. 3.8).

Browsed Shrubs (Outside) vs. Unbrowsed Shrubs (Inside) at the Syke's Exclosure

At the Syke's Coulee exclosure, shrubs with evidence of recent browsing outside the fence were not significantly different ($p > 0.05$) from unbrowsed shrubs within the exclosure in average CAG twig biomass, leaf biomass, protein concentration, fiber (NDF, ADF, or lignin) concentrations, or in ratios of lignin:nitrogen, cell solubles: cell walls (NDS: NDF), or C:N (Table 3.3, Figures 3.9, 3.10, and 3.11). There were, however, significant seasonal differences in a number of shrub characteristics. For example, ADF concentration was highest in August ($38 \pm 0.5\%$) and lowest in November ($30 \pm 0.7\%$). Protein concentration, on the other hand, was highest in May ($9.7 \pm 0.1\%$) and lowest in November ($8.1 \pm 0.1\%$). Seasonal trends in twig and leaf biomass were the same, with the greatest mean biomass in both categories occurring in May, and the least amount of biomass evident in November (Figs. 3.9 a and b). Mean lignin:nitrogen ratios

were highest in November (21.7 ± 1.3) and lowest in May (15.8 ± 0.6), as were C:N ratios (39.3 ± 0.6 in November and 32.2 ± 0.4 in May). Significant interactions did not occur in any categories.

Shrubs with simulated browsing (previously clipped shrubs) inside the exclosure were no different ($p > 0.05$) than unclipped shrubs within the exclosure in CAG twig biomass, fiber (NDF, ADF or lignin) or protein concentrations (Table 3.4).

Forage Digestibility

Results from the bighorn sheep digestion trial (Fig. 3.12) revealed that sheep maintained on a 100% grass/alfalfa hay (control) diet had a significantly higher mean nitrogen digestibility coefficient (59.1 ± 8.0 %, $p < 0.001$) than those fed a 40%:60% mixture of *Cercocarpus* and grass/alfalfa hay (treatment) diet (45.9 ± 3.8 %). Control diets were higher in protein and neutral detergent fiber concentration and lower in lignin than treatment diets (Table 3.5). Although animals on control diets also appeared to have higher mean digestibility coefficients for dry matter (55.1 ± 2.2 %) and neutral detergent fiber (39.0 ± 2.9 %) than those on treatment diets (46.4 ± 6.4 % and 25.4 ± 7.3 %, respectively), these differences were not significant ($p = 0.308$ for dry matter digestibility and $p = 0.201$ for NDF digestibility).

DISCUSSION

Abundance, production, and utilization of *Cercocarpus*

Density of *Cercocarpus* shrubs in stands on the Pryor Mountain Wild Horse Range was higher than that reported for a number of sites in Utah, Nevada, and Montana (Duncan 1975, Davis and Brotherson 1991, Schultz et al. 1990, 1991). In the PMWHR, density ranged from a low of 1,066 individuals/ha at an unbrowsed site (C12) to a high of 54,263 individuals/ha at a site (C5) with heavy utilization by browsers. These figures are more than twice the values reported by Duncan (1975) in Montana, almost four times as high as those of Schultz et al. (1990) for Nevada, and more than ten times as high as what was found by Davis and Brotherson (1991) in Utah.

The disparity in findings is mainly the result of a difference in seedling density (Table 3.1). Mean seedling density in the PMWHR was 8,333/ha, and seedlings were present at all sites studied. Duncan (1975) found no seedlings present in 68% of her sites in Montana, and an average overall seedling density of 134/ha. Davis and Brotherson (1991) reported a lack of seedlings at 47% of their sites, and suggested 5 factors that could negatively affect reproduction or seedling density: 1) shade intolerance, 2) competition between plants for water and nutrients, 3) autotoxicity of litter to seedlings, 4) variations in seed production from year to year, and 5) utilization by wildlife.

Schultz et al. (1991) favored intraspecific competition as the most important explanation for low seedling density. They presented a predictive relationship to describe the structure of *Cercocarpus* stands in which mean crown volume of shrubs was

inversely related to the density of established seedlings. They reasoned that as Cercocarpus stands increase in average age, the average canopy volume and height of individual shrubs in the stand also increases. Eventually, these size increases in individuals result in interference between plants and competition for essential resources. If growth continues, the point is reached where, ultimately, the habitat cannot support additional biomass (Schultz et al. 1991). In the PMWHR, this inverse relationship of mean crown volume to seedling density appeared to hold for sites with the highest and lowest seedling density (Table 3.1). Site C5 had a seedling density of 49,332/ha and a mean crown volume (for plants > 10 cm tall) of 0.18 m^3, whereas site C12 had a seedling density of only 400/ha and a mean crown volume of 13.26 m^3. However, when all sites were included in a regression analysis, the inverse relationship between seedling density and crown volume did not appear to be meaningful in the PMWHR ($r^2 = 0.05$, Fig. 3.13).

In a more recent paper, Schultz et al. (1996) found a greater abundance of established *Cercocarpus* seedlings in *Artemisia*-dominated communities than in adjacent stands of *Cercocarpus*. Schultz et al. (1996) suggested four factors that influence the survival of current-year seedlings: 1) thickness of litter, 2) characteristics of root growth, 3) presence of nurse plants, and 4) herbivory. They found that although litter was perhaps not toxic to seedlings, as Davis and Brotherson (1991) had suggested, a thick layer of it might decrease seedling survival because it prevents *Cercocarpus* roots from making contact with the mineral soil. Instead of growing vertically into the soil, roots apparently first grow laterally through the litter layer (Schultz et al. 1996). Should the

litter layer become desiccated before the roots reach moist soil, the seedling will undoubtedly die.

Herbivory, of course, can also adversely affect seedling survival and establishment. The presence of nurse plants may help to protect seedlings from herbivore attack (Schultz et al. 1996). In areas of low shrub cover, a higher proportion of shrubs are potentially exposed to herbivores. Although shrub cover or litter thickness was not measured at sites in the PMWHR, seedling density was unusually high at a site (C5) where evidence of mule deer, bighorn sheep, horses, and rabbits (tracks, pellet groups, and occasional sightings of animals) was also prevalent. Mean plant height and crown volume were low at this site (Table 3.1), thus cover may have also been low, although density of plants > 10 cm in height was second highest of all sites. There is an additional explanation for the unusually high seedling density at site C5, as well as the overall high seedling density in the PMWHR, perhaps overlooked by Schultz et al (1996).

One answer may lie in enhanced nutrient cycling facilitated by large numbers of herbivores in the area, although there are no comparable data available on herbivore densities in Nevada and Utah. Urinary nitrogen has been found to enrich the soil, thereby stimulating plant growth (Day and Detling 1990, Jaramillo and Detling 1992a). Fecal nitrogen may increase soil nitrogen mineralization (Ruess and McNaughton 1987), also leading to higher rates of plant growth (Bazely and Jefferies 1985, Hik and Jefferies 1990). These effects draw herbivores back to previously fertilized areas (Day and

Detling 1990, Jaramillo and Detling 1992b), causing positive feedback loops and increasing the rates of nutrient cycling (Molvar et al. 1993).

Average *Cercocarpus* shrub height in the PMWHR was much shorter than reported elsewhere. Duncan (1975) reported a mean shrub height east of the continental divide to be 0.9 m. In the PMWHR, the greatest shrub height recorded was 1.2 m, although shrubs 2.0 m tall were observed, and the average height (for plants above 10 cm tall) was 0.2 m. Only four out of 12 sites studied in the PMWHR had any individuals measured over one meter tall. Heights of *Cercocarpus* in Utah averaged 3.4 m, although plants as tall as 9.0 m were occasionally observed (Davis and Brotherson 1991).

The growth habit of *Cercocarpus* in Utah (Davis and Brotherson 1991) varied from treelike (1.75 stems per tree) to shrublike (5.6 stems per tree). Growth forms also varied in Idaho (Scheldt 1969), Wyoming (Miller 1964), and Montana (Duncan 1975). Davis and Brotherson (1991) found a correlation between the branching habit of *Cercocarpus* and soluble salts and percent sand in the soil. Plants in Utah were more shrublike in soils of low soluble salts and high sand content. Although my study did not address soil characteristics or the number of stems per plant, the soils of PMWHR may possibly be higher in sand content and lower in soluble salts than those studied in Utah, thus, the much smaller, apparent shrublike growth habit of *Cercocarpus* here. Common garden studies are needed to determine whether the branching habit is an environmentally adaptive or a fixed genetic response (Davis and Brotherson 1991).

Production in the PMWHR was far greater than that reported in northern Utah by Austin and Urness (1980), where the tree-like form of *Cercocarpus* plants averaged

only 2 g of available forage per plant. Browse production in the PMWHR (averaged across all sites where it was estimated) averaged 0.8 g of available forage for seedlings, 6.1 g for medium-sized shrubs, and 33.2 g for large-sized plants. Production appeared to be higher in 1994 than in 1995 (Table 3.2), but results may be misleading because of a difference in sampling techniques between years. Regardless of the technique used, production during both years was highest at site C5 and lowest at site C6. Shrub utilization by browsers (amount of CAG biomass removed) was also highest and lowest at these same sites during both years.

McInnes et al. (1992) suggested that woody plants may respond to repeated browsing with decreased production and nutrient levels. Compensatory growth in evergreen plants might be expected to be less than that in deciduous woody plants, because evergreens adapted to low-resource environments generally have a lower capacity to acquire resources (Chapin 1980, Bryant et al. 1983, Edenius et al. 1993). Garrison (1953) reported very little twig growth after intensive clipping of the tree-like growth form of *Cercocarpus* in Oregon and Washington. However, he noted that smaller shrubs of the species responded quite differently, appearing to be most productive with a moderate level of browsing. In contrast, Austin and Urness (1980) noted increases of 500-900% in production of *Cercocarpus* when 90 to 99% of the canopy was pruned from mature trees.

Production levels in the PMWHR were highest at a site (C5) where the level of browsing also appeared to be the highest. This may indicate that *Cercocarpus* is quite tolerant to browsing by ungulates. Additionally, in 1994, mean CAG production at

unbrowsed sites (averaged across sites C11 and C12 - 28 kg/ha) was only 21% of the mean CAG production at heavily browsed sites (averaged across sites C1 and C5 - 132 kg/ha). Wandera et al. (1992) found that under conditions of high resource availability, *Cercocarpus* responded to high levels of simulated browsing (removal of 90 % of buds of previous year's growth) by exactly compensating for lost tissues. *Cercocarpus* may, in fact, possess a greater capacity for acquiring resources than one might suspect for a plant growing in nutrient-limited environments, because of its potential for acquiring nitrogen-fixing root nodules (Youngberg and Hu 1972, Lepper and Fleschner 1977). Alternatively, conditions of high resource availability, in the form of increased nutrient cycling, may have increased the potential for compensatory growth. The availability of water and light are, of course, also important in determining how a plant will respond to herbivory (Wandera et al. 1992).

