VEGETATION RESPONSES TO GRAZING IN A HIGH ELEVATION, SOUTHERN APPALACHIAN WET MEADOW

A Thesis

by

Karen Elizabeth Geissinger

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APPROVED BY:

Howard S. Neufeld
Howard S. Neufeld
Chairperson, Thesis Committee

Robert P. Creed
Robert P. Creed
Member, Thesis Committee

Robert D. Sutter
Member, Thesis Committee

Zack E. Murrell
Member, Thesis Committee

Vicki J. Martin
Vicki J. Martin
Chairperson, Department of Biology

Judith E. Domer
Judith E. Domer
Dean of Graduate Studies and Research

ABSTRACT

VEGETATION RESPONSES TO GRAZING IN A HIGH ELEVATION, SOUTHERN APPALACHIAN WET MEADOW

(December 2000)

Karen Elizabeth Geissinger, B.A., Catawba College

M.S., Appalachian State University

Thesis Chairperson: Howard S. Neufeld

This study was designed to test the hypothesis that grazing by cattle affects aboveground net primary productivity (ANPP) and community structure in wetland bogs. My specific study focused on first year changes in Cold Prong Bog, a wet meadow located along the Blue Ridge Parkway (BRP) in North Carolina, following the exclusion of cattle. McNaughton's grazing optimization hypothesis was used as a model for how ANPP might respond to grazing elimination and Connell's intermediate disturbance hypothesis was the model for potential changes in species richness.

In May of 1999, cattle were excluded from a portion of the meadow. Previously, in 1998 baseline data were collected to assess the similarities between the two areas. The point intercept method was used to determine percent cover and species richness, while 1 m^2 plots were used to assess species frequencies. I estimated ANPP in both the grazed (using exclusion plots) and ungrazed areas at various times during the growing season using periodic harvests, and grazing exclusion chambers in the grazed portion of the meadow. I also conducted a clipping study on the ungrazed side. Sala and Austin's peak biomass method was used to estimate productivities in the ungrazed portion of the wetland because the more traditional end-of-season technique underestimated ANPP by nearly 50%.

In 1999, after the exclusion of cattle, percent biomass in both the ungrazed and grazed areas was dominated by two species groupings, grasses and forbs, which combined made up approximately 63% of the total biomass. After the first season of cattle exclusion, nonvascular plant cover significantly increased in the ungrazed area (from 4.0 ± 2.3% to 13.6 ± 2.9%) and there was a tendency, although not significant, toward increased woody cover in this same area. Species richness did not change.

McNaughton's grazing intensity index indicated that 52% of the standing crop was consumed. I could not detect a grazing effect for total ANPP between either the ungrazed (2.85 ± 0.49 g m^{-2} d^{-1}), grazed (2.34 ± 0.54 g m^{-2} d^{-1}) or clipped (2.89 ± 0.38 g m^{-2} d^{-1}) treatments.

In addition, I conducted a greenhouse study to examine the response of two perennial plant species that are preferred browse for cattle in high elevation wet meadows: *Carex lurida*, a native sedge, and *Holcus lanatus*, an introduced pasture grass. Ramets of both species were planted in large pots and allowed to grow for 13 weeks. Half the plants were clipped at two week intervals, and half were fertilized once with urea. Total aboveground production was estimated by periodic harvesting, while leaf gas exchange was measured with a Li-Cor 6200. Clipping reduced total production in *C. lurida* by half (24.0 ± 1.7 g vs 12.6 ± 0.9 g) and in combination with fertilization resulted in the lowest yields (10.8 ± 1.0 g). *H. lanatus* greatly out-produced *C. lurida*: nonclipped fertilized plants had maximum yields (92.3 ± 4.1 g), followed by nonclipped nonfertilized (63.3 ±

3.2 g). Fertilization had no effect on clipped plants (31.0 ± 1.8 g), but clipped plants that were fertilized suffered severe foliar injury.

Photosynthesis showed no treatment effects in *C. lurida*, and was only higher for *H. lanatus* in the two weeks after fertilization. There were no significant trends for stomatal conductance for either species. These results show that clipping inhibits growth in both species, and that *H. lanatus* is more responsive to fertilization than *C. lurida*.

A small experiment was designed to investigate the effects of *Puccinia coronata* on gas exchange rates of *H. lanatus*, using the Li-Cor 6200. Infection greatly reduced photosynthesis in nonfertilized versus fertilized plants but had no effect on stomatal conductance. In fertilized plants infection reduced photosynthesis again compared to nonfertilized plants, but not nearly as drastically. Water use efficiencies declined in response to rust infection. Lower carbon gain and water use efficiencies may affect community level processes in the field, such as succession and productivity. Thus levels of rust infection should be followed in the ungrazed portion of the wetland to see if they become an important factor in the future.

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DEDICATION

I would like to dedicate this thesis to my parents, Paulette and Thomas Geissinger, whose adventure for life continuously inspires me. Thank you for teaching me how to not only dream, but how to achieve my goals as well.

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INTRODUCTION

In the southeastern United States, mountain wetlands are a particularly important habitat for rare and endemic species. They are also some of the rarest and least protected ecosystems in the southern Appalachians. It is estimated that there has been an 85% loss of bog habitat in North Carolina alone, with only 1,000 acres of bog habitat remaining in all the southern Appalachians (Bainbridge *et al.* 1994). Along the Blue Ridge Parkway (BRP), which connects Great Smoky Mountains National Park in NC and TN and Shenandoah National Park in Virginia, there are several hundred rare plants and animals. Of these, approximately 100 are endemic or disjunct to the region and associated with wetland habitats, yet few of these lands are fully protected (Sutter *et al.* 1996). For example, the National Park Service allows cattle grazing on BRP lands in order to maintain a sense of historical continuity in the region. In 1996 there were 370 agricultural leases, with grazing permitted on approximately 3,500 acres of BRP lands, some of them wetlands (Sutter *et al.* 1996).

Because some wetlands on the BRP are reserved for cattle grazing, it is important to understand the effects of herbivory in these rare habitats. Grazing may either negatively or positively affect the rare and endangered species residing in these wetlands, depending on how the community and its individual species react. Large ungulate grazing has been well-studied on rangelands in the western United States and in naturally grazed ecosystems such as the Serengeti; however, much less is known about the ecological impacts of grazing in eastern grasslands and wetlands. Some of these effects include direct consumption of plant parts, recycling of nutrients from dung and urine (McNaughton 1979, McNaughton *et al.* 1983, Ruess 1988, Ball and Ryden 1984), trampling (Murdock 1994), plant growth promoting agents in ruminant saliva (Dyer 1980), and alterations in competition between browsed and non-browsed species (McNaughton 1979, Belsky 1987, Biondini *et al.* 1998).

Currently, there are two main theories surrounding the debate on the effects of herbivory on plant growth. The first argument is based on the idea that plants have evolved numerous defense mechanisms against herbivory and therefore the relationship between plants and grazers is an antagonistic rather than a mutualistic one. This theory states that although animals may benefit plants by pollinating flowers, dispersing seeds, fertilizing soil, and reducing the size of competitors, grazing per se does not benefit plants. For example, the removal of plant parts can reduce surfaces for photosynthesis and the absorption of nutrients and water, and can lower seed production and nutrient and carbohydrate supplies (Belsky 1986). Overall, a reduction in plant size decreases an individual's ability to capture sunlight, nutrients, and water, and therefore decreases competitive success.

The opposing view contends that plants may actually compensate in the presence of herbivores by increasing photosynthetic rates and reallocating substrates to plant parts that have not been grazed (McNaughton 1979, Wallace *et al.* 1984, Nowak and Caldwell 1984). In this case, the argument is that removal of plant tissue can increase photosynthesis due to a decrease in mutual leaf shading, and can lower the rate of leaf senescence thereby prolonging the active photosynthetic period. Grazers can also help to

conserve soil moisture by reducing the transpiration surface and can recycle nutrients from dung and urine (McNaughton 1979).

Grazing effects on productivity have been studied at both the individual and ecosystem levels. In this chapter I address the effects of grazing at the ecosystem level, and in the next section, I focus more on the effects herbivory has on the individual plant.

At the ecosystem level, McNaughton's experiments in Tanzania's Serengeti National Park have demonstrated that grazing strongly regulates aboveground net primary production (ANPP) in grasslands (McNaughton 1979). From these data, he proposed a grazing optimization hypothesis (GOH) which states that ANPP increases as grazing intensity increases, up to some optimal grazing level, at which point it decreases to a level below that of the ungrazed plants (Figure 1). According to this hypothesis, moderate grazing levels may actually increase ecosystem net productivity.

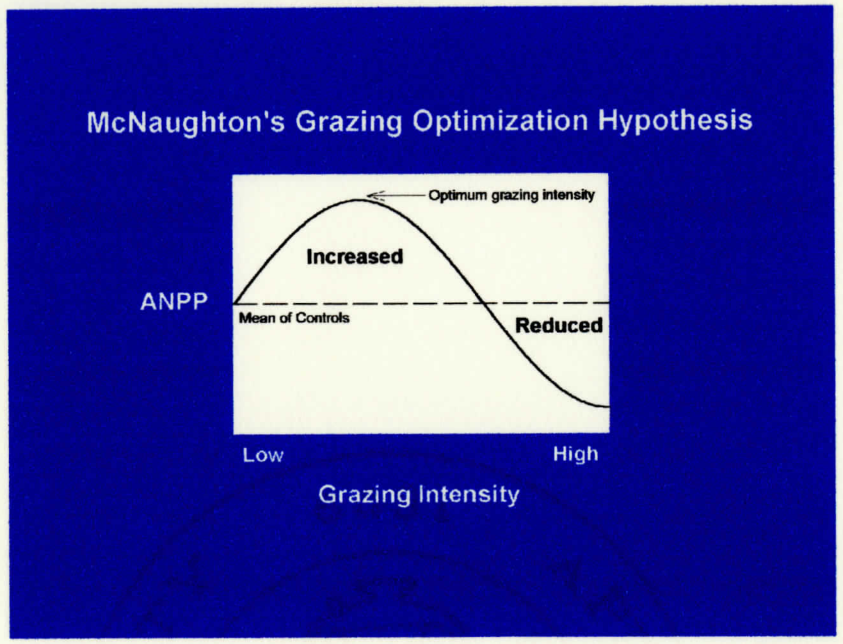

Figure 1. McNaughton's grazing optimization hypothesis which predicts a maximum aboveground net primary production (ANPP) at a moderate grazing intensity and a minimum ANPP at a high grazing intensity.

Several investigators have attempted to test McNaughton's idea that plants can overcompensate after grazing. Williamson *et al.* (1989), using eight grasshopper grazing intensities on blue grama grass, found that grazing never reduced ANPP compared with the ungrazed controls, which they took as evidence for compensatory growth. In addition, they found that following summer drought, light to moderate grazing intensities showed significantly greater ANPP than did a heavy grazing intensity, indicating that soil moisture variability should be considered when investigating herbivore effects on plant growth.

Alward and Joern (1993) also found evidence supporting the GOH, but only for species naturally constrained to lower-resource environments. These results further

demonstrate the need to consider multiple factors when investigating plant-herbivore interactions. Other authors (Belsky 1986, Black 1964) have acknowledged that overcompensation may occur, but only under limited conditions. For example, water and nutrients would have to be sufficient for regrowth to occur, grazing would have to take place early in the growing season in order to give plants adequate time to recover, and no other species could be in a position to gain a competitive advantage over the grazed species (Belsky 1986). In addition, herbivores would have to maintain a species close to its optimal leaf-area index (Black 1964), something that may be difficult to do.

Species richness is another community attribute that can be altered by grazing. Selective herbivory, for example, may be considered a type of disturbance that could possibly prevent competitive exclusion from occurring. Connell's Intermediate Disturbance Hypothesis (IDH) suggests a bellshaped curve of species richness along a stress gradient, predicting a maximum at a moderate disturbance level (Connell 1978). At increased levels of herbivory, richness could be limited due to the stress associated with intense grazing pressure and at low levels richness could be less than at intermediate levels due to competitive exclusion. Therefore moderate grazing may actually increase species richness in some habitats.

Numerous studies have documented increases in species richness in grazed systems (Tremont 1994, Milchunas *et al.* 1988, Kiehl *et al.* 1996, Harnett *et al.* 1996, Noy-Meir 1995). For example, sheep grazing studies conducted in salt marshes in northern Germany and in the Tablelands of New South Wales, indicate that species richness can either be maintained or increased by moderate grazing (Kiehl *et al.* 1996, Tremont 1994). Grazing by bison has been shown to increase plant species diversity in North American tallgrass prairies (Harnett *et al.* 1996) and in Mediterranean grasslands, species richness tends to be higher in grazed areas compared to ungrazed areas. The exclusion of grazers in these grasslands reduces the amount of gaps, which are necessary for the establishment of a variety of annual species (Noy-Meir 1995).

In areas that have been excluded from grazing, species capable of overtopping short species begin to dominate the area, reducing species richness (Belsky 1986, Milchunas *et al.* 1988, McNaughton 1979). For example, Belsky (1986) reports that three categories of species are eliminated in the Serengeti by excluding herbivores. These include 1) short species which get shaded out by taller ones, 2) species that suffer from self-shading, i.e. *Andropogon greenwayi*, which shades itself out because of accumulation of its own dead material that is normally removed by grazers, and 3) species that require specific seed bed attributes, i.e., *Themeda triandra*, a tall, short-lived species that requires high light and high soil temperatures for germination, conditions which are generally provided through the secondary effects of herbivory.

In addition to taller species having a competitive advantage in ungrazed areas, ungulate exclusion has also been associated with increased cover of woody species. Ritchie *et al.* (1998) reported that seven years of herbivore exclusion in an oak savanna significantly increased the cover and biomass of woody plants by approximately 400% and 800% respectively, suggesting that herbivory may prevent the succession of grasslands to woodlands in savanna openings. Similarly, in Kirkman *et al.*'s (in press) ecotone characterization between upland longleaf pine/wiregrass stands and seasonally-ponded isolated wetlands, absence of disturbance (fire in this case) rapidly leads to a shrub-dominated transitional zone.

In some southern Appalachian bogs, increased woody cover due to herbivore exclusion is a particularly important topic now because they are currently being invaded by shrubs and trees. This invasion threatens to accelerate succession toward a forested community, decreasing much of the herbaceous vegetation in these areas (Schafale and Weakley 1990). Since some of the species in these bogs are rare or endangered (the Bog Rose, *Arethusa bulbosa*, Swamp Pink, *Helonias bullata*, and Gray's Lily, *Lilium grayi*; to name a few) this process is of great concern. Thus the study of grazing impacts in these high elevation wetlands is important because it may yield information on the mechanisms involved in maintaining open wetlands amidst deciduous forests.

