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Dynamics of Green Ash Woodlands in Theodore Roosevelt National Park

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ABSTRACT -- Green ash (*Fraxinus pennsylvanica* Marsh.) communities are valuable as sources of biological diversity and shelter for livestock in the Northern Great Plains. Excessive use of stands by livestock tends to convert these woodland communities to less valuable shrublands. We monitored 12 green ash stands in Theodore Roosevelt National Park (TRNP) from 1985 through 1996 to determine changes in species composition, plant density, and canopy coverage in green ash communities that were protected from livestock but exposed to foraging by native ungulates. Over the 12-year sampling period, density of choke cherry (*Prunus virginiana* L.) and Saskatoon serviceberry (*Amelanchier alnifolia* Nutt.) in the tree stratum declined, shrub density showed no consistent trends, and canopy cover of grasses and forbs increased. The changes we observed were more likely attributable to succession and weather conditions than to impacts of native ungulates.

Key words: ecology, *Fraxinus pennsylvanica* Marsh., Green ash, North Dakota.

Woodlands dominated by green ash (*Fraxinus pennsylvanica* Marsh.) comprise 2% or less of the landscape in the Northern Great Plains (Girard et al. 1989, Wood et al. 1989, Hansen et al. 1995) but add structural diversity to the landscape and support

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a wide array of plant and animal species (Boldt et al. 1978, Hopkins 1983, Hansen et al. 1984, 1995, Girard et al. 1987, 1989). Settlement of the Northern Great Plains by Euro-Americans caused extensive changes in green ash communities (Severson 1981). Suppression of fire and elimination of bison (*Bos bison*) may have favored green ash communities (although many woody species in ash communities do resprout following burning [Wasser 1982]), but homestead construction, firewood cutting, farming, and the introduction of livestock have had negative impacts on green ash communities (Severson 1981, Girard et al. 1987, Hansen et al. 1995).

Livestock production is currently regarded as the major human-associated impact on green ash communities (Hansen et al. 1995). Livestock, especially cattle (*Bos taurus*), are attracted to green ash stands because the stands provide forage, shade, protection from wind and insects, and are associated with water sources (Uresk and Boldt 1986, Girard et al. 1987, Hansen et al. 1995). Continuous heavy use of these stands by cattle leads to loss of the tree canopy and replacement of stands by shrub communities (Butler 1983, Hansen et al. 1995). When the tree canopy disappears, biological diversity is reduced as species dependent on trees or the shade from trees disappear, and livestock lose shade and shelter.

Development of grazing systems for livestock that are compatible with green ash communities has been hampered by a shortage of sites managed under low intensity grazing regimes. Studies have shown that excessive grazing by domestic livestock and severe droughts degrade green ash communities (Uresk and Boldt 1986, Girard et al. 1987, Hansen et al. 1995, W. F. Jensen, North Dakota State Game and Fish Department, Bismarck, unpubl. data), but we do not know the normal range of year-to-year variability in plant cover and species composition in green ash stands used only by native ungulates. Without this information, evaluation of the efficacy of different livestock management strategies will be difficult.

We measured plant density and canopy coverage in 12 green ash stands in the South Unit of Theodore Roosevelt National Park (TRNP) in southwestern North Dakota at one to two year intervals from 1985 to 1996. These data allowed us to assess changes in plant coverage, species composition, and stand structure between wet and dry periods in stands protected from domestic livestock grazing for 30 to 47 years. Green ash stands we measured were accessible to low to moderate densities of mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), bison, pronghorn (*Antilocapra americana*), elk (*Cervus elaphus*), and feral horses (*Equus caballus).*

STUDY AREA

TRNP was established in 1947 as the Theodore Roosevelt Memorial Park and received National Park status in 1978. The 18,756-ha South Unit (Fig. 1) encompasses a representative sample of the vegetative communities native to western North Dakota

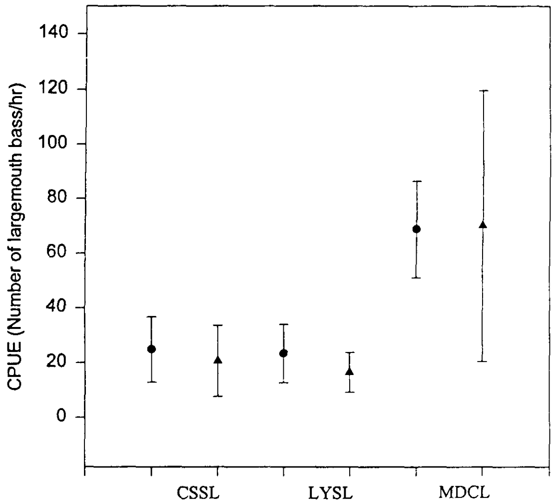

Figure 1. Map of the South Unit of Theodore Roosevelt National Park with stand locations and the release site for introduced elk indicated.