Browse utilization can be measured in several ways. Roundy and Ruyle (1989) measured utilization as the percentage of CAG twig length removed by herbivores. In areas of moderate grazing, cattle removed an average of 44 % of twig length of Jojoba shrubs, whereas in heavily grazed areas, they removed an average of 67 % of the length of twigs (Roundy and Ruyle 1989). In the PMWHR, ungulates removed an average of 38 % of the length of CAG twigs in 1994, and an average of 58 % in 1995. From this estimate of utilization, it appears that browsers consumed a greater percentage of CAG length in 1995 than in 1994, thus, browsing pressure may have been more intense in 1995.

A second way to estimate utilization is to measure the percentage of twigs browsed per shrub. Wambolt (1996) found that browsing levels of *Artemisia* by deer increased with winter severity, reaching a high of 91% leaders browsed per shrub. Deer and sheep in the PMWHR removed an average of 27.1% of CAG twigs per shrub in 1994 and 21.4% in 1995. Ungulates in the PMWHR removed up to 3.7% of current year's production of *Cercocarpus* shrubs during 1993 and 1994, and browsed an average of 60% of mature shrubs per site. By comparison, moose at Isle Royale (McInnes et al. 1992) removed up to 3.0% of shrub production, and browsed from 36 to 83% of shrubs.

Although only a small proportion of total shrub production in the PMWHR was removed by sheep and deer, the tissues typically removed are growing shoot tips (including apical meristems), although leaf-stripping also occurs (pers. obs.). Removal of apical meristems affects shrub morphology by releasing apical dominance and allowing lateral branches to elongate, thus creating a more dense, bushy shrub (Lindroth 1989). Although browsing may increase foliage density, it may also protect interior foliage from browsing by making it physically less accessible to browsers (McNaughton 1984). Removal of growing shoots can also affect the competitive abilities and, ultimately, the survival of the shrub (McInnes et al. 1992). Although I have no data on regrowth rates of *Cercocarpus* following browsing, clipping (or browsing) evergreen woody plants typically decreases growth rates (Archer and Tieszen 1980, Bryant et al. 1983).

Biomass and Nutrient Concentrations in CAG Twigs - Forage Quality

There were no differences in mean CAG individual twig biomass resulting from browsing or simulated browsing at the Syke's Coulee exclosure. And, although average twig biomass was significantly greater in the unbrowsed shrubs growing adjacent to the Bighorn River than in browsed shrubs growing elsewhere, this may have been the result of different growing conditions, rather than an effect of browsing. Shrubs growing next to the river were situated along cliffs, with as much as a 50-60% slope. Soils as well as microclimate were probably different at these cliff sites.

In 1993, protein concentration in *Cercocarpus* shoots was highest in June, averaging 10.0% across sites, and then declined to an average of 8.6% in November. These levels are consistent with those reported elsewhere for this species (Duncan 1975, Austin and Urness 1980). Protein levels in *Cercocarpus* were lower than those of grasses in early spring in the PMWHR (Peterson, Ch. 2), but the shrubs provided a more stable, predictable level of available protein (Duncan 1975), especially for mule deer and bighorn sheep, whose diets included up to 84% and 68% *Cercocarpus* shoots, respectively (Kissell et al. 1996). Although the protein level is more than adequate for maintenance requirements of both these browsers, it is far below the level required for maximum growth in weaned wild ruminants (Robbins 1993, Ullrey et al. 1967, Smith et al. 1975). Additionally, lignin levels in this shrub (mean lignin concentration of *Cercocarpus* CAG twigs = 28.6%, n = 64) are generally much higher than those in grasses, and lignin is regarded as the principal factor limiting digestibility in ruminants (Baker and Hobbs 1987, Robbins 1993, Van Soest 1994). CAG twigs from *Cercocarpus*

were also found to have low levels of condensed tannin (D. Spalinger and C. Robbins, pers. comm.), a secondary plant compound known to reduce protein digestibility and digestibility of neutral detergent solubles in ruminants (Hanley et al. 1992).

Although there were no statistically significant differences in mean fiber or dry matter digestibilities between bighorn sheep consuming the 40%*Cercocarpus*/ 60%grass/alfalfa hay diet and sheep eating 100% grass/alfalfa hay during the digestion trial, there was a significant reduction (13.2 %) in apparent protein digestibility for animals on the *Cercocarpus* diet. However, these two diets contained different levels of protein (Table 3.5), and apparent protein digestibility is a function of dietary protein content because of the large contribution of metabolic fecal nitrogen to total fecal nitrogen, a contribution which is dependent on forage protein concentration. Therefore, animals fed different dietary protein levels would be expected to exhibit different apparent protein digestibility coefficients. But, after calculating the expected difference in apparent protein digestibility due to differences in dietary protein levels, a 3% difference remained in apparent protein digestibilities between treatments. This difference may have occurred because of the presence of condensed tannins in the *Cercocarpus* diet. Condensed tannins are known to dramatically reduce apparent protein digestibilities in isonitrogenous diets by binding with protein in the digestive tract of the animal (Hanley et al. 1992, Robbins 1993). Using an equation formulated by Hanley et al. (1992) to predict the reduction in protein digestibility as a result of condensed tannins in the forage, I calculated that a 4% reduction in apparent protein digestibility would be expected for the *Cercocarpus* diet. So, although *Cercocarpus* appears to be a nutritious

forage because of its relatively high, predictable levels of protein concentration, there appear to be costs associated with its consumption in terms of decreased protein digestibility.

Mean dry matter digestibility in this study was similar to that reported by Baker and Hobbs (1987) for sheep on diets of 100% grass hay and 50% browse/50% grass hay. Mean NDF digestibility, however, was at least 30% lower for sheep in this trial on both experimental and control diets, than that previously reported (Baker and Hobbs 1987). This disparity in results on fiber digestibility could be related to a difference in diet composition (NDF and ADF concentrations were as much as 20% lower in my study and lignin concentrations also varied, being 20% lower in the treatment diet and 28% higher in the control diet), or dry matter intake, which averaged 11 and 15 g /kgW/d for animals on treatment and control diets, respectively in their study and 10 and 7g/kgW/d in mine. Although no significant differences occurred in dry matter digestibility between treatment and control animals in my study, I expect that sheep consuming large amounts of *Cercocarpus* in the PMWHR will exhibit lower dry matter digestibilities than those consuming a diet mainly composed of grasses and forbs, because of the higher lignin levels in *Cercocarpus* twigs.

Browsing by moose (*Alces alces*) and hares has been shown to increase protein concentration in woody plants such as birch, aspen, and alder (Danell and Huss-Danell 1985, Bryant 1981). However, herbivory does not always increase protein concentration in plants. The effects of browsing by mountain hare (*Lepus timidus*) and red deer (*Cervus elaphus*) on protein concentration in heather varied in relation to soil type and

also the type and amount of herbivory (Moss et al. 1981). Browsing by mule deer and bighorn sheep at the Syke's Coulee exclosure in the PMWHR appeared to have no effect on protein concentration of *Cercocarpus* shrubs. However, browsing intensity was not measured on plants outside the exclosure. CAG twig removal inside the exclosure also had no effect on protein levels. This second finding may be the result of small sample size, the low intensity treatment applied to shrubs inside the exclosure, or the timing when the treatment was applied or measured.

In conclusion, *Cercocarpus* stands appear to be in good condition in the PMWHR. The shrub-like growth form that occurs in southcentral Montana and northcentral Wyoming allows easy access by browsers, yet reproduction rates appear to be high, as evidenced by seedling density. Browsing does not appear to have had negative effects on CAG production levels, and this result may be due to the ability of *Cercocarpus* to exactly compensate for tissues lost to herbivory (Wandera et al. 1992). The compensatory growth capacity of *Cercocarpus* may be enhanced in the PMWHR because of resource availability in the form of increased nutrient cycling or, possibly, the presence of nitrogen-fixing root nodules. There is need for further research on this species in order to elucidate with more certainty why *Cercocarpus* communities in the PMWHR appear to be doing so well, when such communities appear to be in jeopardy elsewhere.

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Table 3.1. Shrub density and mean height and crown volume of *Cercocarpus* plants at twelve sites in the Pryor Mountain Wild Horse Range. Height and crown volume data do not include seedlings.

Site	# Seedlings/ha (< 10 cm)	Total # Plants/ha	Mean height (m)	Mean Crown Volume (m^3)
C1	2,000	3,866	0.61	0.37
C2	8,000	10,532	0.40	0.28
C3	4,933	6,799	0.58	0.27
C.	1,200	4,067	0.50	0.32
C5	49,332	54,263	0.40	0.18
C6	1,733	3,733	0.51	0.21
C7	17,333	18,534	0.55	0.36
C8	933	4,533	0.22	3.95
C9	4,000	5,733	0.40	0.29
C10	5,333	7,467	0.44	0.38
C11	4,800	11,467	0.50	0.25
C12	400	1,066	0.50	13.26

Table 3.2. Estimated current annual growth (CAG) production and utilization of *Cercocarpus* shrubs by ungulates at four sites in the Pryor Mountain Wild Horse Range, Montana.

Site	Year	% CAGs Browsed per Shrub	% Shrubs Browsed per Site	Total Biomass Removed (kg/ha)	Total CAG Production (kg/ha)
C1	1993-94	22.1 ± 7.9	70	0.4	110
	1994-95	26.2 ± 5.6	100	3.7	102
C5	1993-94	27.5 ± 6.7	70	11.7	414
	1994-95	22.4 ± 10.5	60	4.8	163
C6	1993-94	21.8 ± 2.5	20	0.4	69
	1994-95	19.4 ± 7.3	40	1.3	38
C7	1993-94	37.2 ± 13.6	50	4.8	153
	1994-95	17.5 ± 4.8	70	2.5	92

Table 3.3. *Cercocarpus* CAG twig characteristics (means ± SE) in browsed (outside) and unbrowsed (inside) shrubs at the Syke's Coulee exclosure.

Twig Variable	Exclosure		
	Inside (Unbrowsed)	Outside (Browsed)	Statistical Significance
Biomass (g)	0.165 ± 0.01	0.153 ± 0.01	NS
Leaf Biomass (g)	0.082 ± 0.01	0.073 ± 0.01	NS
Protein Concentration	9.0 ± 0.12	8.7 ± 0.13	NS
NDF Concentration	43.5 ± 0.7	44.1 ± 0.7	NS
NDS:NDF	1.31 ± 0.03	1.28 ± 0.04	NS
ADF Concentration	34.2 ± 0.9	33.7 ± 0.8	NS
Lignin Concentration	25.3 ± 0.5	26.1 ± 0.9	NS
Lignin:Nitrogen	17.98 ± 0.5	19.83 ± 1.1	NS
Carbon:Nitrogen	35.5 ± 0.5	36.6 ± 0.6	NS

Table 3.4. *Cercocarpus* CAG twig characteristics (means ± SE) inside the Syke's Coulee exclosure in previously clipped and previously unclipped shrubs.