My study was a part of a larger project funded by the National Park Service and developed by The Nature Conservancy. The overall project was designed to evaluate the long-term effects of cattle grazing in Cold Prong Bog, a wet meadow located along the BRP in North Carolina. My work focused on first year changes following the exclusion of cattle in order to evaluate any initial alterations in community structure and function. McNaughton's GOH was used as a model for how ANPP would respond to grazing elimination and Connell's IDH was used as a model for potential changes in species richness.

I had two objectives in this study. First, I wanted to study community structure between the grazed and ungrazed areas. I predicted that 1) grazing would maintain species diversity in wetland habitats, 2) woody cover would increase in the area excluded from cattle, 3) shade tolerant species would become more prevalent in the ungrazed area (Schlapfer *et al.* 1998), and finally 4) sphagnum cover would increase in the ungrazed area due to less trampling and lower nutrient input associated with the removal of cattle (Bainbridge *et al.* 1994, Murdock 1994, Li and Vitt 1994). My second objective was to determine what effect cattle grazing had on net primary productivity by comparing a grazed treatment area to an ungrazed control area.

STUDY SITE

This study was conducted in Cold Prong Bog, a 9.6 hectare (ha) pasture area located along the Blue Ridge Parkway (mile point 297) near Blowing Rock, North Carolina (Figure 2). The Cold Prong Bog wetland complex contains several distinct habitats: a boggy area dominated by sphagnum with a closed canopy, a boggy area dominated by sphagnum with an open canopy, a floodplain levee dominated by a mixture of native and non-native grasses, and a graminoid-Juncus wet meadow (Sutter *et al.* 1996). Soils in this pasture are frequently flooded, Nikwasi loams, ranging from sandy to silty.

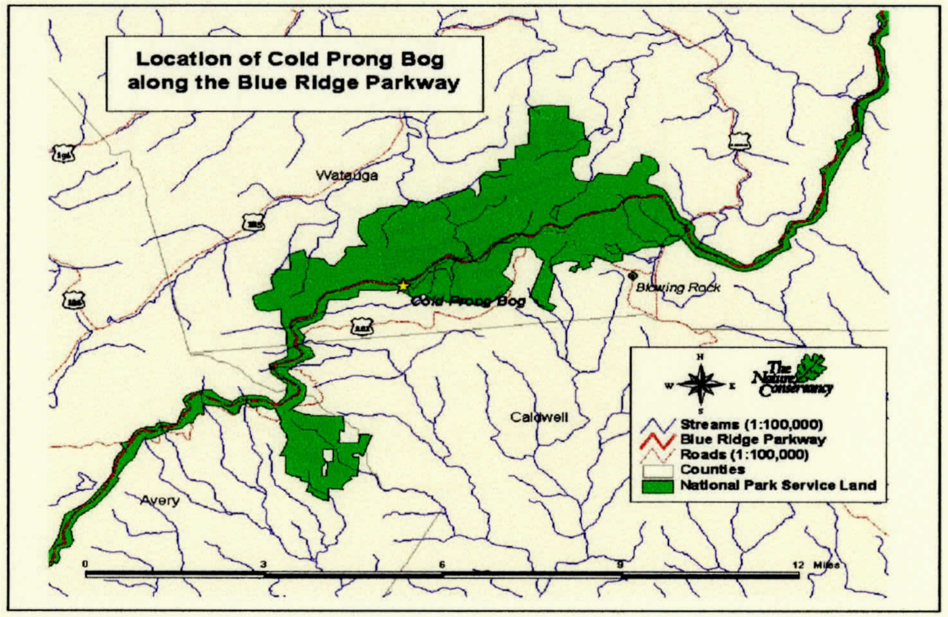

Figure 2. Cold Prong Bog wetland complex location along the Blue Ridge Parkway south of Blowing Rock North Carolina.

The study sites chosen for experimentation were located in the levee dominated by mixed grasses and the graminoid-Juncus wet meadow, primarily due to the limited area in the other habitat types and because this area was subjected to heavy grazing. The current grazing lease for Cold Prong Bog was acquired in 1962, but this area has probably been grazed since at least the 1930's when the Blue Ridge Parkway was established. The stocking density over the two years of experimentation was approximately 1 cow/ha with the grazing season opening within the first two weeks of May and extending through early October.

In the summer of 1998, before grazing was eliminated from a section of the bog, two plots were established for sampling, one each in the grazed and ungrazed treatment areas (Figure 3). During the first week in May 1999 a fence was constructed in order to exclude cattle from grazing in the ungrazed treatment area. Each plot was 10 m by 40 m in size with five 40 m line transects running the length of each plot.

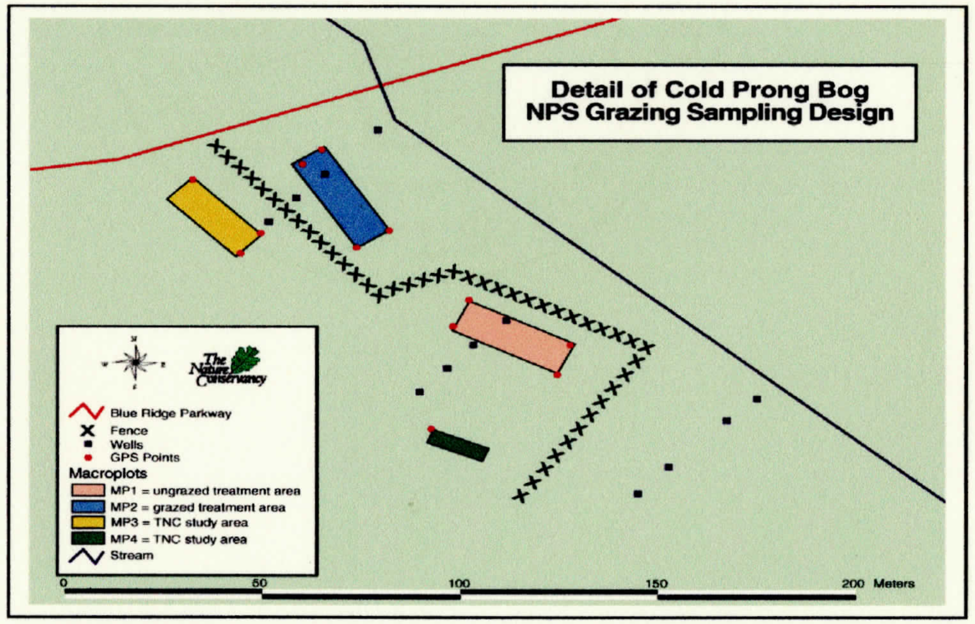

Figure 3. Cold Prong Bog study area after the fence was constructed to exclude cattle from the ungrazed treatment area.

The wetland area comprised only about 0.8 ha. Although this limits the ability to make conclusions about the impacts of grazing, I did extensively analyze conditions in both areas prior to imposition of the treatments to be able to determine if differences later on were the result of cattle or *a priori* effects. In addition, these wetlands are rare in the southern Appalachian mountains (Murdock 1994); they are naturally small (Cold Prong Bog being one of the largest) and there are few other areas of similar community structure (Fleischner 1994).

METHODS

Hydrology and Soil Resistance

During the summer of 1997 a series of 13 PVC wells were constructed in Cold Prong Bog in order to monitor hydrological fluctuations. Three transects were established, each crossing the wetland gradient from the levee to the wettest portion of the bog. Wells were placed 10 m apart for a total of four wells per transect (Figure 3). Seven wells (including one complete transect) were in grazed portions of the wetlands and six in the ungrazed portion. All wells were monitored every week for two years; however, I only looked at data from the four wells that were directly located within my study plots.

In 1998, before cattle were excluded, soil resistance measurements were taken in order to compare soil density characteristics between the ungrazed and grazed areas. Measurements were made with a penetrometer in the center of 15,1 m^2 plots in both the ungrazed and grazed areas.

Community Composition

Percent Cover.- Percent cover was estimated during the second week of August in both 1998, before the cattle were excluded, and in 1999, after cattle exclusion, using the point intercept technique (Elzinga *et al.* 1998). This method estimates cover based on the number of hits for a species out of the total number of points measured. The five transects set up in each treatment area were used as permanent sampling units. A slim steel rod (3 mm in diameter, 1m long) was used and dropped every .30 m along the length of each transect, for a total of 100 points per line. All vegetation touching the pointer at each location was recorded by species. Relative cover was calculated for each species as

percent of total cover per line. Percent cover was then summed for each species group (fern, forb, grass, nonvascular, rush, sedge, and woody).

Frequency.- A quadrat size of 1.0 m^2 was used to estimate species frequency. Three permanent plots were randomly located using a random numbers table along each of the five transects in both treatment areas for a total of 15 plots in each area. Within these plots species were recorded on a present/absent basis. All measurements were done during the second week in August in both 1998 and 1999.

Species richness.- Species richness was calculated using a combination of the quadrat and point intercept data. For total species richness, all species encountered in each 1.0 m^2 plot in each treatment area were counted. These were then compared to the list of species from the point intercept technique in order to create a more comprehensive species list.

From the community structure data I calculated a coefficient of community (CC) for the two years of study,

$$\mathrm{CC} = \frac{2c}{a + b} \qquad (1)$$

where a = the number of species in the ungrazed area, b = the number of species in the grazed area, and c = the number of species present in both areas at the same time (Whittaker 1975).

Species Identification.- Species were identified using Weakley (2000) and Radford *et al.* (1964). There were some difficulties associated with identifying a few of the species in the study area. For example, there were two different species of *Agrostis*, which I have named *Agrostis* sp.1 and *Agrostis* sp. 2. I was unable to identify either of them to species, yet I knew they were distinct taxa. I was also unable to identify one *Sisyrinchium* species. One initial difference between the two study areas prior to the exclusion of cattle was the presence of *Scirpus expandus* in the grazed area but not in the ungrazed area in 1998. In 1999; however, a species of *Scirpus* did occur in the ungrazed area. Although this was not *S. expandus*, it was unidentifiable at the time.

For ease in collecting data I simply placed all moss species, with the exception of *Polytricum commune* and *Sphagnum* sp., in a category entitled "moss". Due to lack of fruiting or flowering parts at the time of sampling, I was unable to identify either *Poa* or *Viola* to species. Finally, there may have been two species of *Festuca*. In 1998 I found one *Festuca* species that I called *Festuca* sp. In 1999 my identification skills improved and I identified a *Festuca* as *F. rubra*. It is very likely that *F.* sp. and *F. rubra* are the same; however, due to the difficulty in identifying *Festuca* species and the possibility that they are different species, they remain in separate categories.

Importance Value.- Importance values (IV's) were calculated for both the grazed and ungrazed areas using the frequency, cover, and biomass data (biomass data are described below). IV's were only calculated for 1999 because biomass data were not collected in 1998. The IV's were calculated as the sum of relative cover, frequency and biomass for each species (Brower 1997). These values were then compared in order to see if any large differences occurred between the two study areas as a result of the elimination of cattle grazing.

Net Primary Productivity

ANPP data were collected in the summer of 1999 after the fence had been constructed. In both the ungrazed and grazed sampling plots two 1.5 m^2 quadrats were randomly located along each of the five transects, for a total of 10 plots per treatment area. These quadrats were separated into 0.25 m^2 subquadrats, which were then randomly designated a month for harvesting: June, August, or September. The midpoint for each harvesting interval was used to determine the length of the growth period. For both the ungrazed and grazed areas, total seasonal productivity was calculated (total ANPP), as well as, two intra-seasonal productivity estimates (represented as NPP_1 and NPP_2).

Ungrazed Area.- In the ungrazed treatment area subquadrats were harvested by species to ground level each of the three sampling months: June (6/2 through 6/7), August (8/3 through 8/11), and September (9/13 through 9/15). The plant material was then dried for approximately two weeks at 65°C, and weighed. In addition a clipping experiment was conducted in the ungrazed treatment area in order to simulate the effects of grazing. One 0.25 m^2 quadrat was randomly located on each of the five transects. These quadrats were clipped to a height of approximately 5 cm at three time intervals (12 June, 15 July, and 13 August) and harvested to ground level on 30 September. All plant material was dried for approximately two weeks at 65° C and weighed. NPP_1 in this area represented the productivity between 5 June and 7 August and NPP_2 represented productivity between 8 August and 14 September. Intra-seasonal productivity was calculated as:

$$NPP_1 \text{ or } NPP_2 = [\text{Biomass}_{(t+1)} - \text{Biomass}_{(t)}] / \Delta\text{days}, \quad (2)$$

where NPP_1 and NPP_2 are g m^{-2} d^{-1}, Biomass $_{(t+1)}$ is the biomass of the harvest at the end of an interval, biomass $_{(t)}$ is the initial harvest for an interval, and Δdays is equal to the number of days between the two harvests. In the ungrazed area the number of days was 64 for NPP_1 and 39 for NPP_2.

Total seasonal productivity was calculated using two methods: end-of-season measurements and peak biomass measurements (Sala and Austin 2000). End-of-season measurements were calculated as:

$$\text{Total ANPP} = \text{Final Biomass} - \text{Initial Biomass} / \Delta\text{days} \qquad (3)$$

where total seasonal productivity was calculated as g m^{-2} d^{-1}, final biomass is the September harvest, initial biomass is the June harvest, and Δdays is the number of days in the growing season. In 1999 this was 103 days.

The peak biomass technique takes into account seasonal differences in the timing of the peak biomass for each species. Productivity using this method is done by summing all the differences in peak (maximum) versus trough (minimum) biomass for each species, and dividing that result by the number of days in the growing season:

$$\text{Total ANPP} = \Sigma(\text{peak-trough})_i / \Delta\text{days} \qquad (4)$$

where $(\text{peak-trough})_i$ is the difference in biomass for species i, and Δdays is the number of days in the growing season.

In the clipped treatment only one productivity interval could be calculated ($CNPP_1$: 12 June through 13 August). Because the final harvest clippings were not separated from the rest of the standing crop below 5 cm, an estimate of productivity between August and September could not be made.

$CNPP_1$ was calculated as:

$$CNPP_1 = (C_1+C_2) / \Delta\text{days} \qquad (5)$$

where C_1 is equal to the June clipping biomass, C_2 is equal to the August clipping biomass and Δdays is the number of days in the clipping interval (64 days).