including approximately 427 ha of the Green Ash - Choke Cherry Habitat Type described by Hansen et al. (1995) (Westfall et al. 1993). These lands were extensively grazed by livestock and influenced by homesteading beginning in the 1880's (Severson 1981, Girard et al. 1987) but have not been farmed since the 1930's or grazed by cattle and sheep (*Ovis aries*) since the early 1950's (Theodore Roosevelt National Park 1984).

Mule deer, white-tailed deer, and a few feral horses were present in 1947. Pronghorn, introduced in 1951, have established a migratory pattern with most of their annual range outside the TRNP boundary fence. Bison were reintroduced in 1956. Elk were introduced in 1985 (Sullivan 1988). Numbers of bison, horses, and elk are actively managed to maintain populations within specific numerical ranges via live capture and removal. No attempts have been made to manipulate deer or pronghorn numbers. Although precise counts were not available for all ungulate species during the 1985 to 1996 period, we estimated the mean densities of large herbivores during this period as: mule deer (0.03/ha), white-tailed deer (0.01/ha), bison (0.02/ha), elk (0.01/ha), pronghorn (<0.01/ha), and feral horses (<0.01/ ha).

METHODS

Vegetation measurement

In 1985, we selected 12 representative stands in the Green Ash - Common Choke Cherry Habitat Type (Hansen et al. 1995) for measurement. In each stand, a 20-m

baseline was established in the center of the stand parallel to the drainage on which the stand was located. We attempted to minimize heterogeneity within sampled areas by including only interior areas of stands and excluding stands in which we could not locate a 20 by 3 m strip with tree cover. We measured vegetation in three strata. The ground stratum was sampled by estimating canopy coverage of all grasses, forbs, shrubs, and nonliving ground cover less than 50 cm in height at 1-m intervals along the transect baseline in 20 by 50-cm (1985 and 1986) or 25 by 51-cm (1988 to1996) plots. Cover estimates in individual plots were based on a modification of a canopy coverage rating system developed by Daubenmire (1959). Canopy coverage for each category over the entire transect was calculated by using the median percentage value within each coverage class (I = 0; II [less than 1%] = 0.5%; III [1 to 5%] = 2.5%; IV[greater than 5 to 25%] = 15%; V [greater than 25 to 50%] = 38%; VI [greater than 50% to 75%] = 62%; VII [greater than 75 to 95%] = 85%; and VIII [greater than 95%] = 98%) as a point estimate and averaging the values recorded in 20 individual plots per transect. Density of plants in the shrub stratum (woody species less than or equal to 2 m in height) was calculated by counting shrub stems by height class (less than 50 cm, 50 to 100 cm, and greater than 100 to 200 cm) in seven 1-m^2 plots placed at 3-m intervals along the transect baseline. Density of plants in the tree stratum (woody plants greater than 2 m in height) was measured in a 20 by 3-m plot parallel to each transect baseline. Plants with multiple stems were counted as separate trees if the stem branching occurred at ground level or lower.

Baselines were marked with metal posts to aid in relocation. A tape measure stretched between end points of the baseline allowed us to resample the same plots in different years. Plant species nomenclature follows the Flora of the Great Plains (Great Plains Flora Association 1986). Our analyses were limited to a subset of species and groups of species that we regarded as potential indicators of change (Table 1).

Independent variables

Changes in vegetation during the monitoring period were related to indices of ungulate use of monitored stands, seasonal temperatures, and seasonal precipitation. None of our monitored stands was burned during the 12-year period so we were unable to assess the effects of fire. We never saw pronghorn, bison, or horses or any evidence of their presence within the plots we measured. Elk and deer had access to our sites and were considered the most likely ungulates to have an impact on vegetation at sampling sites. Fecal pellets at sample sites and duration of exposure to ungulate foraging were used to assess elk and deer impacts.

Forty-seven elk were introduced into the South Unit of TRNP in 1985. Numbers increased to approximately 400 by 1993 (Theodore Roosevelt National Park, unpubl. data). In January 1993, 200 elk were removed from the population. The estimate in 1996 was 300 to 400. Between 1985 and 1992, elk distribution in TRNP expanded from the introduction site to cover all areas of the South Unit that were inside the

Table 1. Vegetation parameters included in analyses of change in green ash stands during 1985 to1996 in Theodore Roosevelt National Park, North Dakota.