Twig Variable	Previously Clipped	Previously Unclipped	Statistical Significance
Biomass (g)	0.15 ± 0.01	0.17 ± 0.01	NS
Protein Concentration	9.1 ± 0.16	9.1 ± 0.16	NS
NDF Concentration	41.6 ± 0.8	43.3 ± 0.86	NS
ADF Concentration	33.0 ± 1.2	32.1 ± 0.9	NS
Lignin Concentration	25.1 ± 0.7	25.4 ± 0.6	NS

Table 3.5. Chemical composition (%) and gross energy of grass/alfalfa - browse diets fed to Rocky Mountain bighorn sheep (100% dry matter basis).

	40 % *Cercocarpus*/ 60 % grass/alfalfa	0 % *Cercocarpus*/ 100 % grass/alfalfa
Dry Matter	92.8	91.0
Neutral Detergent Fiber	46.2	49.1
Acid Detergent Fiber	31.7	32.2
Lignin	9.8	6.3
Crude Protein	13.6	18.1
Gross Energy, kcal/g	4.6	4.4

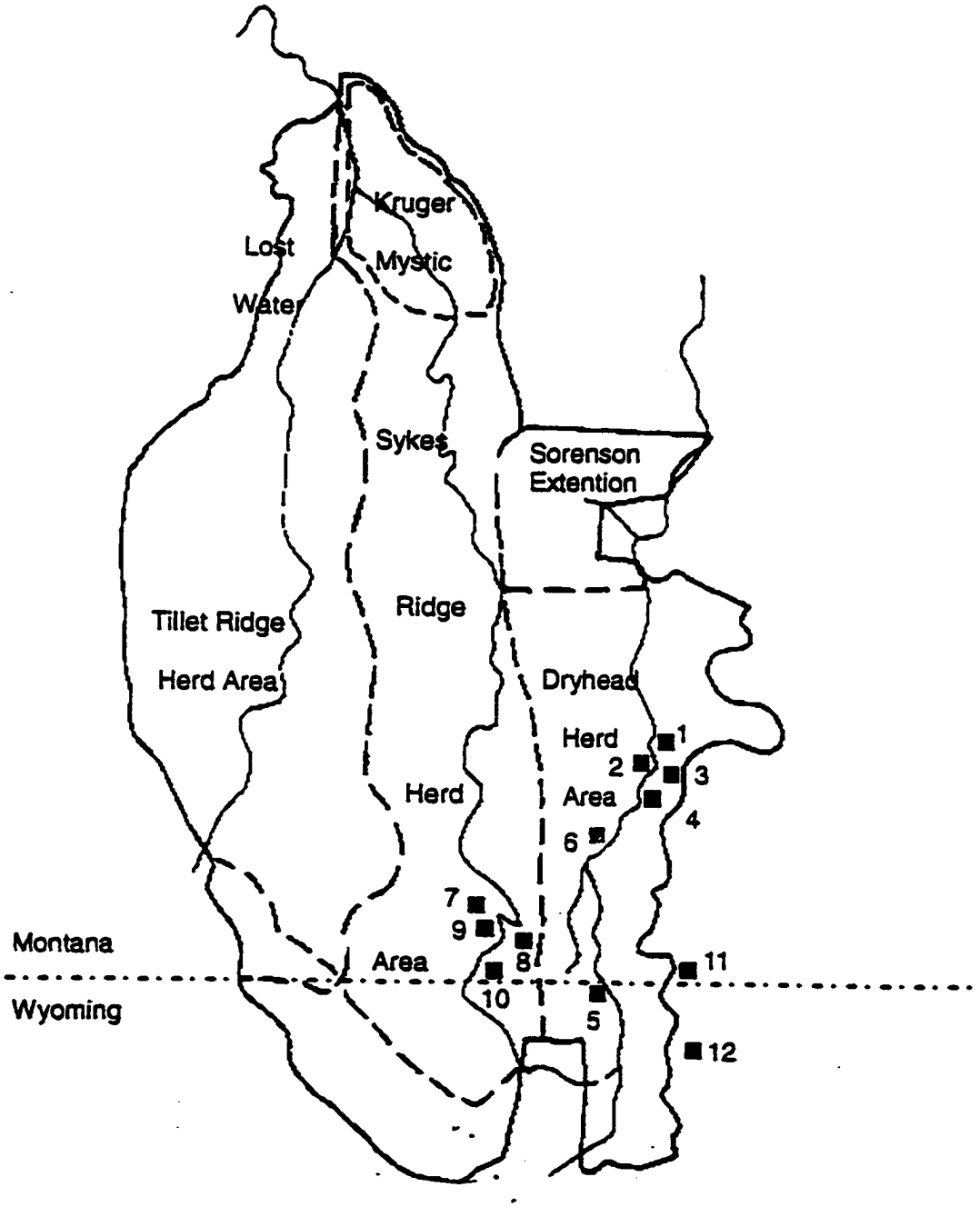


Figure 3.1. Twelve Cercocarpus research sites located in the Pryor Mountain Wild Horse Range. Solid lines within the map represent roads and dashed lines represent boundaries of 3 wild horse herd areas.

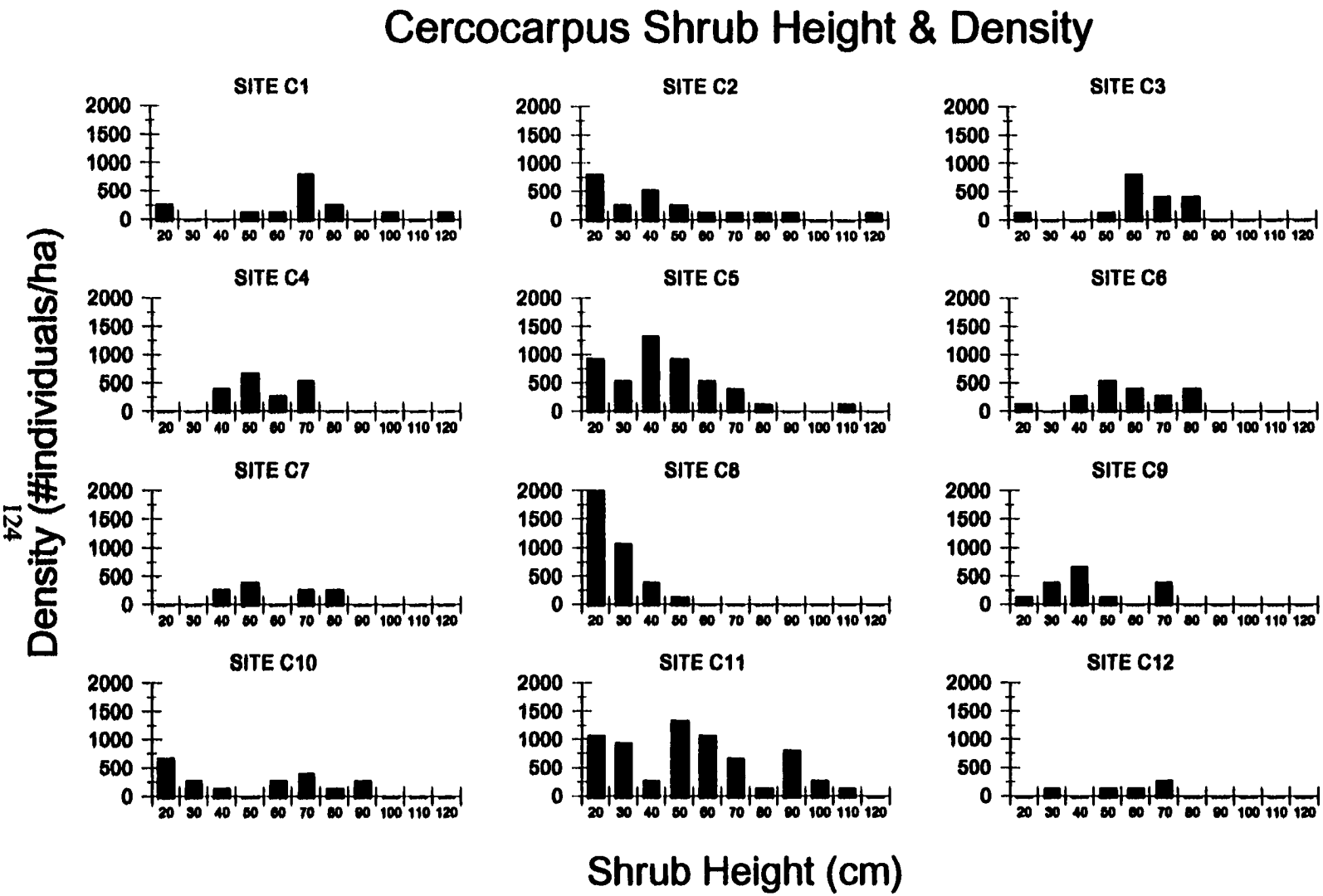


Figure 3.2. Height and density of Cercocarpus shrubs greater than 10 cm in height at 12 sites in the Pryor Mountain Wild Horse Range. Shrub height categories (20 cm, 30 cm, 40 cm, etc.) Include a range of heights (10.1 - 20.0 cm, 20.1 - 30 cm, etc.).

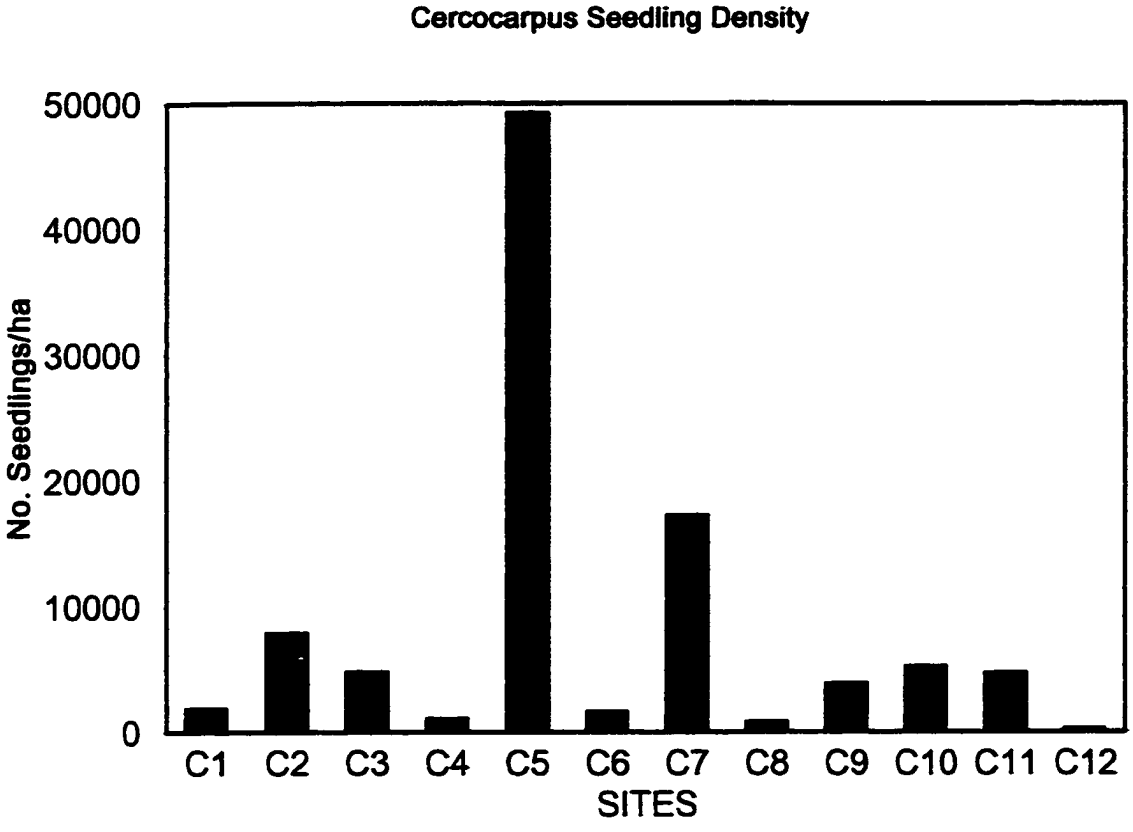


Figure 3.3. Density of *Cercocarpus* seedlings (individuals < 10 cm tall) at 12 sites. Sites C1 through C10 are browsed sites, and C11 and C12 are unbrowsed sites in the Pryor Mountain Wild Horse Range.