Total seasonal productivity of the clipped plants was calculated as:

$$\text{Total CNPP} = C_1+C_2+SC / \Delta\text{days} \qquad (6)$$

where SC is equal to the standing crop taken in September and all other terms are as before.

Grazed Area. - In the grazed area I had to account for the plant material lost due to consumption by the cattle. Therefore temporary exclosures were placed around one of 10 randomly located 0.25 m^2 subquadrats on 23 April. Plant material located inside the exclosures was allowed to grow for approximately four weeks (23 April through 9 June) after which it was harvested by species. At this time the exclosures were moved to another 0.25 m^2 area within the same quadrat. This portion of the quadrat had been grazed up until this point and plant material now enclosed was freed from grazing pressure for approximately another four weeks (9 June through 31 July).

At the end of this time interval the method was repeated one more time (31 July through 10 September), for a total of three harvests. Sampling dates were June (6/9 through 6/12), August (7/29 through 7/31), and September (9/1 through 9/10). An additional harvest was conducted at the end of the season (19 September through 23 September) in the 0.25 m^2 portions of the quadrat that had been continually grazed throughout the season in order to determine final standing crop. All plant material was separated by species, dried at 65° C for approximately two weeks, and weighed.

NPP_1 in this area represented productivity between 10 June and 30 July and NPP_2 represented productivity between 31 July and 5 September. Intra-seasonal productivity estimates were calculated as:

$$NPP_1 \text{ or } NPP_2 = [\text{Biomass}_{(\text{exclosure})} - \text{Biomass}_{(\text{grazed})}] / \Delta\text{days} \quad (7)$$

where $\text{Biomass}_{(\text{exclosure})}$ is the biomass within the exclosure, $\text{Biomass}_{(\text{grazed})}$ is the biomass at the end of the season harvest (which was continually grazed throughout) and Δdays is the number of days in the growing season (138 days). Normally, one compares $\text{Biomass}_{(\text{exclosure})}$ to the biomass outside the exclosure at each harvest time (McNaughton *et al.* 1996) but due to the limited area available for sampling, I had to restrict myself to an end-of-season sample. This could bias the estimate, but based on my observations, the areas outside of the exclosures did not change much in stature nor in my estimation, biomass either. Therefore I used an end-of-season value. Total productivity was equal to the sum of each intra-seasonal productivity estimate.

Grazing Intensity and Consumption.- Grazing intensity and consumption calculations were derived from McNaughton (1985). Grazing intensity (GI) was calculated as:

$$GI = \left[1 - \frac{Cg}{Cu}\right] \times 100 \quad (8)$$

where C_g is the mean biomass in the grazed area, C_u is the mean biomass in the ungrazed area, and GI is the percent of the standing crop missing due to grazing. Consumption was calculated as:

$$C = ANPU - ANPG \quad (9)$$

where ANPU is aboveground net primary production in the ungrazed area, ANPG is aboveground net primary production in the grazed area, and C is the amount of plant material consumed by cattle and expressed as g/m^2.

Species Groupings and Biomass.- Biomass data were further analyzed at both the species groupings and species levels, in order to determine which groups of species and which individual species were contributing the most to the productivity of the wetland. Species were separated into five major groupings: woody species, forb species, grass species, a grouping containing both the ferns and nonvascular species, and a grouping combining the rush and sedge species. Species grouping biomass was expressed as a percent of the total community biomass. Species data within species groupings were expressed in absolute terms in grams.

Statistical analysis.- In order to compare percent cover for both 1998 and 1999, a two-sample t-test was conducted for each species group using Microsoft Excel. All initial productivity calculations and comparisons among treatments were performed using SAS (1989). Productivity values among the ungrazed, grazed and clipped treatments were analyzed with Analysis of Variance, using the General Linear Model procedure. For all statistical tests, $p<0.05$ was considered significant and transforming the data did not change the results, so all analyses were done on just the untransformed data. All data are reported as mean ± standard error.

RESULTS

Site Characteristics Prior to Cattle Exclusion (the 1998 season):

Soil resistance, hydrology, and species composition were evaluated in 1998, prior to the elimination of cattle in order to assess the similarities between the two study areas.

Soil Characteristics and Hydrology.-Soil resistance was similar for both areas with values of 2.43 ± 0.96 kg/cm^2 in the ungrazed area and 2.38 ± 0.93 kg/cm^2 in the grazed area. Hydrological fluctuations for both areas are shown in Figure 4. Ground water in both areas rarely came to the surface. Only after a heavy rain would the surface briefly become saturated. In the ungrazed area the water table ranged from –17 to –77 cm below ground level while in the grazed area it ranged from –29 to –73 cm. The ungrazed area had greater water fluctuations than the grazed area in 1998 although the reasons for these differences are not known. However, the general trend over time was similar for both areas.

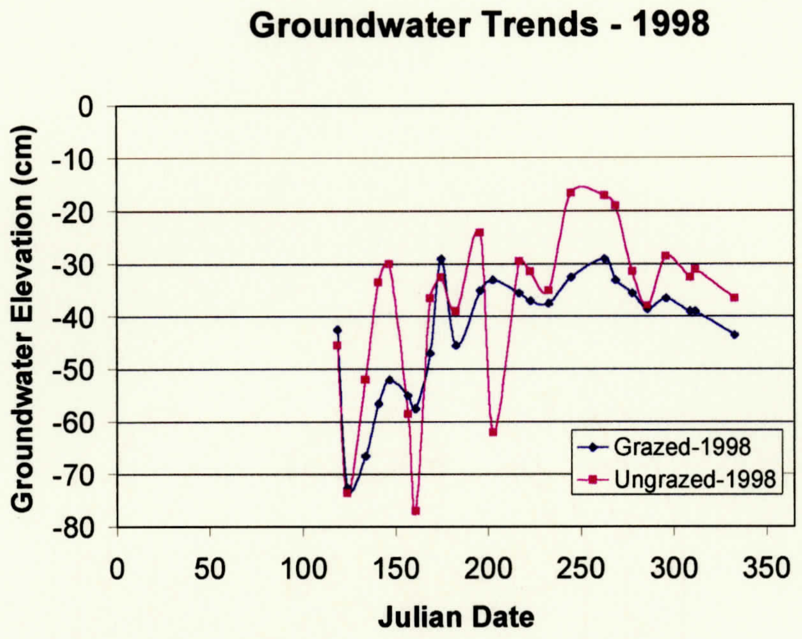

Figure 4. Groundwater trends for the ungrazed and grazed areas of Cold Prong Bog in 1998. Values represent water elevation below ground level.

Community Attributes.-There were no significant differences in percent cover for any of the major species groups (fern, forb, grass, nonvascular, rush, sedge, and woody) between the ungrazed and grazed treatment areas (Figure 5). Before cattle were excluded, 40 species were recorded in the ungrazed area and 42 in the grazed area (Appendix A). There were, however, some differences in actual species composition. *Mitchella repens* and *Senecio aureus* were found in the ungrazed area and not the grazed area, while *Hypericum mutilum, Scirpus expandus, Sisyrinchium sp.,* and *Veronica officinalis* were found in the grazed but not the ungrazed area.

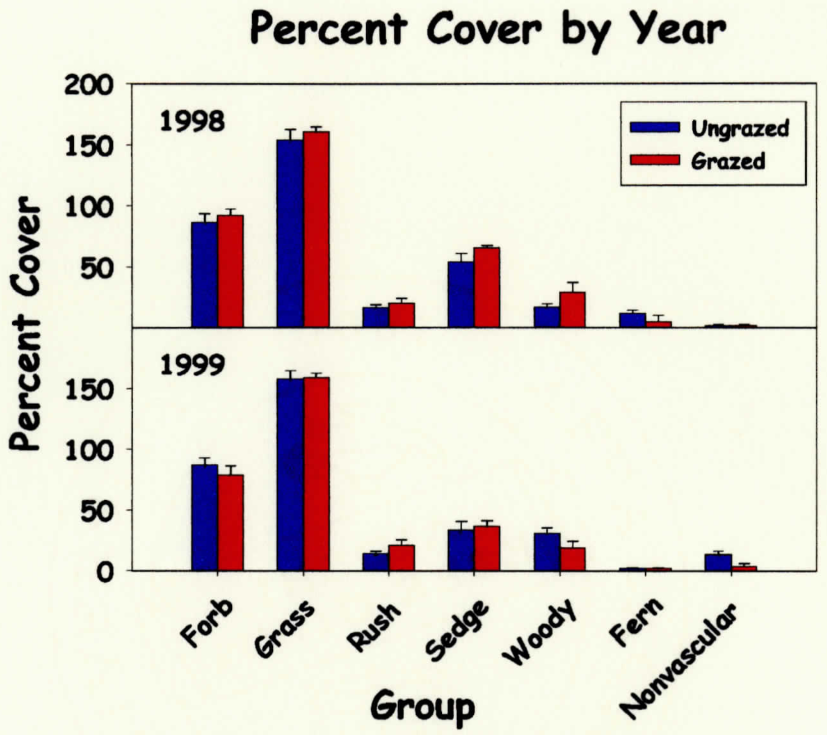

Fig. 5. Mean percent cover of the seven major species groups before (1998) and after (1999) cattle exclusion (n=5). Vertical bars represent mean ± SE and (*) represents significance at the p≤0.05 level.

Site Characteristics After Cattle Exclusion (the 1999 season):

Soil Characteristics and Hydrology.-Soil resistance measurements were not repeated in 1999. Hydrological fluctuations were similar to those in 1998 with the water table in the ungrazed area ranging from –14 to –70 cm below ground level and from –24 to –55 cm in the grazed area (Figure 6). The water table again did not reach the surface except after heavy rains and it fluctuated more in the ungrazed area, but still showed the same trend over time as the grazed area.

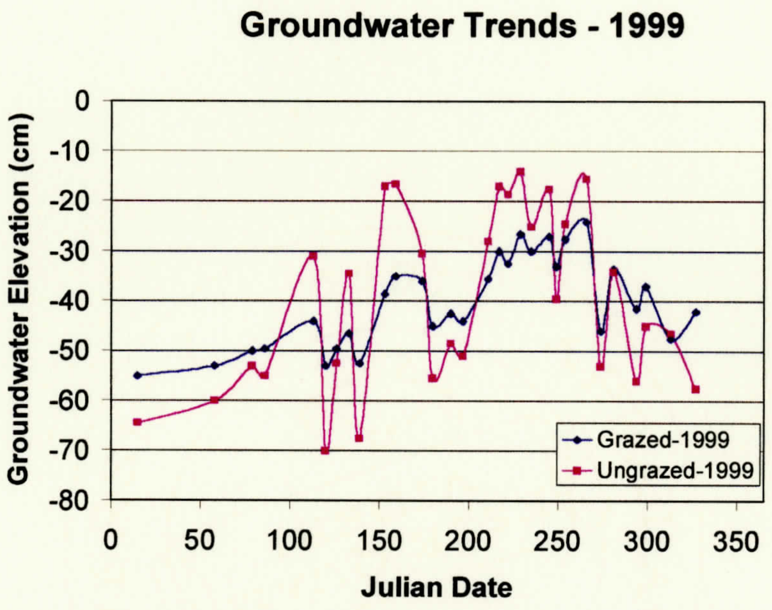

Figure 6. Groundwater trends for the ungrazed and grazed areas of Cold Prong Bog in 1999. Values represent water elevation below ground level.

Community Attributes

Percent Cover.-There were slight differences in percent cover between the two areas after elimination of grazing (Figure 5). Nonvascular species showed a significant increase in 1999 in the ungrazed area, with percent cover tripling from 4.0 ± 2.3% to 13.6 ± 2.9%. There was also a trend, although not significant, toward a higher percent cover of woody

species in the ungrazed area. There were no significant differences for any of the other species groups.

Species richness.-Total species richness in the ungrazed and grazed areas was the same, with 47 species recorded in each area (Appendix A). Although these numbers were equal, there were as in 1998, some differences in species composition. For example, the following species were found in the ungrazed area but not in the grazed area in 1999: *Acer rubrum, Kalmia latifolia, Lygodium palmatum, Nyssa sylvatica, Scirpus sp.,* and *Smilax glauca*. Furthermore, these species had not been found in either the ungrazed or grazed areas in 1998, which also accounts for some of the differences in species richness between the two years. Six species were located in the grazed area but not the ungrazed area, and included *Achillea millifolium, Carex intumescens, Dichanthelium clandestinum, Scirpus expandus, Sisyrinchium sp.,* and *Veronica officinalis*. All of these species had been previously found in the grazed area in 1998 except *D. clandestinum* and *C. intumescens*. Of the six species found in the grazed area but not in the ungrazed area in 1999, only *A. millifolium* was recorded in the ungrazed area in 1998.

Species richness was relatively similar between the ungrazed and grazed areas in both 1998 and 1999 with the exception of a few species, mostly woody, accounting for the small changes in richness between the two sampling years. The coefficient of community, an index of species similarity between two communities, illustrates this fact with a value of 0.927 in 1998 and 0.872 in 1999.

Importance Value.-The importance values for all species are shown in Appendix B. The grazed and ungrazed areas had seven of their top ten species in common, including

Vernonia noveboracensis, Holcus lanatus, Viola sp., Festuca rubra, Agrostis sp., Juncus effusus, and *Potentilla canadensis*. There were 16 species that had differences in IV's between the grazed and ungrazed areas that were greater than 10. Of these 12 had higher IV's in the ungrazed area (*Dichanthelium dichanthelium, Danthonia compressa, Glyceria melicaria, Mitchella repens, Clematis virginiana, Carex scoparia, Carex swanii, Acer rubrum, Juncus coriacious, Rubus argutus, Polytricum commune*, moss) and only four were of higher importance in the grazed area (*Carex* sp., *Hypericum canadense, Eupatorium perfoliatum, Sisyrinchium* sp.). Differences in IV's could not be narrowed down to either relative cover, relative frequency or relative biomass since they were a result of varied combinations of the three categories.

Aboveground Net Primary Productivity.- Results from the two intra-seasonal net primary productivity intervals for both the grazed and ungrazed areas (NPP$_1$ and NPP$_2$) are provided in Figure 7. An outlier plot was detected in the ungrazed area during the September harvest with a biomass amount that was seven standard deviations above the mean. This was due mainly to a large clump of *Vernonia noveborascensis* located in that plot.

V. noveborascensis is common throughout the study area, highly clumped in distribution, and appears late in the growing season. It is also not browsed by cattle. Therefore I decided to analyze the productivity data both with and without this outlier. For NPP$_1$, productivity in the grazed area was 2.92 ± 0.54 g m^{-2} d^{-1}. This was significantly higher ($p = 0.045$) than productivity in the ungrazed area with the outlier

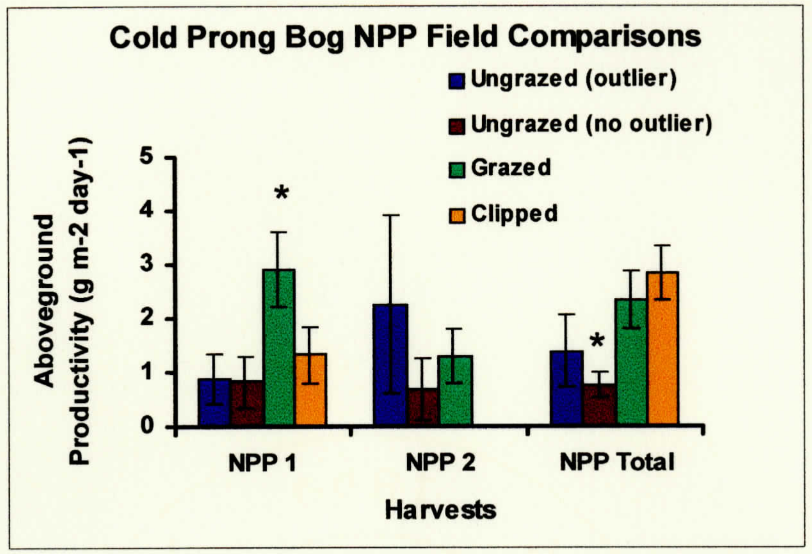

Fig. 7. Aboveground production (ANPP) of grazed, ungrazed, and clipped vegetation at three productivity intervals in 1999: two intra-seasonal intervals (NPP$_1$ and NPP$_2$) and one total seasonal ANPP estimate calculated using the end-of-season method. Vertical bars represent mean ± SE and * represents a significant difference within a group at the $p<0.05$ level 7.

(0.88 ± 0.47 g m^{-2} d^{-1}) and without ($p = 0.05$) the outlier (0.83 ± 0.52 g m^{-2} d^{-1}), and also significantly higher ($p = 0.045$) than the clipped treatment (1.33 ± 0.51 g m^{-2} d^{-1}). By the second interval (NPP$_2$), there were no significant differences between the ungrazed area with the outlier (2.26 ± 1.66 g m^{-2} d^{-1}) or without the outlier (0.68 ± 0.58 g m^{-2} d^{-1}) versus the grazed area (1.3 ± 0.50 g m^{-2} d^{-1}).

Results from the end-of-season method for calculating ANPP (Sala and Austin, 2000) are shown in Figure 7. Total seasonal ANPP on the grazed side was 2.34 ± 0.54 g m^{-2} d^{-1}, which was not significantly different from the clipped production of 2.85 ± 0.49 g m^{-2} d^{-1}. Total seasonal ANPP results on the ungrazed side varied depending on if the outlier was present. With the outlier (1.4 ± 0.66 g m^{-2} d^{-1}) the ungrazed production was not significantly different from either the grazed or clipped production. ANPP for the ungrazed area without the outlier (0.77 ± 0.23 g m^{-2} d^{-1}), however, was significantly different ($p = 0.013$) from both the grazed and clipped treatments.

A review of the seasonal trends in biomass data for all the plots showed that some species were peaking at different times during the growing season (Figure 8). For example, *Holcus lanatus* peaked early in the growing season, then steadily declined throughout the season, while *Vernonia noveboracenis* peaked late in the season. Other species had most of their growth in the middle of the season, such as, *Dichanthelium dichotomum* var. *dichanthelium*, which slowly accumulated biomass from June to August and then declined from August to September.

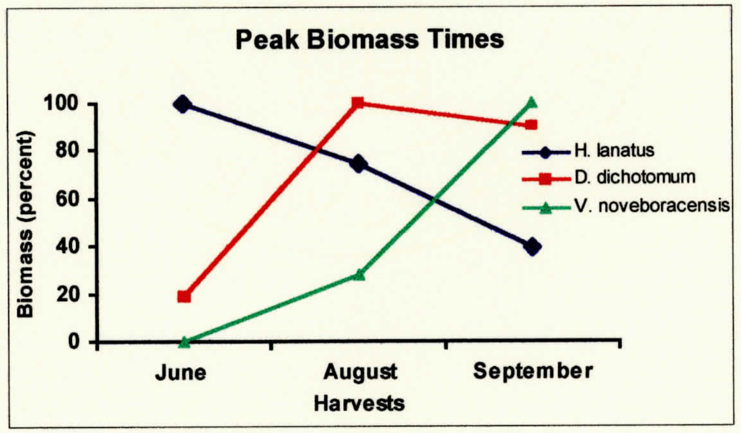

Fig. 8. Peak biomass times (expressed as a % of total biomass) of three species in the ungrazed area of Cold Prong Bog in 1999: *Holcus lanatus, Dichanthelium dichotomum* var. *dichanthelium, Vernonia noveboracensus.*

Such divergent growth patterns can result in underestimation errors when calculating productivity by using only end-of-season biomass estimates (Sala and Austin 2000). To see how great these errors might be, I compared the-end-of season method with the peak method for calculating productivity (Figure 9). Based on this comparison, I probably underestimated productivity in the ungrazed area by almost 50% by using the end-of season method. Therefore, I chose the peak biomass technique to compare total seasonal ANPP among the three treatments (Figure 10). When I did this I found no significant differences among the ungrazed, grazed or clipped treatments (2.89 ± 0.38 g m^{-2} d^{-1}, 2.34 ± 0.54 g m^{-2} d^{-1}, and 2.85 ± 0.49 g m^{-2} d^{-1} respectively).

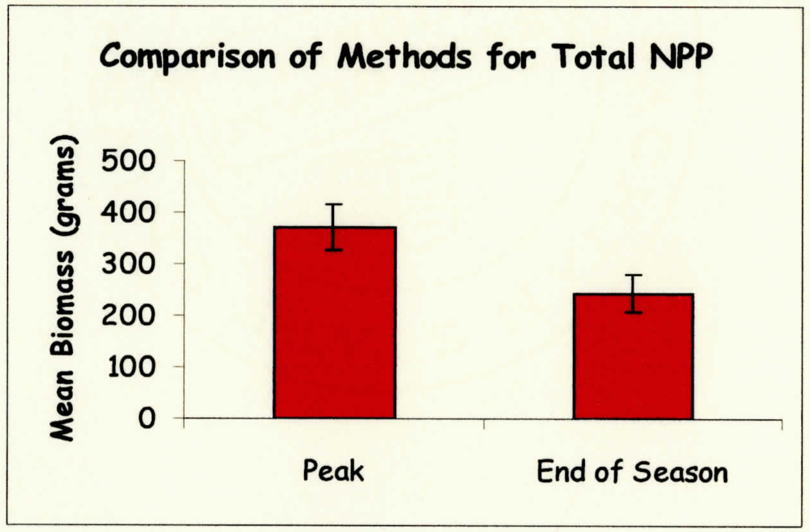

Fig. 9. Total seasonal productivity estimates of ungrazed vegetation in 1999 by two methods: the peak biomass method and the end-of-season method (n=10). Vertical bars represent mean ± SE.

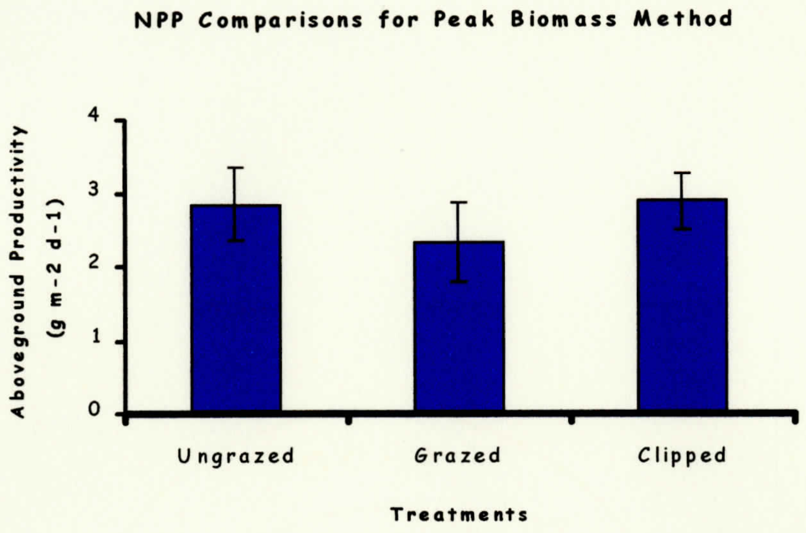

Fig. 10. Total seasonal aboveground production of ungrazed, grazed, and clipped vegetation in 1999 using the peak biomass technique (n=10). Vertical bars represent mean ± SE.

Grazing Intensity and Consumption.-McNaughton's grazing intensity index (McNaughton 1985) ranges from 0%, when there is no difference in the standing crop between the grazed and ungrazed sites, to 100% when there is no standing crop at all on the grazed site. In my study, the grazing intensity index indicated that 52% of the standing crop had been removed by the cattle. The consumption calculation (McNaughton 1985), a measure of how much biomass was being consumed by the cattle, was 113.3 g/m^2 for the period 2 June to 10 September (101 days).

Species grouping and Species Biomass.-In 1999, after the exclusion of cattle, percent biomass was dominated by two species groupings, the grasses and the forbs, which combined made up approximately 63% of the total biomass in both the ungrazed and grazed areas (Figure 11). For the remaining three species groupings the percent biomass varied depending on whether it was in the ungrazed or grazed area. The rush-sedge species grouping made up approximately 12% of the biomass in the ungrazed area, but 20% in the grazed area. The woody species grouping contained 12% of the biomass in the ungrazed area, and 15% in the grazed area, while the fern-nonvascular species grouping had 13% of the biomass in the ungrazed area compared to less than 1% in the grazed area.

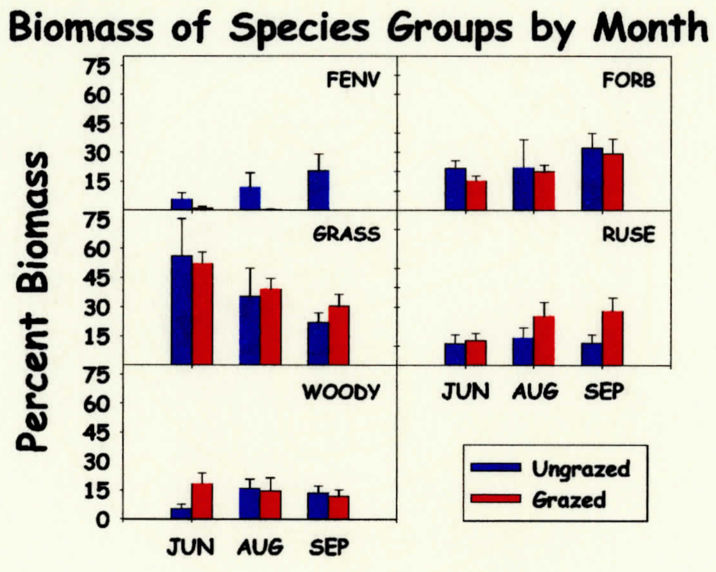

Fig. 11. Biomass (expressed as a percent of total biomass) by month for the five major species species groupings in Cold Prong Bog in 1999 in the grazed and ungrazed treatment areas. (FENV=fern and nonvascular species, RUSE=rush and sedge species). Vertical bars represent mean ± SE and n=10.

Within the grass species grouping the two most abundant species were *Holcus lanatus* and *Anthoxanthum oderatum*. These species were followed in importance by the two *Festuca* species. In the ungrazed area, *Festuca* sp. dominated, while in the grazed area, *Festuca rubra* dominated. As stated earlier, it is likely that these two *Festuca* species are the same. In the forb species grouping, *Vernonia novaboracensis* made up most of the biomass, followed by *Solidago* sp. and *Viola* sp. in both areas. In the rush-sedge species grouping there was an initial difference between the two treatment sites with *Scirpus expandus* growing in the grazed area, but not the ungrazed area. Other common species in the grazed area included *Juncus effusus* and *Carex lurida*. *Juncus effusus* and *Carex lurida* were also common species in the ungrazed area, followed by *Carex vulpinoidea*. Within the woody species grouping the main species for both the grazed and ungrazed areas were *Rubus argutus* and *Rosa palustrus*.

DISCUSSION

Slight changes in community structure were detected in 1999, after cattle exclusion, with the only significant increase being the cover of nonvascular species in the ungrazed area. I had predicted that nonvascular species, in particular sphagnum, would increase in the ungrazed area due to the removal of secondary effects of cattle. For example, I hypothesized that trampling was limiting nonvascular cover and that removal of cattle would result in its increase (Murdock 1994). This may have been the case for *Polytricum commune*, a common nonvascular species in Cold Prong Bog, which had higher relative cover, frequency and biomass values in the ungrazed area compared to the grazed area, making it the fourth most important species in the ungrazed area, but only the 21st most important in the grazed area.

I also hypothesized that the exclusion of cattle would enable sphagnum, which is adapted to very low nutrient environments (Krohne 1998) and cannot tolerate high nutrient loads (Bainbridge et al. 1994), to recover due to a reduction of nutrients from dung and urine. Since wetlands are extremely sensitive to hydrologic changes, sphagnum moss can be an important community regulator in these areas due to its ability to hold up to 20 times its weight in water (Brewer 1994). In very dry years this water holding capacity may be increasingly important because sphagnum can conserve water and prevent the upper soil layers from completely drying out (Murdock 1994). However I could not yet detect changes in sphagnum cover at this time. Sphagnum showed similar importance in both the ungrazed and grazed area with a value of 30 in the ungrazed area and 29 in the grazed area.

In addition to an increased cover of nonvascular species, there was also a tendency toward increased cover of woody species in the ungrazed area, although these results were not statistically significant. Previous studies have suggested that woody species encroachment can facilitate succession in wetland habitats and if future research in Cold Prong Bog finds that this trend is significant, then succession toward a more forested community may be a consequence of this increased woody cover. Increased woody cover has also been shown to favor shade-tolerant species (Schlapfer *et al.* 1998).