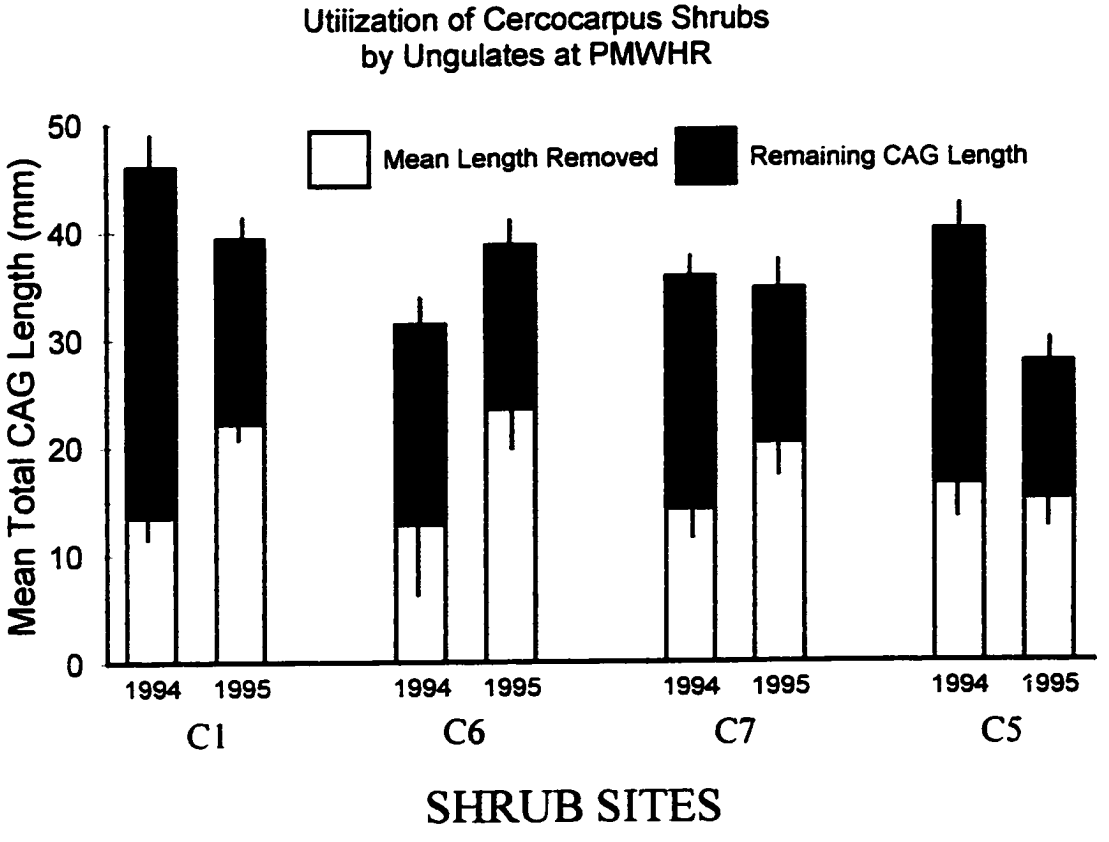


Figure 3.4. Mean length of unbrowsed and browsed *Cercocarpus* current annual growth (CAG) twigs (±SE) at 4 sites in the Pryor Mountain Wild Horse Range.

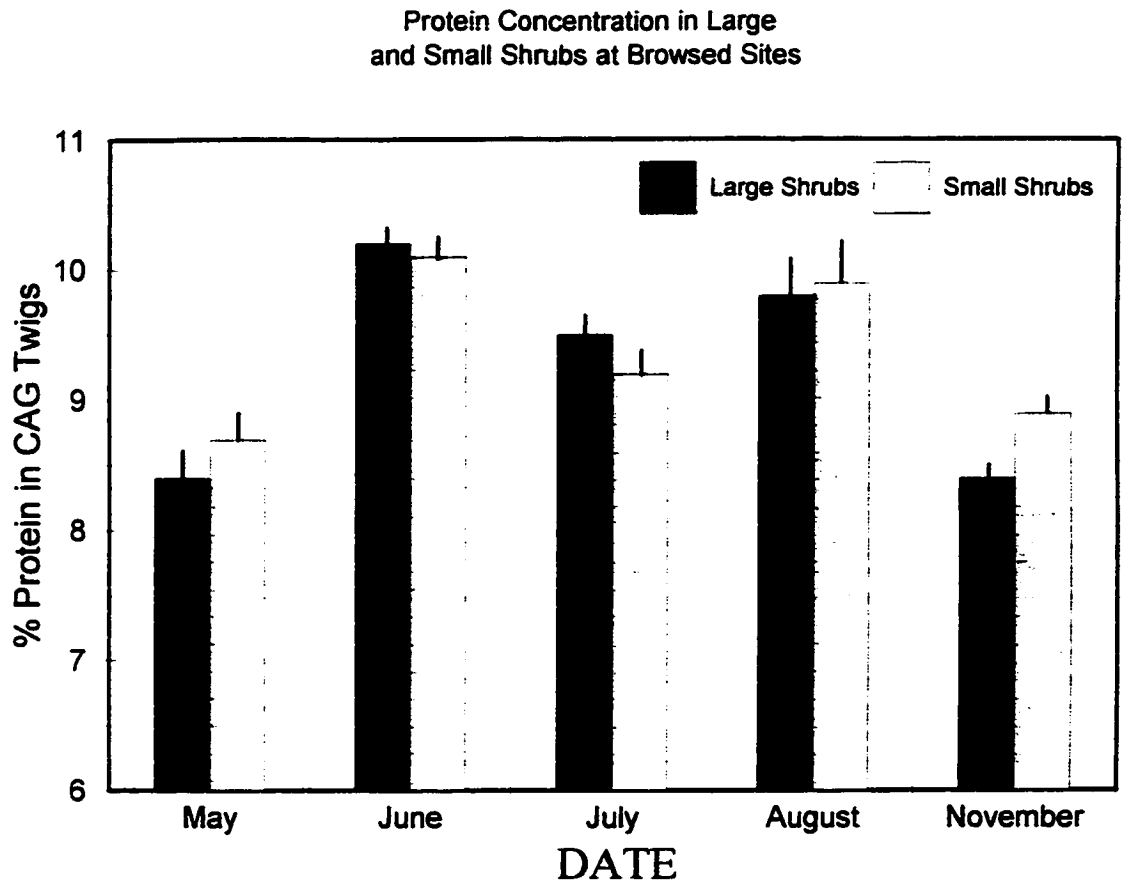


Figure 3.5. Mean protein concentration (± SE) in CAG twigs of large (> 40 cm in height) and small (≤ 40 cm) *Cercocarpus* shrubs (averaged across 10 browsed sites, n = 50) in the Pryor Mountain Wild Horse Range.

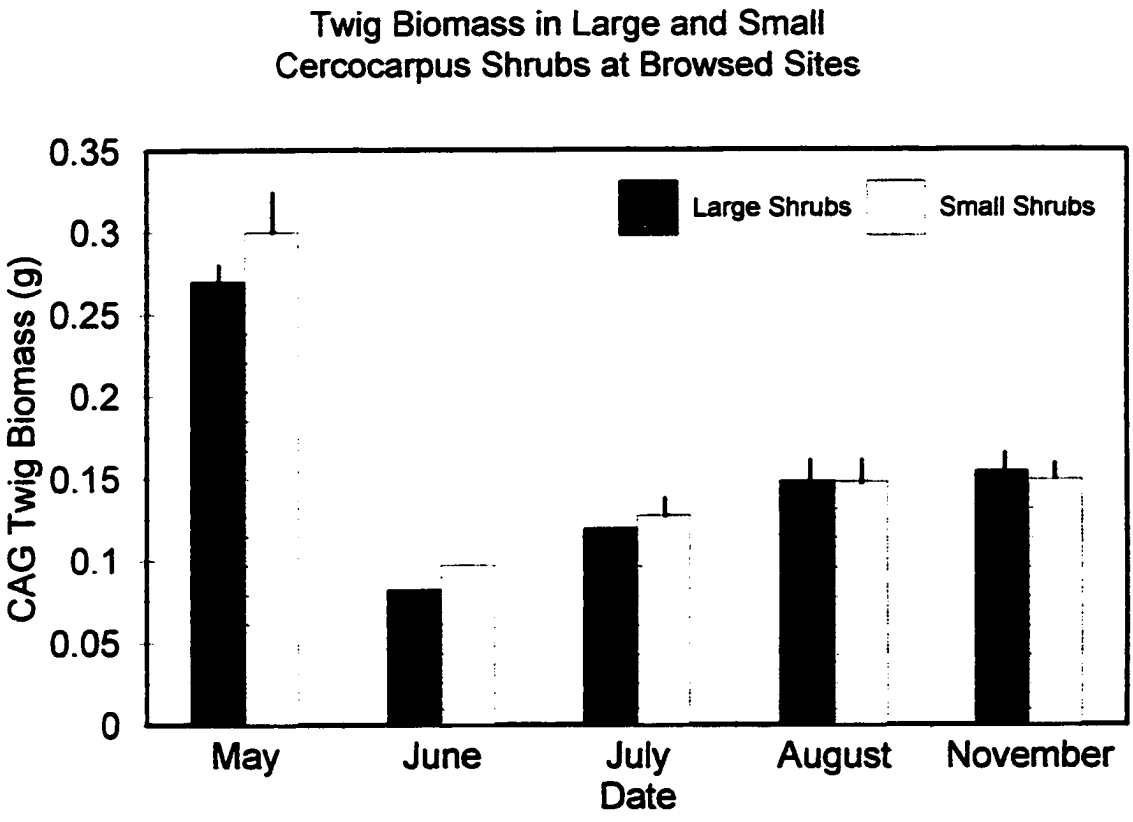


Figure 3.6. Mean biomass (± SE) of CAG twigs of large (> 40 cm in height) and small (≤ 40 cm) *Cercocarpus* shrubs (averaged across 10 sites, n = 50) in the Pryor Mountain Wild Horse Range.

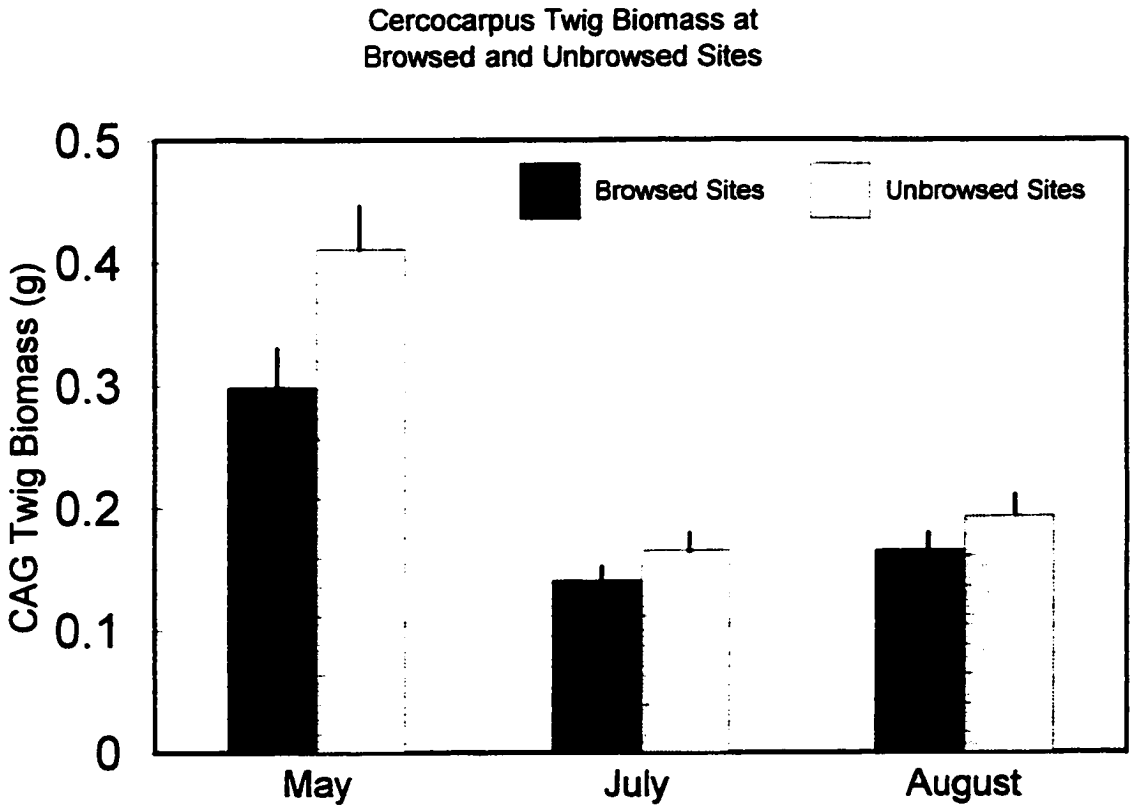


Figure 3.7. Mean biomass (± SE) of CAG twigs of *Cercocarpus* at two browsed and two unbrowsed sites (n = 20) in the Pryor Mountain Wild Horse Range.

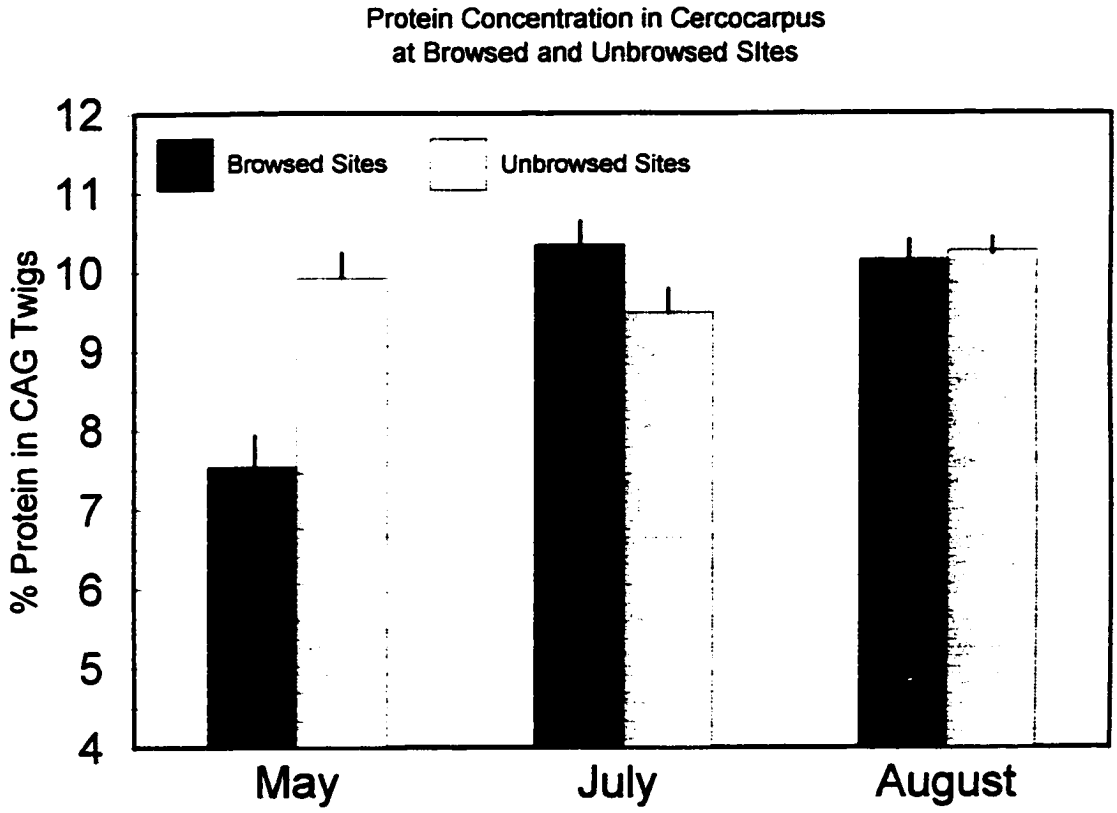
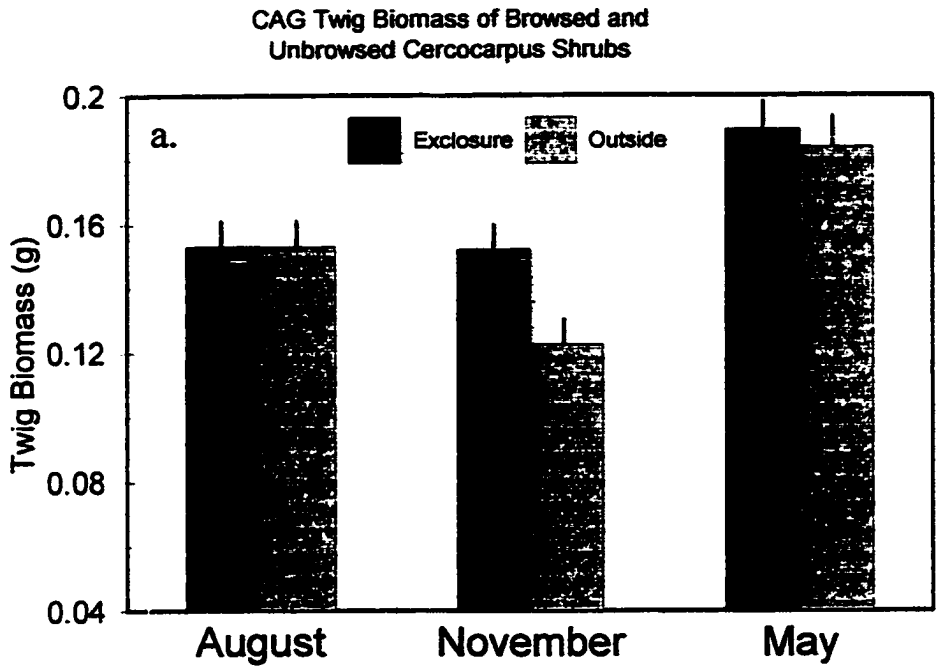


Figure 3.8. Mean protein concentration (± SE) in *Cercocarpus* CAG twigs at two browsed and two unbrowsed sites (n = 20) in the Pryor Mountain Wild Horse Range.



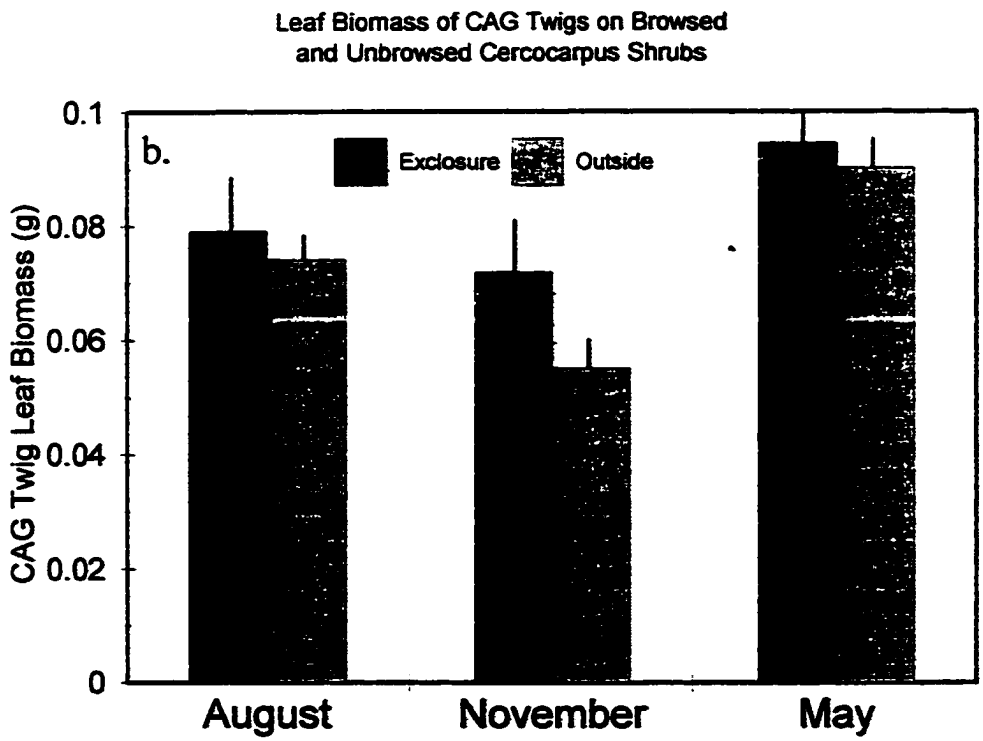


Figure 3.9. Mean biomass (± SE) of *Cercocarpus* CAG twigs (a) and leaves (b) inside and outside the Syke's Coulee exclosure (n = 20) during 1993-94 in the Pryor Mountain Wild Horse Range.