The absolute number of woody species also increased in the ungrazed area following cattle exclusion, which can partially account for the slight increase in species richness in the ungrazed area before and after cattle exclusion (42 species in 1998 and 47 species in 1999). However, differences were not a result of any apparent trend since species richness also increased in the grazed area between years (40 species in 1998 and 47 species in 1999). These differences were not accounted for by increased woody cover, but rather by an increased appearance of sedge and forb species.

In both 1998 and 1999 there were similar species richness values for the grazed and ungrazed areas and similar community coefficient values for both years of study, suggesting that one year of cattle exclusion in Cold Prong Bog is too early to detect changes in species composition. Because there were no changes, I am not yet able to determine where Cold Prong Bog lies on Connell's Intermediate Disturbance curve (Connell 1978). Because Cold Prong bog is composed primarily of perennial species, it

may take several years of cattle exclusion before changes in species richness become apparent.

Although one season of cattle exclusion was not enough to significantly alter species richness between the two areas, it did alter the cover of certain species groups. The increased cover and occurrence of some woody species is consistent with the findings of Ritchie *et al.* (1998), who reported that herbivore exclusion in an oak savanna significantly increased the cover and biomass of woody plants, suggesting that herbivory may prevent the succession of grasslands to woodlands in savanna openings. Today, the use of large ungulates is becoming more prevalent as a management tool with goals ranging from the creation of wilderness areas to maintenance of species diversity. Oene *et al.* (1999) used a modeling approach to analyze the effects of plant-herbivore interactions on succession in nutrient-rich wetland systems and found that cattle grazing leads to a more open environment, while ungrazed areas tend to succeed toward willow-dominated vegetation.

It is possible that cattle grazing may actually be inhibiting succession in Cold Prong Bog. Although the area studied was classified as a southern Appalachian wet meadow, this area did grade into the actual bog portion of the wetland. Because of it's close proximity to the boggy habitat it is possible that some of the effects associated with successional processes in southern Appalachian bogs may eventually result in similar patterns in the meadow portion of Cold Prong Bog. One of the predictable features of bogs in general is that they will eventually be invaded by shrubs followed by forest tree species (Brewer 1994). Although it is likely that some bogs in the southern Appalachian mountains are undergoing succession that will eventually lead to a forest community, succession has been occurring at increasing rates in the past few decades for reasons not entirely understood (Schafale and Weakley 1990).

Currently there are two main theories as to why these areas may be undergoing rapid succession. The first is that there were once periodic or chronic natural disturbances that kept these communities open but which today are missing. Present excavation records show that during the late Pleistocene, and up until 10,000 years ago, there were perhaps 20 mammalian herbivores grazing in these areas, including, mastodon, moose, caribou and mammoth. After these species became locally extinct, herbivores such as elk, deer and bison became important regulators of community structure and function (Weigl and Knowles 1995). Other potential natural disturbances included fire and clearing by Indians (Brewer 1994, Schafale and Weakley 1990).

The alternative hypothesis states that the original native herbaceous vegetation once created an unfavorable environment for shrub and tree species, but that recent modifications to the environment are making it difficult for this exclusion to continue. These modifications include agricultural practices such as heavy grazing, ground water pumping or other human activities, and increased nutrient input (Schafale and Weakley 1990). Even minor alterations, such as clearing the surrounding uplands or channelizing adjacent streams can lead to the drying-out of these habitats. Prolonged dry periods can enable woody species which are normally absent from bogs to invade. Establishment of shrub and tree species can then lead to further drying of the bogs because they consume large amounts of water (Murdock 1994). A similar argument for the role of ungulate

herbivores in maintaining a meadow-like habitat has been made for the grass balds that are common in the southern Appalachians (Weigl and Knowles 1995).

The increased rate of succession in these bogs is important because today we are seeing a significant loss of wetlands throughout the United States. Within the past two centuries over one-half of the wetlands in the United States, outside of Alaska and Hawaii, have been destroyed (Murdock 1994). Bogs in particular are one of the most important habitats for rare species in the Southeast, yet 85% of the bog habitat has been lost in North Carolina, with only 1,000 acres remaining in the all of the southern Appalachians (Bainbridge 1994).

In addition to affecting community structure, grazing can also alter community function in wetland habitats. There were initial differences in aboveground net primary productivity (ANPP) during the first intra-seasonal productivity interval (NPP_1) with ANPP significantly higher in the grazed area compared to either the ungrazed or clipped treatments. The reason for these initial differences is unknown but could possibly be due to initial biomass differences carried over from the previous growing season between the two areas (Sala and Austin 2000). By the second intra-seasonal productivity interval (NPP_2) and throughout the remainder of the growing season, the grazed and ungrazed areas were similarly productive.

Analyzing total seasonal productivity is more difficult because the method used depends on community characteristics and seasonal variability in plant growth. Sala and Austin (2000) propose three methods for estimating ANPP in "fast-turnover" ecosystems, such as grasslands and steppes. Methods #1 and #2 assume there is just one biomass peak during the study period and therefore one can overlook intermediate peaks in biomass by assuming a single maximum. Method #3, the peak biomass technique, avoids this source of error by taking into account the seasonal peaks and troughs of each species. In my study area, the peak biomass technique for estimating total seasonal ANPP should be used in future studies since failure to use this method resulted in a nearly 50% underestimation of ANPP.

There are at least two explanations for the similarities in total seasonal ANPP among the grazed and ungrazed treatments. First changes in aboveground net primary productivity were simply not detectable during the first year of cattle exclusion in Cold Prong Bog because of plot to plot variability. Second, current grazing intensities in these wet meadows does not alter ANPP to a measurable extent.

It is possible that the grazing intensity of 1 cow/ha in Cold Prong Bog still allows productivity to occur at a level naturally encountered in the bog in the absence of grazing. With this explanation in mind, Cold Prong Bog could be located at one of two separate locations on McNaughton's GOH curve (Figure 1). First, grazing may be at such a low intensity that ANPP is not optimized at all, leaving the grazed area at point a on the curve. Alternatively, it is possible that the grazing intensity was between moderate and high, placing Cold Prong Bog at point b on the GOH curve, where the grazing curve transects the mean of controls, or ungrazed plants. In order to validate this hypothesis, studies controlling the number of cattle allowed to graze in a certain portion of the meadow will have to be conducted, employing a range of stocking densities.

The grazing intensity index (McNaughton 1985) for the study area indicated that 52% of the standing crop was being removed during the growing season. These data suggest that the grazing intensity in Cold Prong Bog is moderately low compared to a tropical savanna in India, where free range herbivores remove 66% to 89% of the standing crop annually (Pandey and Singh 1992). Consumption over the 105 day interval in my study was only 113 g/m^2, much less than the 476 to 734 $g\ m^{-2}\ yr^{-1}$ found by Pandey and Singh (1992). Of course, their grazing interval was much longer than mine which only covered a third of a year. In the Serengeti, grazing intensities can reach as high as 92% (McNaughton 1985). Therefore, it is more likely that Cold Prong is located at point a on McNaughton's GOH.

One of the preferred browse species in this bog is *Holcus lanatus*, an introduced weedy grass of pastures from Europe. The ability of this species to tolerate grazing may have contributed to the overall ability of the ANPP in the grazed area to keep up with that in the ungrazed area, while self-shading, and more severe competition may have constrained productivity in the ungrazed area.

The clipped treatment was used to determine the effects of grazing through simulated defoliation. Numerous authors point out that caution should be used when using mechanical removal to simulate natural defoliation (Paige 1998, Archer and Tieszen 1980, Baldwin 1990, McNaughton 1986, Belsky 1986). Artificial herbage removal is not completely representative of actual grazing because mechanical removal may not be equivalent to the natural timing, frequency, or amount of tissue eaten by herbivores (Paige 1999, Baldwin 1990). In addition, herbivores may also alter a plant's physiology through growth promoting hormones found in ungulate saliva (Dyer 1980), and grazing may be less detrimental than clipping if plant parts are left intact, promoting a transfer of nutrients from uninjured to injured parts (Archer and Tieszen 1980).

Nonetheless, the clipped treatment employed in Cold Prong Bog was comparable to the grazed treatment for total seasonal ANNP. That the clipped treatment had similar ANPP to that on the grazed side suggests that I was able to simulate the impacts of grazing fairly closely, and further supports my ideas concerning regulation of ANPP by grazing in this system.

Results from this study suggest that the elimination of cattle grazing in these wet meadows did not decrease ANPP in the first year, but grazing intensities were sufficient to alter cover of certain species groups. I predict that over the next several years, as the cover of various species changes because of lack of grazing, that there will be measurable alterations in ANPP and species richness. For example, as shade tolerant species begin to predominate in the ungrazed area, differences in ANPP and species diversity between the ungrazed and grazed areas may accentuate. Furthermore, I predict that the system will go more toward a forested wetland as shrub and tree species increase in cover and number. This work serves as a baseline against which to compare future studies.

CHAPTER TWO: Greenhouse Experiments

INTRODUCTION

The ecological effects of grazing have been extensively monitored in both terrestrial and riparian habitats in the western United States and in tropical grazing ecosystems, such as those found in the Serengeti of Africa (Skovlin 1984, McNaughton 1979). Experiments in the grasslands of Tanzania's Serengeti National Park have demonstrated that native grazers, such as, wildebeest, zebra, and Thomson's gazelle, strongly regulate aboveground net primary production (McNaughton 1979). Likewise, stimulation of aboveground productivity by grazers has been reported in Yellowstone National Park, which supports some of the largest concentrations of native ungulates in North America including elk, bison and the Pronghorn antelope (Frank and McNaughton 1993, Tracy and Frank 1998).

However, the effects of grazing in eastern wetlands and grasslands are not as well known. In the southern Appalachians the primary large grazers today are cattle and deer; however, some studies suggest that in the past mammalian herbivores, such as, mammoth, mastodon, bison, horse, tapir, musk ox, and ground sloth all occurred in the southern Appalachians (Weigl and Knowles 1995). These mammals were present up until 10,000 years ago, after which only bison, elk, and deer remained in the mountains (Billings and Mark 1957). It has been only in the last 200 years that the elk and bison were extirpated, and now only the deer remain. Thus until very recently, grazing was a natural process in these communities. But in the last 150 years or so, domestic livestock have now taken the place of the native herbivores (Weigl and Knowles 1995).

Large ungulates can affect plants not only through direct consumption of plant parts, but also by trampling (Murdock 1994), and by plant growth promoting agents found in ruminant saliva (Dyer 1980). They can also cause alterations in competition between browsed and non-browsed species (McNaughton 1979, Belsky 1987, Biondini *et al.* 1998), and increase the rate of nutrient cycling through the rapid return of nutrients to the soil in the form of dung and urine (Ball and Ryden 1984, Hamilton *et al.* 1998, McNaughton 1979, McNaughton *et al.* 1983). In grazing ruminants, for example, only 5-10% of the ingested nitrogen is stored while 75-90% is excreted, increasing the available nitrogen pool to surrounding plants (Ball and Ryden 1984).

In the previous chapter experiments designed to look at grazing effects at the community level showed that changes in aboveground net primary productivity (ANPP) were not detectable during the first year of cattle exclusion in Cold Prong Bog. However, grazing intensities in the study area were sufficient to alter the percent cover of certain species groups. In this chapter I describe experiments that evaluated the effects of simulated grazing and urine additions at the individual plant level. These experiments were conducted to better understand the mechanisms by which species currently browsed by cattle respond to grazing, and if the plants exhibit any responses indicating adaptation to a history of grazing.

I conducted a controlled experiment in which I examined the response of two perennial plant species to examine the interacting effects of clipping and urination. The two species studied were *Carex lurida*, a native sedge, and *Holcus lanatus*, an introduced pasture grass from Eurasia. These species were selected because they were both preferred browse by cattle and because they were abundant throughout the Cold Prong Bog wetland complex. They were also chosen because I felt it would be interesting to compare the responses of a native and an introduced species.

Clipping and urine application have both been shown to alter productivity and photosynthetic rates in a variety of sedge and grass species. Defoliation may have either negative or positive effects, depending on how the community and individual species react to grazing (Belsky 1986, McNaughton 1979). One of the positive effects of grazing is the ability of plants to compensate for the moderate effects of herbivory. Compensatory growth is the positive response of plants to injury and can be divided into two mechanistic categories: extrinsic and intrinsic (McNaughton 1983a,b). Extrinsic mechanisms directly or indirectly modify the environment. For example, indirect effects include increased light, increased water use efficiency, and increased nutrient supplies to remaining tissues. Direct modification involves the transfer of plant hormones, hormone analogs, or growth factors from herbivores to the plant (McNaughton 1983a,b). Intrinsic mechanisms are physiological changes within the plant, such as, meristem activation, enhanced rates of cell division, and rejuvenation of residual tissues (McNaughton 1983a,b). Compensatory rates of photosynthesis are also important to the growth of a plant following herbivory. Compensatory photosynthesis is defined as the increase in photosynthetic rates of foliage on partially defoliated plants relative to foliage of the same age on undefoliated plants (Nowak and Caldwell 1984).

In a study looking at the photosynthetic responses of three African graminoids, Wallace *et al.* (1984) showed that clipping increased photosynthetic rate in all three species, possibly due to stimulation of stomatal opening. However, compensatory responses vary among species. Caldwell *et al.* (1981) found that following defoliation

Agropyron desertorum, a grazing-tolerant bunchgrass introduced to the western U.S. from Eurasia, reestablished a canopy with three to five times the photosynthetic surface area of *Agropyron spicatum*, a grazing-sensitive bunchgrass native to North America. In both grasses, however, leaf blades of regrowing tillers had higher photosynthetic capacity than blades on unclipped plants.

In addition to these species-specific responses to grazing, the response of plants to herbivory involves numerous other factors including the plant's genetic makeup, the intensity and frequency of defoliation, plant developmental stage at the time of herbivory and which plant tissues are affected (McNaughton 1983a, Trlica and Rittenhouse 1993). *Themeda triandra*, a perennial grass common to semi-arid Africa, responds better with low clipping or grazing intensities. In field experiments in the Serengeti, *T. triandra* stands cut every 8 weeks yielded 30% and 60% more plant material then stands cut every 4 and 2 weeks, respectively (Coughenour *et al.* 1985).

Watt and Hagar (1980) found that *Holcus lanatus* grew better with higher clipping heights while height of clipping did not affect *Lolium perenne* yields. Both plants responded better with less frequent clippings. *Carex* species, in contrast, have been shown to grow better with lower clipping heights. For example, raising the clipping height from 5 to 15 cm in both grass-sedge (*Poa* spp., *Deschampsia,* and *Carex* spp.) and sedge (*Carex* spp.) associations reduced total forage yields by over 50% (Dovel 1996).