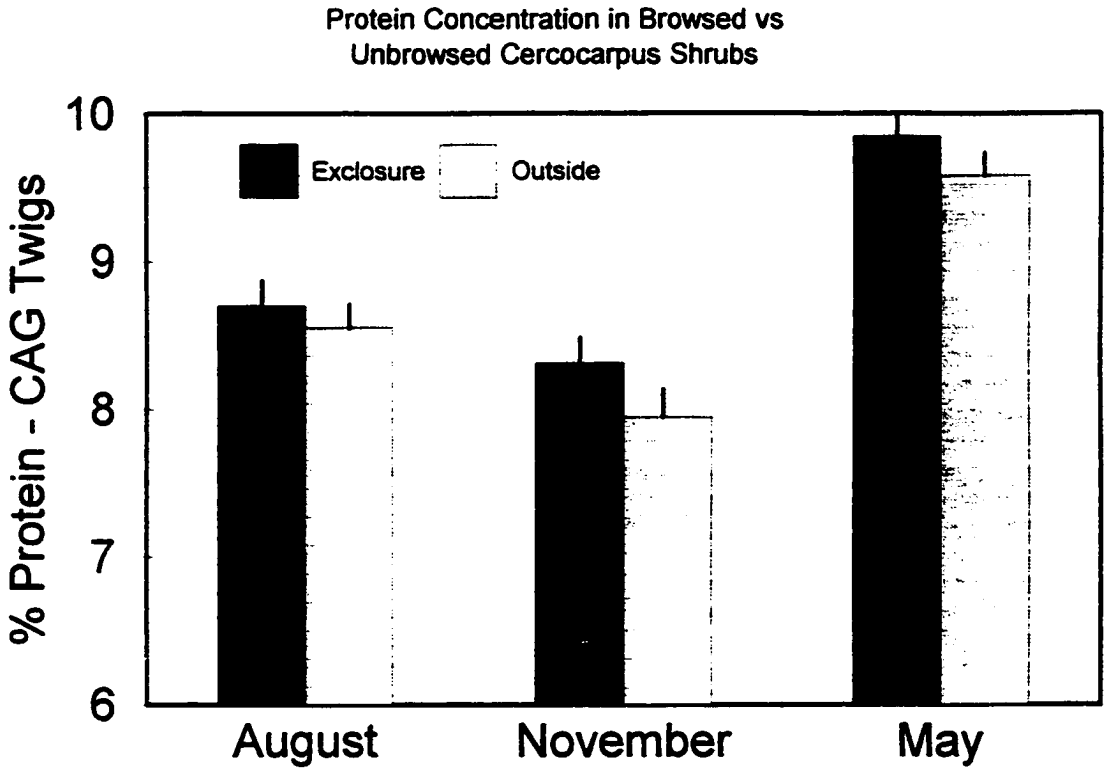


Figure 3.10. Mean protein concentration (± SE) in *Cercocarpus* CAG twigs inside and outside the Syke's Coulee exclosure (n = 20) in the Pryor Mountain Wild Horse Range.

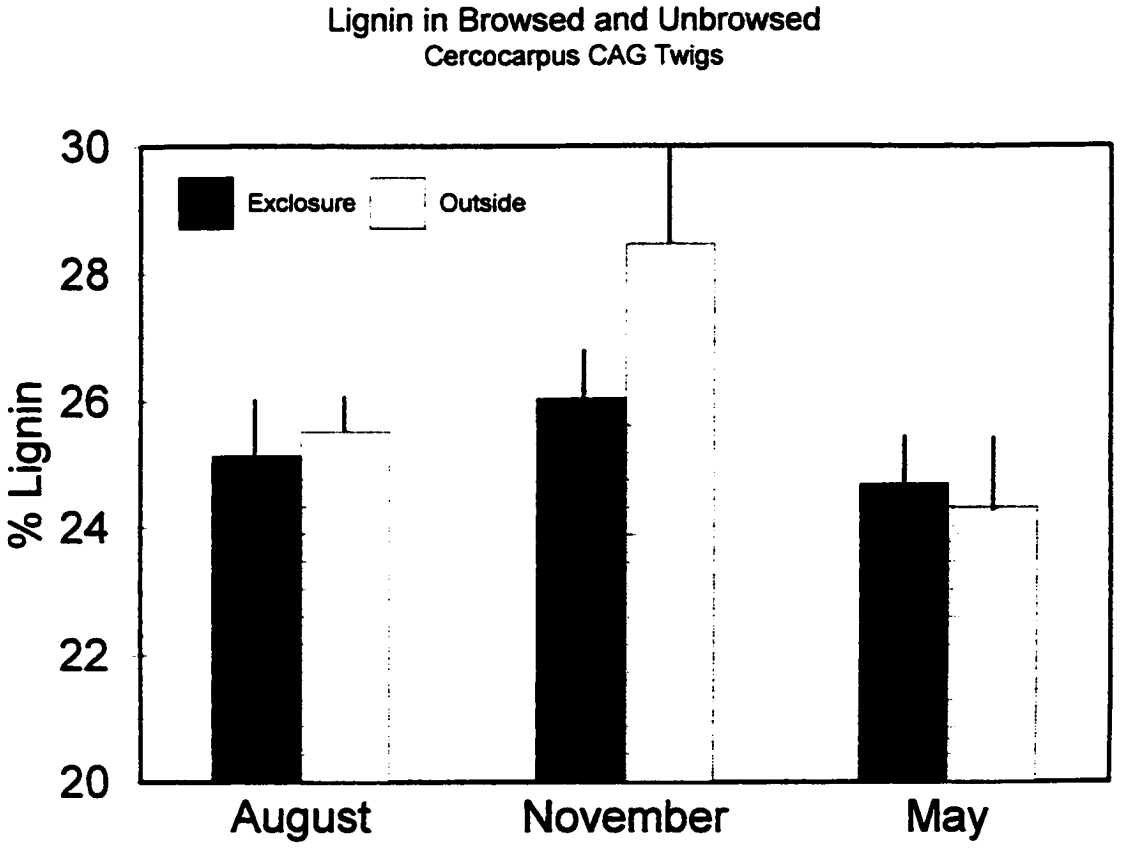


Figure 3.11. Mean lignin concentration (± SE) in *Cercocarpus* CAG twigs inside and outside the Syke's Coulee exclosure (n = 8) in the Pryor Mountain Wild Horse Range.

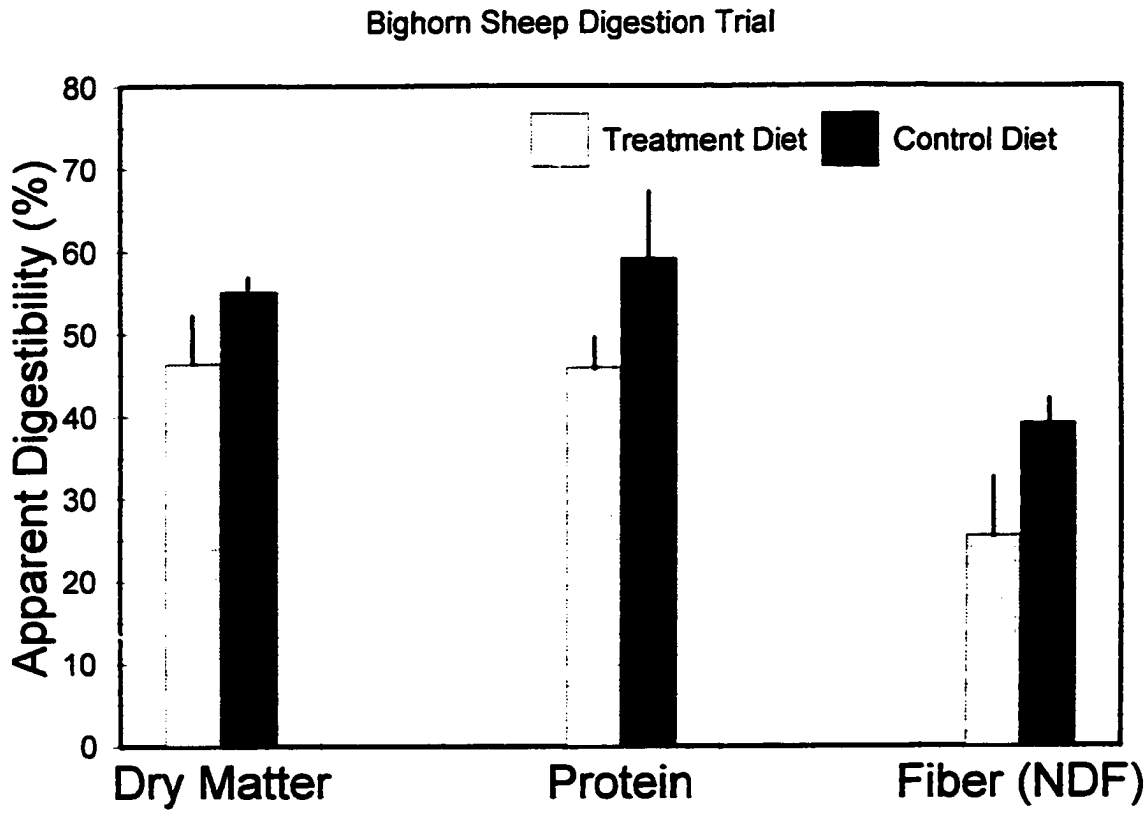


Figure 3.12. Mean dry matter, protein, and fiber (NDF) digestion coefficients (±SE) for captive bighorn sheep (n = 4) fed a 100% grass/alfalfa hay diet (control) and a 40% *Cercocarpus*: 60% grass/alfalfa hay diet (treatment). Differences in apparent protein digestibility were significant at $p < 0.001$, but other differences in digestibility were not significant.