Abiotic factors, such as light, temperature, and nutrient and water availability can also account for differential plant responses to clipping (McNaughton 1983a). The addition of nitrogen fertilizer, in combination with clipping, has been shown to increase the quality and quantity of plant tissue in *Sporobolus kentrophyllus*, a short-grass species found in the Serengeti (Hamilton *et al.* 1998). *Kyllinga nervosa*, a C_4 sedge native to the Serengeti, has also been shown to overcompensate under moderate grazing and high nitrogen conditions (McNaughton *et al.* 1983). In many instances, herbivores prefer vegetation subjected to urine fertilization, due to the increased nutrient content of the tissues (Steinauer 1995).

Plants may also respond differently to grazing depending on their grazing history. Species that have a long history of grazing rapidly restore leaf area following tissue removal and often have increased gas exchange rates in the remaining leaf tissues (Wallace *et al.* 1984, McNaughton 1979, Painter and Detling 1981). For example, *Holcus lanatus* plants in pastures with a long history of grazing have been shown to produce more tillers in response to clipping than plants from newer pastures, suggesting selection for compensatory growth in the face of grazing (Aarssen and Turkington 1987). Similarly, defoliated *Festuca idahoensis* plants with a previous grazing history had higher stomatal conductance rates, perhaps a result of greater soil moisture associated with grazed areas (Doescher *et al.* 1997).

Compensatory growth may have evolved in response to continuous or heavy grazing (McNaughton *et al.* 1983). Owen *et al.* (1981) suggest that grasses and grazers co-evolved during the Miocene and, due to the selective pressure of these grazers, grasses now possess certain adaptations as evidence for this interaction. For example, grasses are relatively palatable to grazers compared to most other land plants, they possess a basal meristem that is low enough not be damaged by grazers feeding from above, and they can reproduce vegetatively (Owen *et al.* 1981).

Milchunas *et al.* (1988) adds that small stature, belowground nutrient reserves and rapid growth also allow grasses to tolerate grazing. Grasses produce an excess of nutritious vegetation, which could have evolved in response to grazers and, in addition, they do not usually possess leaf absicission layers and therefore must depend on grazers to prevent the accumulation of dead material, further suggesting a coevolved relationship. In addition to being palatable and highly nutritious, plants produce vitamin D_3. This vitamin currently has no known function in plants, but is necessary for animal growth (Belsky 1986).

Domestic livestock grazing is one of the most prevalent activities influencing native ecosystems in western North America with approximately 91% of all federal lands in the 11 contiguous western states currently being grazed (Belsky and Blumenthal 1997, Fleischner 1994). In the east, the National Park Service allows cattle grazing on Blue Ridge Parkway (BRP) lands in order to maintain a sense of historical continuity in the region. In 1996 there were 370 agricultural leases, with grazing permitted on approximately 3,500 acres of Parkway lands, some of them wetlands (Sutter *et al.* 1996). It is not known for how long grazing by cattle has been allowed on the BRP, but in Cold Prong Bog grazing has been permitted since at least 1962 when the current grazing lease for this area was originated.

It is reasonable to assume that *Holcus lanatus*, a dominant non-native pasture grass growing in Cold Prong Bog, has a history of grazing, since in its original habitat in British grasslands it dominates grazed swards (Watt and Hagar 1980). It is possible that *Carex lurida*, which is a native, perennial sedge located in the study area, has encountered past grazing from extinct or extirpated grazers and more recently from deer; however, it is difficult to ascertain its grazing tolerance. Therefore, experiments were designed to test the reaction of both species to simulated grazing and urination, and to help predict how such responses may affect successional patterns in the portion of the bog now freed from grazing.

METHODS

Plant Material and Growing Conditions.- For this experiment I selected two perennial species, both of which are preferred browse for cattle in high elevation wet meadows: *Holcus lanatus*, an introduced pasture grass, and *Carex lurida*, a native sedge species. Ramets of both species were collected on 9 July 1999 from a grazed portion of Cold Prong Bog, which is located along the Blue Ridge Parkway (mile point 297) near Blowing Rock, North Carolina. Plants were then transferred to the Appalachian State University greenhouse courtyard and placed in 7.6 liter nursery pots containing Scotts Metro-Mix 360 soil. All plants were clipped to approximately 5 cm and placed under a 30% shade cloth for three days in order to relieve any transplanting stress. After removal of the shade cloth plants were allowed to grow for one month before imposition of treatments. On 20 July all plants received a single application of Anderson's Professional Turf 14-14-14 three-month slow release fertilizer. All plants were well-watered throughout the experiment.

Near the end of the experiment, some of the *H. lanatus* plants became infected by a rust fungus (*Puccinia coronata*). All plants, infected and uninfected, were treated at three separate intervals with a fungicide (1 September and 10 September with Cleary's 3336F, and 14 September with Biosafe Systems Zero-tol).

Aboveground Net Primary Productivity.- Clipping experiments were designed to test the effects of simulated grazing and a one-time simulated urination event on the aboveground net primary production (ANPP) of the two species. Eighty plants of each species were chosen and placed in a completely randomized design. Plants were selected based on similar initial size. Initial size estimates were made for each plant on a scale from 1 (smallest) to 5 (largest) to use as a covariate for any subsequent analyses. Twenty plants of each species were randomly assigned, in rows of 10, to one of four treatments: nonfertilized-nonclipped (NF-NC), fertilized-nonclipped (F-NC), fertilized-clipped (F-C), and nonfertilized-clipped (NF-C).

I observed that in the field, cows tended to graze *H. lanatus* plants closer to the ground than *C. lurida* plants. I therefore used different clipping heights for each species in the greenhouse experiment: 5 cm for *H. lanatus* and 10 cm for *C. lurida*. Both species were clipped at two-week intervals for a total of four clippings (9 August, 23 August, 6 September, and 20 September). During each clipping, plants were held vertically taut in order to eliminate any variation due to lateral growth. Clippings were oven dried for two weeks at 65 C°, and then weighed.

Urea was chosen as the primary nitrogen source to simulate a urination event. The majority of nitrogen excreted by cattle is found in urine and of this nitrogen, 70% is in the form of urea (Williams and Haynes 1994). An average cow in the eastern United States would urinate 1839 Kg N per ha per year, or 112 g N m^{-2} y^{-1} (Dr. Matt Poore, Extension Beef Nutritionist, Department of Animal Science, North Carolina State University). To achieve this amount, each plant received 12 grams of urea mixed in 0.6 liters of water in a one-time application. I assumed that a plant would receive only one urination event within the same season.

Over a three day period from 5-7 October, and two weeks after the final clipping, plants were harvested, oven dried for approximately 3 weeks at 65° C, and weighed. Because *H. lanatus* plants became infested with the rust fungus late in the experiment, whole-plant estimates of the severity of rust infection were made before harvesting using a scale ranging from 0 (having no infection) to 5 (most heavily infected) in case late clippings or final total biomass were severely affected by the infection.

Gas Exchange Measurements.- Forty plants were randomly chosen for laboratory measurement of gas exchange, with 5 plants of each species measured per treatment. Plants were well-watered the day before analysis and kept in the headhouse of the greenhouse the night before measurement in order to maintain environmental conditions as consistent as possible prior to measuring gas exchange rates. Laboratory temperature was kept at 24°C. Because of the amount of time involved in measuring all 40 plants, *C. lurida* and *H. lanatus* plants were each measured on sequential days in order to minimize diurnal variation in gas exchange rates. All measurements were made between 10 am and 2 pm each day.

Gas exchange measurements were made with a Li-Cor 6200 portable photosynthesis system at a light intensity of 1,175 μmol m^{-2} s^{-1} using a metal halide lamp. The most recently, fully expanded leaf of each plant was placed horizontally in a 0.25 liter cuvette, and allowed to acclimate for approximately four minutes, after which a series of three or four measurements were taken. Most plants reached constant rates after approximately six to eight minutes, and the last two or three measurements were averaged. Net photosynthesis and stomatal conductance were recorded. Plants were measured every two weeks (19 and 20 August, 3 and 4 September, 16 and 17 September, and 30 September and 1 October), approximately 11 days after each clipping interval to determine if there were any long-term residual impacts due to either clipping or fertilization. It also allowed clipped leaves enough time to grow long enough to fit into the cuvette.

Rust effects.- Near the end of the greenhouse experiment, I noticed that the *H. lanatus* plants had become infected by a rust fungus. Dr. Larry Grand, from the Department of Plant Pathology at North Carolina State University in Raleigh, NC, identified the fungus as *Puccinia coronata*. This infestation first became evident in early September when air temperatures suddenly began to drop. As noted earlier, fungicide was applied at three separate times. However it did not decrease rust levels. Therefore I decided to investigate the impacts of this fungus on gas exchange of these plants. I also chose to end the clipping experiment early before the rust effects became even more severe.

Eight *H. lanatus* plants were chosen for photosynthesis measurements, four nonfertilized and four fertilized. Only nonclipped plants were chosen because the rust did not seem to have such noticeable effects on the clipped plants. On 7 October measurements were taken in the greenhouse courtyard with a Li-Cor 6200 photosynthesis system at a light intensity of 1,650 μmol m^{-2} s^{-1} using natural sunlight. Average leaf temperature during the experiment was 21.7 °C while relative humidity ranged from 45% to 64% with an average of 51%. On each plant, a healthy, uninfected leaf and an infected leaf were selected for measurement of photosynthetic rate and stomatal conductance. The percent leaf area infected was also estimated for each of the infected leaves.

Statistical analysis.- Biomass at each clipping interval was analyzed with SPSS using a Repeated Measures General Linear Model (SPSS Inc. 2000). Total productivity was calculated as the sum of the final harvest weight and the cumulative clipping dry weights and analyzed in SAS using Analysis of Covariance, with initial size as the covariate (SAS Institute 1989).

Gas exchange results were analyzed separately for photosynthesis and stomatal conductance in SPSS also using the Repeated Measures General Linear Model Procedure. A paired t-test was used to analyze differences between rust infected and uninfected leaves and a two-sample t-test was used to analyze fertilizer effects. Finally, regression analysis was used to assess the relationship between rust infection and photosynthesis. Duncan's Multiple Range Test was used for post-hoc means comparisons. For all statistical tests, $p<0.05$ was considered significant. Data are reported as mean ± standard error.

RESULTS

Aboveground Net Primary Productivity.- There were significant treatment effects for *Holcus lanatus* (Figure 1). Nonclipped plants had greater productivity than clipped plants. Fertilized-nonclipped plants had the highest yields (92.3 ± 4.1 g), followed by nonfertilized-nonclipped plants (63.3 ± 3.2 g). Clipped plants showed no significant differences between fertilizer treatments, and had an average yield of 31.0 ± 1.8 g. Plants that were clipped and fertilized did, however, suffer severe foliar damage, which I attribute to burning of the leaf blade by the urea.

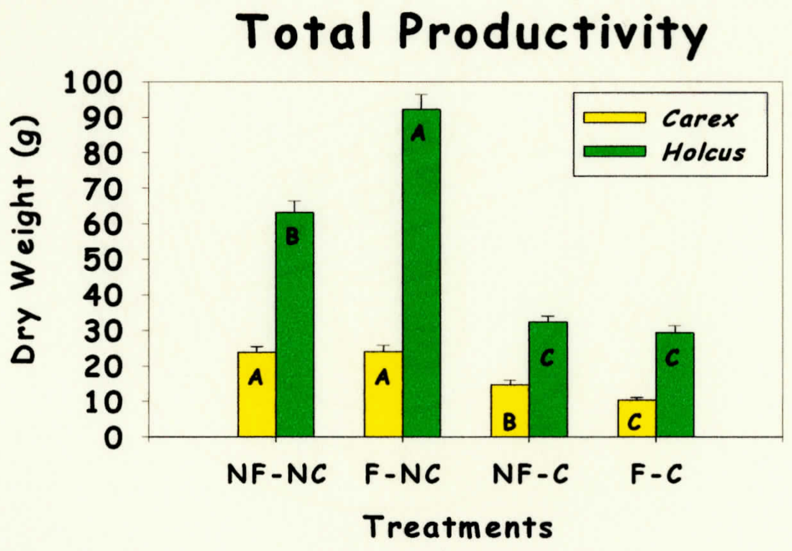

Figure 1. Effects of clipping and urea on total aboveground production of *Holcus lanatus* and *Carex lurida* plants (n=20). Vertical bars represent mean ± SE and letters represent a significant difference at $p < 0.05$.

Clipping significantly reduced total productivity by approximately half (24.0 ± 1.7 g vs 12.6 ± 0.9 g) in the *Carex lurida* plants (Figure 1). Within the nonclipped treatment there were no significant differences between fertilization treatments. For the clipped plants there was a trend toward higher total productivity in the nonfertilized plants.

Nonfertilized and fertilized plants produced 14.8 ± 1.3 g and 10.4 ± 1.0 g, respectively.

For *H. lanatus,* clipping biomass was significantly reduced at the fourth clipping, after the urea had been added (2.1 ± 0.7 g for the fertilized plants and 5.2 ± 0.5 g for the nonfertilized plants). For the *C. lurida* plants there were no significant differences between treatments for any of the clipping intervals (Figure 2).

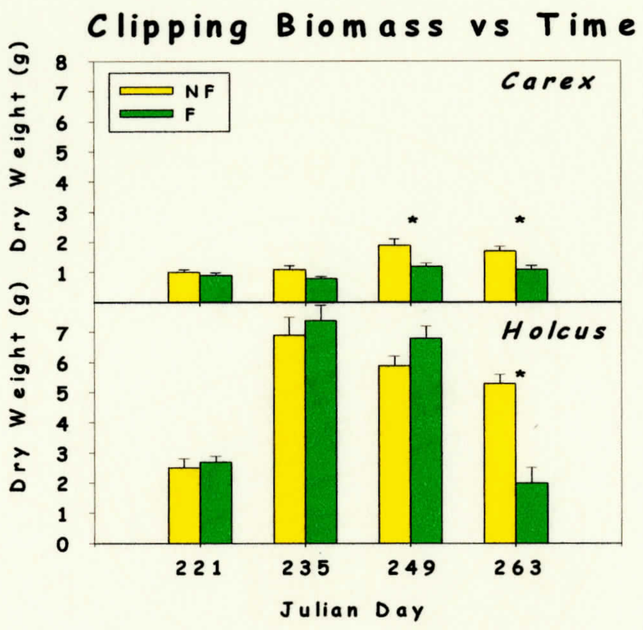

Figure 2. Effects of clipping and urea on dry weight of *Carex lurida* and *Holcus lanatus* (n=20) at four clipping intervals. Vertical bars represent mean ± SE and * represents a significant difference at p<0.05.