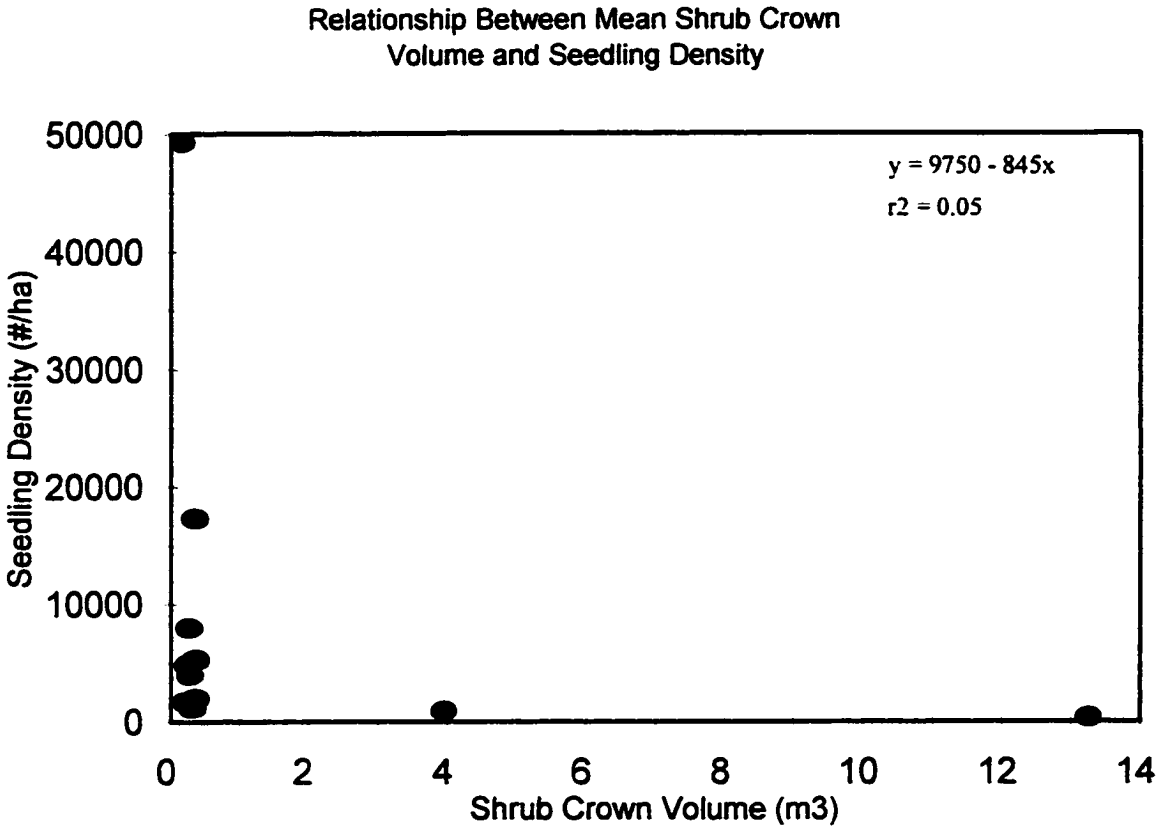


Figure 3.13. Relationship between the mean shrub crown volume and seedling density of *Cercocarpus* at 12 sites in the Pryor Mountain Wild Horse Range.

APPENDIX 3.1

Table A3.1. Site-specific regressions of CAG twig biomass as a function of CAG twig length used in estimating total CAG biomass utilization.

Site	Regression Equation	R^2 Value
C1	$Y = -24.31 + 2.82X$	0.962
C5	$Y = 1.76 + 2.46X$	0.758
C6	$Y = -36.01 + 4.26X$	0.859
C7	$Y = -1.13 + 2.74X$	0.811

Table A3.2. Mean biomass and protein concentration (± SE) of CAG twigs from large and small *Cercocarpus* shrubs averaged by site across sample dates.

Site	CAG Biomass (g)		% Protein per CAG	
	Large Shrubs	Small Shrubs	Large Shrubs	Small Shrubs
C1	0.20 ± 0.0	0.23 ± 0.0	9.1 ± 0.4	9.9 ± 0.4
C2	0.19 ± 0.0	0.21 ± 0.0	9.0 ± 0.3	8.3 ± 0.3
C3	0.18 ± 0.0	0.17 ± 0.0	9.6 ± 0.2	10.1 ± 0.2
C.	0.14 ± 0.0	0.18 ± 0.0	9.3 ± 0.2	9.7 ± 0.2
C5	0.14 ± 0.0	0.14 ± 0.0	9.4 ± 0.4	9.5 ± 0.3
C6	0.13 ± 0.0	0.13 ± 0.0	10.4 ± 0.5	10.6 ± 0.5
C7	0.15 ± 0.0	0.17 ± 0.0	8.6 ± 0.4	8.9 ± 0.2
C8	0.15 ± 0.0	0.12 ± 0.0	8.3 ± 0.2	8.7 ± 0.3
C9	0.13 ± 0.0	0.20 ± 0.0	8.9 ± 0.2	8.5 ± 0.2
C10	0.14 ± 0.0	0.09 ± 0.0	9.0 ± 0.4	9.5 ± 0.3
C11	0.23 ± 0.0	0.23 ± 0.0	9.8 ± 0.2	8.6 ± 0.7
C12	0.26 ± 0.0	0.30 ± 0.1	10.5 ± 0.2	10.1 ± 0.2

IV. CONCLUSIONS AND RECOMMENDATIONS

There are several general conclusions which can be drawn from this study. First, and possibly most important for management considerations, grazing and browsing levels in the PMWHR during this study were light to moderate in comparison to those reported elsewhere (Coppock et al. 1983, Detling 1987, Lacey and Van Poollen 1981, Whicker and Detling 1988,). The percentage of grass and forb production removed by grazers was up to ten times as high as the percentage of *Cercocarpus* CAG production removed by browsers. One possible explanation for this difference is that all three species of ungulates utilized at least some grass and forbs in their diets, whereas only bighorn sheep and mule deer consumed *Cercocarpus* (Kissell et al. 1996).

Grassland productivity was as much as 3 to 4 times greater at upper elevation sites than at the low elevation Dryhead Herd Area sites. The more mesic upper elevation grasslands also offered higher quality forage with nitrogen levels in C_3 live grasses as much as 63% higher than those found in low elevation C_3 grasses.

Cercocarpus stands in the PMWHR appeared to be productive and healthy overall, although shrub decadence was observed in several areas. Seedling density here was far greater than that reported elsewhere (Duncan 1975, Davis and Brotherson 1991, Shultz et al. 1991). High seedling density may have resulted from: 1) a recent good seed crop, which occurs only at irregular intervals (Davis and Brotherson 1991),

2) an adequate litter layer for seedling establishment (Schultz et al. 1991), 3) adequate temperatures and levels of precipitation, or 4) an increase in nutrient cycling facilitated by browsing herbivores (Day and Detling 1990, Jaramillo and Detling 1992).

The 930 ha of *Cercocarpus* stands in the PMWHR comprise the majority of crucial mule deer winter habitat (BLM 1984). This shrub may be equally important to bighorn sheep, as it was the dominant component in their diets during three out of four seasons during 1993-1995 (Kissell et al. 1996). However, although this forage provides a stable, predictable level of protein for both sheep and deer, it was found to cause significant reductions in protein digestibility in captive bighorn sheep. Additionally, the protein concentration in CAG twigs never reached levels high enough to support maximum growth in weaned ruminants (Duncan 1976, Robbins 1993). In fact, Kissell et al. (1996) suspected that low forage quality was the leading factor responsible for the rapid decline of the sheep population during their 3 year study.

Reductions in protein digestibility may be associated with high lignin levels in *Cercocarpus*. However, this woody evergreen plant also contains low levels of condensed tannins (D. Spalinger and C. Robbins pers. comm.), which are known to negatively affect protein, dry matter, and fiber digestibility in ruminants (Hanley et al. 1992). Mule deer may be better able to handle these secondary plant chemicals in their diets than bighorn sheep because deer produce salivary tannin-binding proteins, which act to neutralize the tannins' effects (Hagerman and Robbins 1993). Sheep are not known to produce these proteins, thus, *Cercocarpus* may be of a lower nutritional value for them (Robbins et al. 1991).

Bighorn sheep are generally classified as intermediate grazers (McArthur et al. 1991), although in the PMWHR they might better be described as browsers. According to Kissell et al. (1996), sheep consumed *Cercocarpus* more often than did the 'true browser' of the system, mule deer, during three years of study in the PMWHR. Diets of bighorn sheep elsewhere are dominated mainly by grasses (Wikeem and Pitt 1991). Browse, however, becomes an important component in their diets when herds are restricted to low elevations (Rominger and Bailey 1988) or deserts (Krausman et al. 1989), where grasses and forbs are sparse and often of low quality. Low elevation grasslands in the PMWHR were always far less productive than the upper montane grasslands, where forage quality of C_3 graminoids was also superior.

Graminoids were the major component in horse diets throughout the study of Kissell et al. (1996). Although horses consumed *Cercocarpus* in an earlier study (Coates and Schemnitz 1989), this shrub was not detected in their diets during 1993-1995 (Kissell et al. 1996). Many studies have shown that grazing bovids generally use forbs and woody plants to a greater extent than do equids (Hansen and Clark 1977, Olsen and Hansen 1977, Krysl et al. 1984). The reason for this difference is not yet fully understood, although some ruminants are known for their ability to detoxify secondary metabolites (Van Soest 1994). Equids appear not to possess similar detoxification abilities (Duncan 1992).

Although there is considerable overlap between equid and bovid diets in the PMWHR (Kissell et al. 1996), little competition likely existed between them for food during summer, fall, and winter, since sheep fed so heavily on *Cercocarpus*. Feral horses

may, in fact, have acted as facilitators of sheep and deer by reducing graminoids which compete with *Cercocarpus* shrubs for water and nutrients (Reiner and Urness 1982). Horses, therefore, may actually have enhanced winter habitat for both mule deer and bighorn sheep.

Spring appeared to be the time of greatest dietary overlap between horses, deer, and sheep (Kissell et al. 1996). This is generally the time of year when all 3 species of ungulates are faced with the high energy demands of lactation, which can usually be met with spring growth of nutritious grasses and forbs. However, as populations of horses, sheep, and deer were increasing in the Pryor Mountain Wild Horse Range during 1993-1994, the standing crop of herbaceous vegetation, most notably live graminoids, in the low elevation Dryhead Herd Area decreased dramatically, probably because of low amounts of precipitation and increased herbivory. This pattern was not apparent in the montane grassland sites.

Although results from this study show that grazing and browsing levels in the PMWHR were light to moderate (see Chapter 2 and 3), there is always the potential for ungulate populations to expand in the PMWHR. Feral horse populations often attain high growth rates (Eberhardt et al. 1982, Berger 1986), and the Pryor Mountain herd is no exception (Garrot and Taylor 1990). In 1997, there were reportedly 208 horses in the PMWHR before round-up (BLM 1997). Bighorn sheep, which re-populated the PMWHR in the 1970's with a small group of individuals from a transplanted herd in the Bighorn Mountains (Coates and Schemnitz 1989), also exhibited a high rate of population growth, peaking at 211 animals in 1994 before beginning to decline (Kissell

et al. 1996). During the study of Kissell et al. (1996), the mule deer population reached a level of ~700 animals before it also decreased.

There are 18,944 ha available to feral horses in the PMWHR, however, 7,104 ha were designated as unsuitable for grazing because of a preponderance of rock and a paucity of vegetation (BLM 1984). In addition, the availability of the undesignated Sorenson extension area of the Bighorn Canyon National Recreation Area for horse use was discontinued in the fall of 1992, resulting in a further loss of 1076 ha of potential forage. Even more recently, a fence separating Custer National Forest from the PMWHR was repaired, discontinuing ~12 years of unauthorized summer grazing by ~30 horses (BLM 1997). Thus, the grazing impact on authorized BLM horse range has increased somewhat over the last 6 years. Furthermore, 66% of the producing range has been described as being in poor condition, probably resulting from previous heavy livestock use of the area, whereas only 33% of the range is in fair to good condition (BLM 1997).

Management Recommendations

The main management tool historically utilized by the BLM to sustain the current level of all-around health of the PMWHR range has been the round-up, removal, and subsequent adoption of feral horses. This procedure is not only costly in terms of tax dollars and the health and welfare of horses, but it has also been met repeatedly with opposition from the general public (Bama 1998). Feral horses, in fact, are not the lone culprits in the degradation of the PMWHR range; mule deer and bighorn sheep are also guilty of consuming and trampling vegetation.

Other management strategies that might be incorporated in an overall plan to improve or maintain range condition could include: 1) prescribed burning of diseased or dead stands of conifers and/or decadent *Cercocarpus* stands with or without 2) reseeding of desirable perennial forage species, 3) increased hunting pressure on deer and sheep, 4) fertility control of all three species, 5) rest and rotation grazing with the use of moveable fences (including the possibility of making the Sorenson extension area available to horses again), 6) construction of additional water cachements with maintenance or repair of existing ones, and 7) more long term monitoring studies of all three ungulate populations and their forage to better understand habitat use and fluctuating patterns in plant productivity.

Prescribed burning programs have the potential to improve and enlarge habitats for large herbivores (Hobbs and Spowart 1984, Cook et al. 1994). As such, they could be utilized in areas of the PMWHR where there are diseased or dead stands of pine and fir at upper elevations or decadent, unproductive stands of *Cercocarpus*, especially at lower elevations. However, although there is ample information available on prescribed burns in several types of plant communities, there have been few, if any, studies conducted on the response of *Cercocarpus ledifolius* to burning. Because of the overall abundance and health of Cercocarpus stands in the PMWHR, this may be an ideal location for such research.

Burning in grassland and mountain shrub communities, other than *Cercocarpus*, has been shown to increase the productivity of perennial grasses and herbs (Martin 1983, Cook et al. 1994) and also to improve the nutritional quality of diets for bighorn sheep

and mule deer (Hobbs and Spowart 1984, Cook et al. 1994). Improved dietary quality for ungulates in the Hobbs and Spowart (1984) study resulted, in part, from an increase in green grass on burned plots, where soils were warmer than those on unburned plots, thus, favoring grass growth during winter. These authors also showed that the positive effects of burning on ungulate nutrition were more persistent in mountain shrub communities than in grasslands. Cook et al. (1994) found the crude protein content of herbs to be higher on burned plots from late spring through early fall for two years post-burn.

Ungulates appear to be attracted to burned areas (Vogl and Beck 1970, Davis 1977), thus, prescribed burns might also be used as a strategy to attract deer, sheep, and horses away from heavily or over-grazed parts of the range (Coppock and Detling 1986). However, it may take a year of higher than average precipitation for perennial grasses to become well established (West and Hassan 1985), so it would be prudent to prevent animals from grazing burned areas until the new vegetation has become established.

If fire consumes a large portion of undesirable diseased or dead conifers or decadent *Cercocarpus* shrubs and does little damage to the desirable herbaceous species, then the landscape that has been created may be better wildlife and feral horse habitat. However, this assumes that desirable native species can regenerate themselves. *Cercocarpus* does not resprout after burning, and in areas other than the PMWHR, it has been found to be difficult to establish from seed (Davis and Brotherson 1991). However, several perennial grasses with a strong potential for reseeding themselves increased markedly after burning (Martin 1983). Bluebunch wheatgrass (*Pseudoroegneria spicata*) was back to pre-burn levels in a sagebrush-grass community within two years (West and

Hassan 1985). but its successful recovery was largely due to vegetative growth. Although artificial seeding appears to be mandatory only when cheatgrass (*Bromus tectorum*) is a major component of the preburn community (Young et al. 1976, West and Hassan 1985), it could be beneficial in areas of low herbaceous vegetation cover, such as the Dryhead Herd Area of the PMWHR. Of course, cost of reseeding is likely a concern. The price of seeding with native grass species varies from year to year, but a recent quote (R. Zakely pers. comm.) estimates a mixture of 60% *P. spicata*, 20% *Bouteloua gracilis*, 10% *Stipa comata*, and 10% *Poa secunda* (grasses found at low elevation sites in the PMWHR [Fahnestock 1998]) seed to cost approximately $1225 per seeded ha. The ideal situation would be to reseed with seed collected from plants actually growing in the area, but the cost for collecting and planting such seed might be exorbitant (R. Zakely pers. comm.).

A more controversial approach to managing ungulate populations which are expanding in numbers, yet existing on fixed amounts of area, such as national parks, is fertility control. Continuing urban sprawl, coupled with shrinking wildlife habitat, and increasingly negative attitudes toward hunting, trapping, and poisoning, have triggered a rapid rise in fertility control investigations. In 1998, two bighorn ram and 166 mule deer permits were issued to hunters in the Pryor Mountains (C. Eustace pers. comm.). Increased hunting pressure on bighorn sheep and mule deer populations in the PMWHR might aid in combating the habitat degradation problems that are associated with overpopulation, but it is likely not nearly as popular with the general public as fertility control. Fertility control has been tried with several species of animals, among them,

kangaroos (Bamberg 1991), white-tailed deer (Plotka and Seal 1989, Kirkpatrick et al. 1997), foxes (Pech et al. 1997), rabbits (Robinson et al. 1997), grey squirrels (Moore et al. 1997), mice (Jackson et al.1998), and feral horses (Daels and Hughes 1995, Kirkpatrick et al. 1997).

Obviously, there are many benefits to be realized using fertility control in populations of wild or feral animals that are exceeding their carrying capacity. The most compelling reason for use, according to Kirkpatrick and Turner (1985) is that the approach is a humane one, far more socially acceptable today than hunting, trapping, or poisoning. There are economic benefits, as well. Long-acting contraceptives, in some cases, can now be administered remotely with tranquilizer guns, thereby avoiding costly capture and handling programs (Kirkpatrick and Turner 1985). For example, the cost of rounding up and removing ~ 70 feral horses on the PMWHR was estimated at $78,000 in 1997, whereas the price for a single dose of the immunocontraceptive vaccine, PZP, is about $25 (BLM 1997, Bama 1998). Fertility control, in some instances, has the added advantage of being a flexible management tool, because of its reversibility (Kirkpatrick and Turner 1985).

However, even though fertility control is a popular idea with the general public and is being promoted by humane organizations, the media, and researchers involved in its development, there continue to be unresolved questions concerning the impacts it will have on wildlife health (for a review of these concerns, see Nettles 1997). Thus, the American Association of Wildlife Veterinarians has recommended that fertility control in free-ranging wild animals only be used when certain criteria are met (Nettles 1997).

Among these, contraceptive methods should be used so as to not alter the gene pool of the species (or subspecies) or to adversely affect the health of the treated animal. Fertility control should also be limited to site-specific, well-defined subpopulations of species that are not classified as threatened or endangered (Nettles 1997). And finally, wildlife contraceptives should be easy to administer, cause minimal disruption to social structure and behavior, be fully reversible, and also cost effective (Daels and Hughes 1995).

One such method that appears to be safe, effective, and practical in horses is an intrauterine device (IUD) for fertility control in mares (Daels and Hughes 1995). Another solution, at least for feral horses and white-tailed deer, is the immunocontraceptive vaccine PZP, which essentially makes mares and does reject their own eggs. This vaccine can be delivered by darting the animal and does not affect existing pregnancies, nor does it alter behavior or social structure. In addition, it is reversible and does not pass into the food chain when the animal dies. It has recently been used to stabilize the feral horse population on Assateague Island National Seashore in Maryland with some success (Kirkpatrick et al. 1997).

A somewhat less contentious approach to managing deteriorating range conditions and other problems associated with rapidly increasing animal populations existing on fixed areas of land is the rest-rotation grazing system (Werner and Urness 1998). An idea developed in the late 1950's to protect vegetation from the harmful effects of selective herbivory (Hormay and Evanko 1958), rest-rotation grazing systems apparently help restore plant vigor, and promote seed production and seedling

establishment by giving different areas of vegetation a periodic rest from grazing (Hormay and Talbot 1961). Rest-rotation grazing systems, however, have received mixed reviews from wildlife managers because they have been used most often to improve livestock forage at the expense of wildlife values (Yeo et al. 1990). These systems apparently result in increases in grasses, rather than in shrubs, thus, favoring grazers rather than browsers (Hormay and Talbot 1961, Yeo et al. 1993). Additionally, some authors question the suitability of these grazing systems as methods for improving rangeland conditions in steep, mountainous terrain (Yeo et al. 1990), although others have shown improved use of upland areas in such terrain (Holecheck et al. 1989).

When multiple species are involved, as is the case in the PMWHR, the problem associated with this type of grazing system is that, depending on the type of fencing used, bighorn sheep and mule deer would likely be able to utilize forage in areas that are being 'rested' from horses. The regrowth response of the targeted forage depends, however, not only on the timing and intensity of the herbivory, but also on associated environmental and ecological conditions, such as soil moisture and plant competition (Trilica and Rittenhouse 1993, Briske and Richards 1994, Werner and Urness 1998). Thus, short-term forage production in rested areas may not be reduced. At the Sorenson extension site in the PMWHR, for example, which has continually been accessible to deer and sheep, but not to horses (since fall 1992), the standing crop of live grass was no different inside and outside the exclosure in 1992, when horses had access. After the horses were removed, however, mean live grass biomass was greater outside than inside the exclosure, and deer and sheep presumably were still utilizing the area (see Chapter

2). Werner and Urness (1998), on the other hand, found no differences in phytomass between areas subjected to or protected from elk herbivory in 1994, but average phytomass in protected areas was significantly higher than that in areas subjected to herbivory in 1995.

A rest-rotation grazing system has its drawbacks, the biggest one being that such a system requires a large investment of time and money to install and maintain. However, this type of system has proven, in many cases, to be a useful tool in the redistribution of habitat use by wildlife and livestock species and, therefore, in the prevention of range deterioration. More long term studies of the plants and animals that inhabit the PMWHR, specifically regarding habitat use and range condition, would no doubt be helpful in determining how best to install such a system.

Water catchments may also be useful in influencing habitat use patterns. There are currently two water catchments in the PMWHR, one on Sykes Ridge and the other one on Tillet Ridge. The Sykes Ridge catchment was inoperable during all three years of my study, and it is doubtful whether or not the other catchment was fully functional. Since funding must be appropriated for maintenance of existing facilities before any new construction is considered by the BLM (1984), perhaps the water catchments should be repaired first, and more long-term studies of animal distribution and movement patterns be conducted before investing too heavily in a system of rest-rotation grazing.

Grazing and browsing pressure by ungulates in the PMWHR was light to moderate during the three years of my study, but this situation obviously could change in the future. Even under light grazing pressure, 25% of the total range area produces no

forage, 66% of the producing range is in poor condition, and 33% of the producing range is considered by the BLM (1997) to be in fair to good condition. Not all of the management strategies offered above may be useful at present, but if ungulate populations continue to increase in the future, and/or managers decide that having more range in good condition is a desirable long-term goal, then perhaps one or more of these recommended tools could be utilized, either alone or in concert with one another, in improving the overall health of the Pryor Mountain Wild Horse Range.

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