Gas Exchange.- There were no significant differences in either photosynthesis or stomatal conductance for the first two measurements periods for the *H. lanatus* plants. By the third measurement, 10 days after the urea had been added, there was a significant increase in photosynthetic rate but no significant effect on stomatal conductance. The fourth and final gas exchange measurements showed no treatment effects (Figure 3). For the *Carex lurida* plants there were no significant treatment effects with the exception of

stomatal conductance, which was significantly higher in the clipped plants on the fourth measurement period (Figure 4).

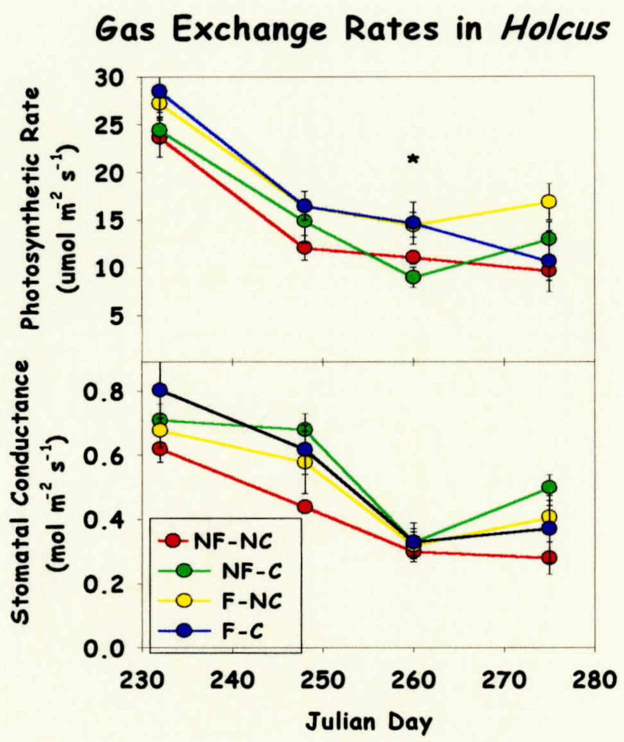

Figure 3. Rates of net photosynthesis and stomatal conductance for *Holcus lanatus* plants at four measurement intervals (n=5). Vertical bars represent mean ± SE and * represents a significant difference at p<0.05.

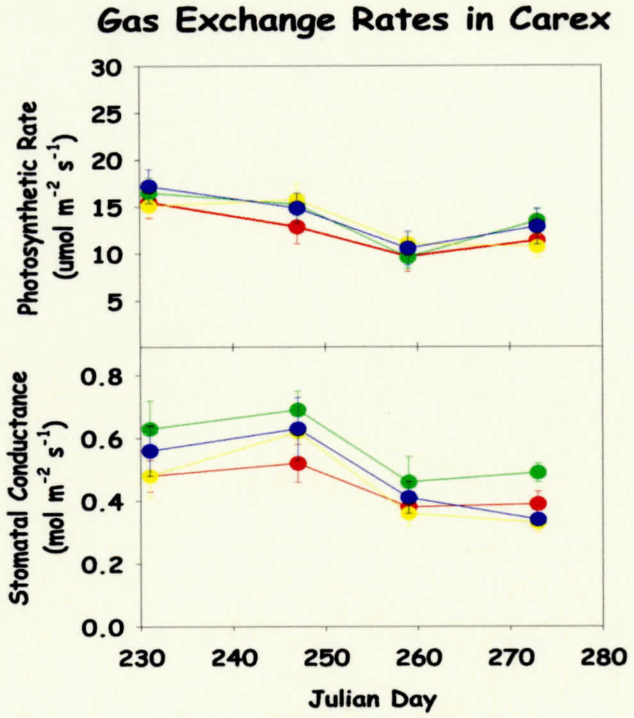

Figure 4. Rates of net photosynthesis and stomatal conductance for *Carex lurida* plants at four measurement intervals (n=5). Verticle bars represent mean ± SE and * represents a significant difference at $p<0.05$.

Rust effects.- The highest rust infection levels occurred on nonfertilized-nonclipped plants followed by fertilized-nonclipped plants. Clipped plants had the lowest levels of rust, and had approximately 50% less visible rust than nonfertilized-nonclipped plants (Figure 5). Because clipped plants seemed relatively unaffected by the rust fungus, only nonclipped plants were chosen for investigation of their gas exchange responses.

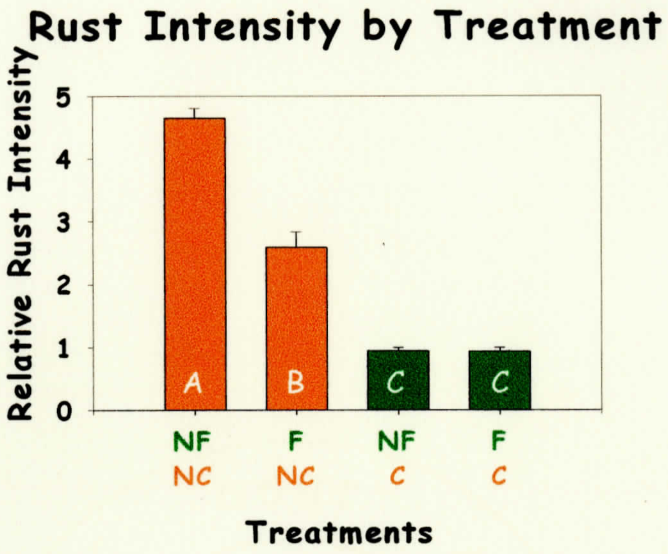

Figure 5. Relative rust intensity by treatment for *Holcus lanatus* plants (n=20). NF = non-fertilized, F = fertilized, NC – not clipped, and C = clipped. Letters represent a significant difference at $p<0.05$.

There was a significant decrease in photosynthetic rate for infected leaves in both the nonfertilized and fertilized plants (Figure 6). Infected leaves on nonfertilized plants had a mean photosynthetic rate of 2.4 ± 0.9 umol $m^{-2} s^{-1}$ while uninfected leaves had a mean rate of 14.8 ± 0.7 umol $m^{-2} s^{-1}$. Infected leaves on fertilized plants had a mean photosynthetic rate of 12.05 ± 1.5 umol $m^{-2} s^{-1}$ while uninfected leaves had a mean rate of 16.6 ± 1.2 umol $m^{-2} s^{-1}$. Across fertilizer treatments, there were no significant differences in photosynthesis for uninfected leaves. But for infected leaves, photosynthetic rates were significantly lower in the nonfertilized compared to the fertilized plants.

Photosynthesis rates drastically declined as percent leaf area infected increased (Figure 7). Linear regression showed a highly significant relationship ($r^2 = 0.80$,

$p < 0.0026$). However, the four highest photosynthesis rates were all from the fertilized treatment, and the lower four rates all from the nonfertilized treatment.

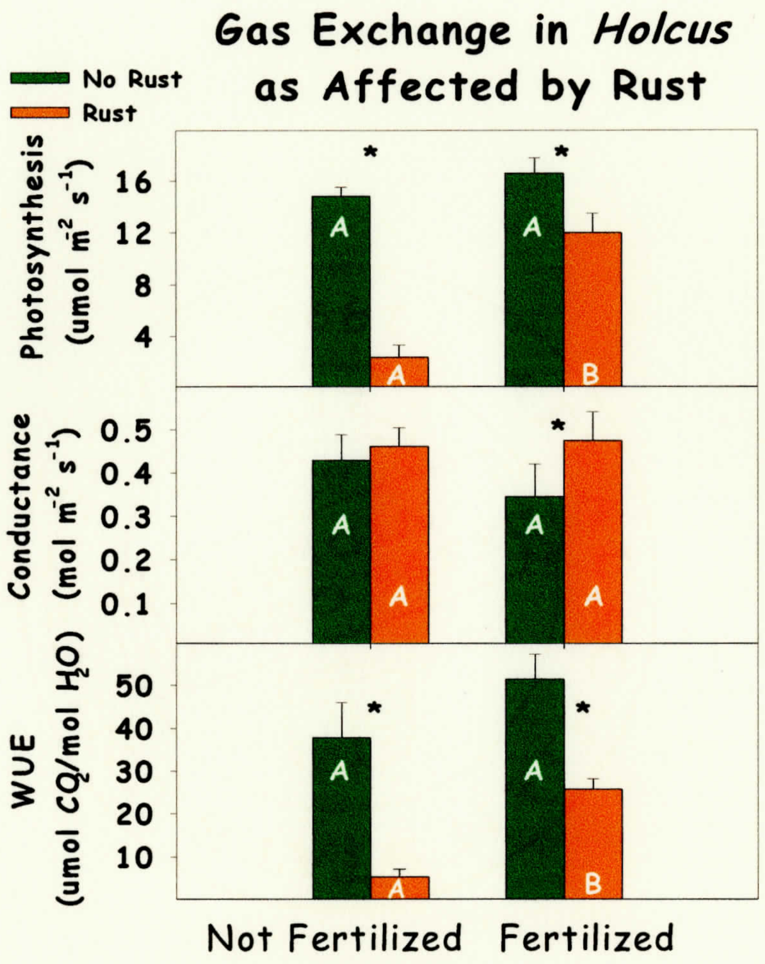

Figure 6. Rates of net photosynthesis, stomatal conductance, and water use efficiency (WUE) in uninfected *Holcus lanatus* leaves for unclipped fertilized and unclipped nonfertilized plants (n=8). Letters represent significant differences between treatments (not fertilized and fertilized) and * represents significant differences within a single treatment. Vertical bars represent mean ± SE and * represents p<0.05 significance level.

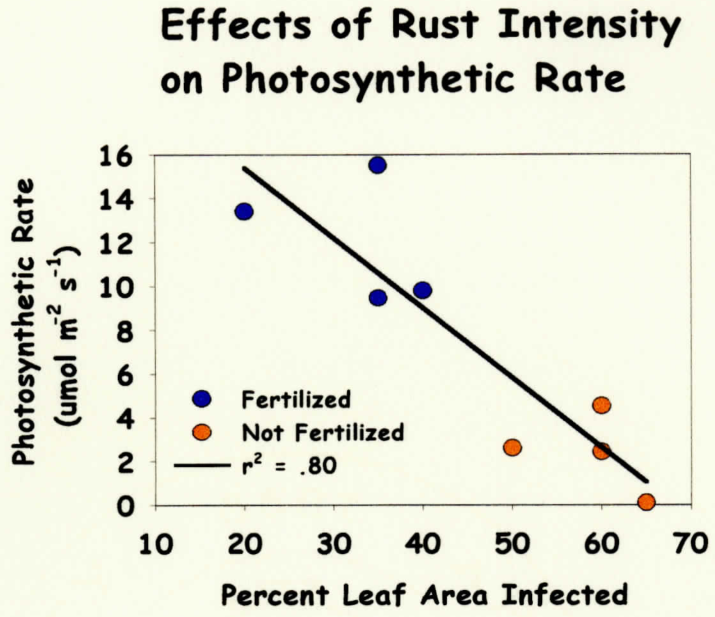

Figure 7. Linear regression for photosynthesis by rust intensity for unclipped fertilized and nonfertilized *Holcus lanatus* leaves (n=4 and r^2 = .80).

There were no significant differences for stomatal conductance in the nonfertilized treatment between uninfected and infected leaves; however, in the fertilized treatment stomatal conductance was significantly reduced for uninfected leaves compared to infected leaves (0.35 ± 0.08 mol $m^{-2} s^{-1}$ vs 0.43 ± 0.06 mol $m^{-2} s^{-1}$, respectively) (Figure 6). There were no significant differences between treatments for either the infected or uninfected leaves.

Water use efficiencies (WUE) followed the same trend as the photosynthesis measurements (Figure 6). Within a treatment, there were significant decreases in WUE for infected leaves in both the nonfertilized (37.8 ± 8.2 vs 5.3 ± 1.8 μmol CO_2/mol H_2O for healthy and infected leaves, respectively) and fertilized (51.6 ± 5.7 vs 25.8 ± 2.4 μmol CO_2/mol H_2O for healthy and infected leaves, respectively) treatments, caused mainly by the drop in photosynthetic rates and not by changes in stomatal conductance. The fertilizer treatments had no effect on WUE for uninfected leaves but for infected leaves WUE was almost six times in the nonfertilized plants when compared to the fertilized plants.

DISCUSSION

Plants of different life form and grazing history often vary in their tolerance to herbivory. Plants can either overcompensate by exhibiting both compensatory growth and photosynthesis (McNaughton 1979, Nowak and Caldwell 1984), or undercompensate, exhibiting lower yields than control plants (Belsky 1986, Painter and Belsky 1993). In other plants herbivores may have little or no effect at all on plant function (Lee and Bazzaz 1980). In these experiments *Holcus lanatus*, an introduced pasture grass, greatly outproduced *Carex lurida*, a native sedge species. However, in both species production was decreased in clipped plants compared to unclipped plants.

Previous studies examining the effects of clipping on *H. lanatus* plants have demonstrated that growth of this species is influenced by previous grazing history. Aarssen and Turkington (1985) used three different-aged pastures and found that *H. lanatus* plants from the oldest pasture had significantly greater shoot biomass, total biomass, and tiller number compared with the two younger pastures. When compared to unclipped controls, shoot and total biomass of clipped plants from the youngest pasture were significantly decreased, but not so in the two older pastures. These results suggest that in the oldest pasture selection has favored genotypes with the ability to withstand grazing pressures. Cold Prong Bog has been grazed for at least 38 years (and probably longer) and this time frame is comparable to the oldest pasture in the study by Aarssen and Turkington which has been grazed for approximately 46 years. Watt and Hagar (1980) found that *H. lanatus* plants grew better with higher clipping heights and less frequent clipping, reaching their greatest yields when clipped to 10 cm and at 6 week intervals. Clipping studies have shown that the amount of herbage residue, or amount of forage left after grazing, is important to the regrowth ability of some plants (Dovel 1996, Milligan 1981). My clipping intervals were only 2 weeks, which may have been too short to maximize yields.

Carex species have also been shown to react differently to varying clipping heights and intensities. For example, Dovel (1996) reported that forage yields in both grass-sedge (*Poa* spp., *Deschampsia,* and *Carex* spp.) and sedge (*Carex* spp.) wetland meadow associations increased as clipping height decreased, with maximum yields produced when clipped to 5 cm. McNaughton (1979) reported a similar trend for *Kyllinga nervosa*, a C_4 sedge native to the Serengeti, which yielded maximum net aboveground productivity at a clipping height of 4 cm and daily clipping intervals. He points out, however, that he knows of no other species that can withstand such intense defoliation.

The sedge species used in the above cited experiments quite possibly were obligate grazophils, plants whose presence depends on herbivory, and therefore could withstand such intense grazing (McNaughton 1979). The long-term grazing history of *C. lurida* is not known though. *C. lurida* plants in this experiment, which were clipped to a height of 10 cm and at 2 week intervals, showed a significant decrease in growth due to this defoliation regime. If these findings are a consequence of *C. lurida's* inability to tolerate grazing (in other words if *C. lurida* is not an obligate grazophil), it is possible that a grazing height of 10 cm is below the minimum herbage residue requirements for this species. Alternatively it may be possible that *C. lurida* plants were clipped too frequently. Further studies will need to be done to determine optimum clipping heights and intervals.

This decrease in productivity for clipped plants in both *C. lurida* and *H. lanatus* plants is not consistent with the community results from Chapter One. In the field total ANPP was not significantly different between the grazed, ungrazed, and clipped treatments, yet the greenhouse clipping experiments reduced production by almost 50% in both species. There are several possible explanations for these differences. As stated earlier, it is possible that cattle return rates in the field were longer than the simulated 2 week clipping interval used in the greenhouse study. In addition, Scotts Metro-Mix 360 soil was used as potting soil instead of actual soil from the Cold Prong wetland complex. Also, soil characteristics such as, soil nutrient content and aeration were different from the field, which may have affected plant responses in some way.

It is also possible that clipping in the greenhouse failed to adequately simulate grazing in Cold Prong Bog. For example, herbivores may alter a plant's physiology through growth promoting hormones found in ungulate saliva (McNaughton 1986, Dyer 1980), and grazing may be less detrimental than clipping if plant parts are left intact, promoting a transfer of nutrients from these areas to injured parts (Archer and Tieszen 1980). However, the clipped treatment employed in Cold Prong Bog was comparable to the grazed treatment for total seasonal ANPP (2.85 ± 0.49 g m^{-2} d^{-1} and 2.34 ± 0.54 g m^{-2} d^{-1}, respectively), although the clipped productivity was slightly lower than the grazed productivity. Therefore, what might be viewed as detrimental at the individual plant level may be beneficial at the community level (Belsky 1986, 1987, Trlica and Rittenhouse 1993). It is likely that if *C. lurida* and *H. lanatus* are detrimentally affected in the field by grazing, that other species may compensate for their decreased productivity.

There are two other effects of cattle grazing that cannot be simulated simply by using shears. These include trampling and nutrient recycling from dung and urine. I attempted, in this greenhouse experiment, to control for one of these factors by investigating the effects of a one-time urination event on ANPP of the two selected species. Urea was chosen as the primary nitrogen source because most of the nitrogen excreted by cattle is in this form (Williams and Haynes 1994). In the field urea is rapidly hydrolyzed to ammonia and has a greater environmental impact than feces nitrogen, which only slowly enters the available nitrogen pool (Dr. Matt Poore, Extension Beef Nutritionist, Department of Animal Science, North Carolina State University, personal communication).

In my experiments, fertilized-nonclipped *H. lanatus* plants had the highest yields, which were significantly higher than nonfertilized-nonclipped *H. lanatus* plants and, in addition, nonclipped *H. lanatus* plants responded to fertilization more than nonclipped *C. lurida* plants. This suggests that this fast growing grass species is better able to take advantage of nutrient recycling as a result of the presence of cattle while the slow and steady growth of *C. lurida* is not as affected by these additions.

Although clipped *C. lurida* plants were not affected by fertilization, growth of clipped *H. lanatus* plants in the fertilization treatment was significantly reduced at the fourth clipping interval, after the addition of urea. It is possible that our estimate of the amount of urea the plants would receive from cattle was too high. In a study investigating urine impacts on growth of Serengeti species, Hamilton *et al.* (1998) calculated 40 g N m^{-2} as representative of a urine hit produced by large native mammalian herbivores. The concentrations I applied was nearly three times as high as this. It may be that concentrations are higher in the southeastern United States as compared to native, migrating animals. However, clipped *H. lanatus* plants suffered severe foliar damage following the application of urea, which supports my contention that perhaps the urea concentration was too high. I never observed such burning in the field.

Haggar (1976) found that in mixed swards of *Holcus lanatus* and *Lolium perenne*, *H. lanatus* had consistently lower growth rates compared to *L. perenne* under high fertilizer treatments and higher growth when only receiving low fertilizer treatments. These results suggest that this species may be very sensitive to nutrient additions. However, in my study nonclipped plants showed increased yields when fertilized suggesting there may be an interaction between fertilization and clipping treatments.

In addition to outproducing *C. lurida* and being able to make better use of nutrient additions, *H. lanatus* plants also generally exhibited higher gas exchange rates than *C. lurida* plants. However, clipping and fertilization had relatively little effect on gas exchange rates in both species. Clipping had no residual impacts on gas exchange rates of either species. These results are different from the findings of other investigators who report increased rates of photosynthesis following grazing and clipping (Painter and Detling 1981, Wallace 1990, Detling *et al.* 1979).

Detling *et al.* (1979) found that three to 10 days following clipping photosynthesis rates of *Bouteloua gracilis* were 21% higher than unclipped controls. I looked at effects over a similar time frame (11 days after clipping), however it may be possible that photosynthetic rates in the species I investigated may have initially diverged between treatments, but the 11 day time interval may have been adequate for rates to return to pre-clipping levels.

Other species have been reported to have similar photosynthetic rates between clipped and unclipped treatments. *Themeda triandra* clipped at infrequent intervals exhibited photosynthetic rates not significantly different from unclipped controls (Wallace *et al.* 1984). In my study, only *H. lanatus* responded to fertilization with a temporary two week stimulation of photosynthesis, demonstrating that nutrient additions can initiate a short-term photosynthetic response in these plants.

Infection by pathogens is yet another biotic interaction that can affect the photosynthesis and growth of a plant and it's ability to compete with other species. A late season infection by the rust fungus *Puccinia coronata* on *H. lanatus* plants mainly affected the unclipped plants. The clipped plants seemed relatively unaffected by this fungus, most likely due to the constant removal of spores as leaf material was clipped.

The significant decrease in photosynthetic rate for infected leaves in both the nonfertilized and fertilized-nonclipped treatments is consistent with the effects of *Puccinia coronata* on other species, such as oats (*Avena sativa*). Scholes and Rolfe (1995) found that as rust infection developed on oat leaves, photosynthesis progressively declined in infected versus healthy leaves with visible symptoms appearing 5 days after inoculation and photosynthetic rates decreasing to only 13% of the control plants just 6 days later.

A reduction in photosynthesis may contribute to community changes in the field because reduced carbon acquisition could eventually lower both the growth and reproductive success of a species. Barley plants infected with brown rust had reduced growth over 16 days, primarily due to a reduction in net photosynthesis and transport of carbohydrates from infected leaves (Owera *et al.* 1981). This reduced growth could, in

turn, alter competitive relationships in the field as infected plants would be less able to compete with more vigorous, healthy plants.

Interestingly, gas exchange rates for infected leaves varied between treatments, with decreased photosynthetic rates in the nonfertilized treatment. This suggests that the impact of an infection by *P. coronata* may be more severe in nitrogen limiting habitats and therefore become a greater threat in the ungrazed area of Cold Prong Bog, which due to the loss of cattle would have less nutrient recycling from dung and urine deposits.

Water use efficiencies (WUE) followed the same trend as the photosynthesis measurements and as a result may contribute to hydrological changes in the bog. Healthy leaves take up more CO_2 per unit water transpired but as a result of the rust fungus, infected leaves took up less CO_2 for the same amount of water lost. This lowered WUE, combined with decreased photosynthetic rates suggests that infection might lead to changes in the cycling of materials through changes in carbon, nitrogen and water fluxes. However, this is most likely to occur only if infection is severe and widespread.

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APPENDIX A

Species list for the ungrazed and grazed areas of Cold Prong Bog in 1998, before the exclusion of cattle and in 1999, after the cattle had been excluded from the ungrazed area. Species were recorded using a combination of the quadrat and point intercept data. A more detailed explanation is provided in the methods section.

Species List	Ungrazed Area 1998	Ungrazed Area 1999	Grazed Area 1998	Grazed Area 1999
Acer rubrum		√		
Achillea millifolium	√		√	√
Agrostis #1	√	√	√	√
Agrostis #2	√	√	√	√
Anthoxanthum oderatum	√	√	√	√
Carex atlantica	√	√	√	√
Carex debilis	√	√	√	√
Carex intumescens				√
Carex lurida	√	√	√	√
Carex scoparia	√	√	√	√
Carex swanii	√	√	√	√
Carex vulpinoidea	√	√	√	√
Clematis virginiana		√		√
Danthonia compressa	√	√	√	√
Dichanthelium boscii	√	√	√	√
Dichanthelium clandestinum				√
Dichanthelium dichotomum var dichanthelium	√	√	√	√
Eupatorium perfoliatum		√		√
Festuca rubra		√		√
Festuca sp.	√		√	
Galium tinctorium	√	√	√	√
Glyceria striata	√	√	√	√
Glyceria melicaria	√	√	√	√
Holcus lanatus	√	√	√	√
Hypericum mutilum		√	√	√
Ilex verticillata	√	√	√	√
Juncus coriacious	√	√	√	√
Juncus effuses	√	√	√	√
Juncus subcoriacious	√		√	
Kalmia latifolia		√		
Lycopus virginicus	√	√	√	√
Lygodium palmatum		√		
Mitchella repens	√	√		√
Moss	√	√	√	√
Nyssa sylvatica		√		
Osmunda cinnamomea	√	√	√	√
Oxalis striata	√	√	√	√
Poa sp.	√	√	√	√
Polygonum sagittatum	√	√	√	√
Polytricum commune	√	√	√	√
Potantilla canadensis	√	√	√	√
Rosa palustris	√	√	√	√
Rubus argutus	√	√	√	√
Rumex acetocella	√	√	√	√
Sambucus canadensis		√		√
Scirpus expandus			√	√
Scirpus sp		√		
Senecio aureus	√	√		
Sisyrinchium sp.			√	√
Smilax glauca		√		
Solidago rugosa	√	√	√	√
Trifolium repens	√	√	√	√
Vernonia noveboracensis	√	√	√	√
Veronica officinalis			√	√
Viburnum nudum	√	√	√	√
Viola sp.	√	√	√	√

APPENDIX A (Concluded)

APPENDIX B

Species rank by Importance Value for the ungrazed and grazed areas in Cold Prong Bog. The Difference column is the magnitude of difference in ranking from ungrazed to grazed. Importance Value calculations are explained in the Methods section.

Ungrazed Area Rank	Species	Grazed Area Rank	Difference
1	*Vernonia noveboracensis*	4	-3
2	*Rubus argutus*	13	-11
3	*Holcus lanatus*	2	1
4	*Polytricum commune*	21	-17
5	*Viola sp.*	6	-1
6	*Festuca rubra*	1	5
7	*Agrostis #2*	3	4
8	*Juncus effusus*	5	3
9	*Solidago rugosa*	17	-8
10	*Potentilla canadensis*	10	0
11	*Carex lurida*	14	-3
12	*Rosa palustris*	7	5
13	*Dichanthelium dichotomum var dichanthelium*	26	-13
14	*Rumex acetosella*	12	2
15	*Poa sp.*	9	6
16	*Anthoxanthum oderatum*	18	-2
17	*Agrostis #1*	15	2
18	*Lycopus virginicus*	11	7
19	*Carex debilis*	23	-4
20	*Carex scoparia*	34	14
21	*Carex vulpinoidea*	28	-7
22	*Danthonia compressa*	40	-18
23	*Carex swanii*	36	-13
24	*Acer rubrum*	47	-23
25	*Carex sp.*	8	17
26	*Galium tinctorium*	27	-1
27	*Juncus coriacious*	46	-19
28	*Trifolium repens*	24	4
29	*Polygonum sagittatum*	39	-10
30	*Sphagnum sp.*	29	1
31	*Unidentifyable Grass*	19	12
32	*Viburnum nudum var. cassinoides*	25	7
33	*Smilax glauca*	-	33
34	*Moss*	45	-11
35	*Ilex verticillata*	37	-2
36	*Vaccinium corymbosum*	43	-7

APPENDIX B (Concluded)

37	*Dichanthelium boscii*	41	-4
38	*Mitchella repens*	52	-14
39	*Oxalis stricta*	31	8
40	*Clematis virginiana*	51	-11
41	*Sambucus canadensis*	32	9
42	*Hypericum canadense*	30	12
43	*Glyceria striata*	48	-5
44	*Carex atlantica*	38	6
45	*Glyceria melicaria*	33	12
46	*Lygodium palmatum*	-	46
47	*Scirpus sp.*	-	47
48	*Thelypteris noveboracensis*	-	48
49	*Eupatorium perfoliatum*	20	29
50	*Kalmia latifolia*	-	50
51	*Nyssa sylvatica*	-	51
52	*Osmunda cinnamomea*	49	3
53	*Senecio aureus*	-	53
54	*Veronica officinalis*	44	10
55	*Sisyrinchium sp.*	42	13
-	*Scirpus expansus*	16	-16
-	*Dichanthelium clandestinum*	22	-22
-	*Achillia millifolium*	35	-35
-	*Carex intumescens*	50	-50
-	*Dichanthelium sp.*	53	-53

VITAE

Karen Elizabeth Geissinger was born in Berwick, Pennsylvania on February 18, 1975. She graduated from Port Saint Lucie High School in Port St. Lucie, Florida in 1993. She then went to Catawba College in Salisbury, North Carolina on a partial soccer and academic scholarship and completed a Bachelor of Arts degree in Environmental Science in May 1997. She entered the graduate program in Biology at Appalachian State University in August 1997 and was a co-winner of the Odum Award for best presentation of an ecological topic at the Association of Southeastern Biologists Annual Meeting in April 2000. This was awarded by the Southeastern chapter of the Ecological Society of America. She is currently employed by Birkitt Environmental Services, Inc. in Tampa, Florida as an Ecologist.