Category	Definition/expected trend
Tree stratum (stem counts)	
Green ash (> 2 m)	Expected to decrease under heavy grazing or drought
Choke cherry (> 2 m)	"
Saskatoon service-berry (> 2 m)	"
All trees and saplings (> 2 m)	"
Shrub stratum (stem counts)	
Green ash (≤ 2 m)	Expected to decrease under heavy grazing by livestock or native ungulates and drought
Choke cherry (≤ 2 m)	"
Saskatoon service-berry (≤ 2 m)	"
Snowberry (≤ 2 m)	Includes *Symphoricarpos albus* (L.) and S. *occidentalis* (Hook.). Expected to increase under heavy grazing by gramivores.
All species (0-50 cm)	Expected to decrease under heavy grazing or drought but possible increase under gramivore grazing.
All species (> 50-100 cm)	Expected to decrease under heavy grazing, drought, or severe winters.
All species (> 100-200 cm)	Expected to decrease under heavy grazing, drought, or severe winters.
Ground stratum (% cover)	
Bare ground	Expected to increase under heavy grazing or drought
Litter	Expected to decrease under heavy grazing or drought but could also decrease if hidden under heavy herbaceous living plant cover.
Shrubs 0-50 cm	Expected to decrease under heavy grazing or drought but could increase under heavy use by gramivores.
Graminoids	Expected to decrease under heavy grazing and drought.
Climax graminoids	Includes only the three most common species (Virginia wild rye [*Elymus virginicus* L.], little-seed ricegrass [*Oryzopsis micrantha* (Trin. & Rupr.) Thurb.], and Sprengel's sedge [*Carex sprengelii* Dew. ex Spreng.]) in stands. Expected to decrease under heavy grazing and drought.

Table 1. Cont.

Category	Definition/expected trend
Exotic grasses	Includes all introduced grass species, but Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss.) comprised > 90% of exotics in stands. Expected to increase under heavy grazing and decrease under drought.
All forbs	Includes all forb species identified in stands. Expected to increase under heavy grazing by gramivores and decrease under drought conditions.
Palatable forbs	Includes all native forb species/genera that were found in stands and identified as comprising > 2% of seasonal diets of elk or deer in TRNP (Genera included: *Achillea* L., *Astragalus* L., *Campanula* L., *Fragaria* L., *Galium* L., *Glycyrrhiza* L., *Heuchera* L., *Monarda* L., *Oxalis* L., *Thalictrum* L., *Toxicodendron* P.Mill., *Vicia* L., and *Viola* L.
Invasive forbs	Exotic forbs that had demonstrated potential to dominate ground cover in green ash stands in southwestern North Dakota. Included: Arctium minus Bernh., *Cirsium arvense* (L.) Scop., *Euphorbia esula* L., *Convolvulus arvensis* L., and *Polygonum convolvulus* L.

boundary game fence (approximately 95% of the South Unit). Potential duration of use by elk in stands we sampled at the time of the 1996 vegetation measurements varied from zero to 12 years.

White-tailed and/or mule deer had access to all of our sample sites from 1985 to 1996. Fall surveys conducted by the North Dakota State Game and Fish Department indicated that mule deer numbers declined by more than 50% between 1985 and 1996 (North Dakota State Game and Fish Department, unpubl. data). No data were available for white-tailed deer numbers in TRNP, but white-tailed deer were much less common than mule deer in areas where our stands were located.

Weather, especially precipitation and temperature, exert major influences on green ash stands (Girard et al. 1987). Temperatures during 1985 to 1996 were well within historic norms. The warmest and coolest summers of the monitoring period were 1988 and 1993, respectively (Fig. 2). Winter temperatures were generally milder than average with the mildest winter before the 1992 growing season and the coldest before the 1996 growing season. Precipitation during the growing season was greater than 20% below the 30-year average in 1984, 1985, 1988, 1989, and 1990 (Fig. 3). Precipitation was greater than 20% above average in 1986, 1987, and 1993. We included 11 variables related to weather (Table 2) in our analyses. Weather data were obtained from a weather station maintained by TRNP in the South Unit. We attempted

to measure all stands before herbaceous plants became desiccated, but in some years we were forced to measure one or more stands after the optimal mid-July to mid-August sampling period. We included month of vegetation measurement as an index to phenology to determine if deviations from our optimal sampling period had detectable impacts on values.

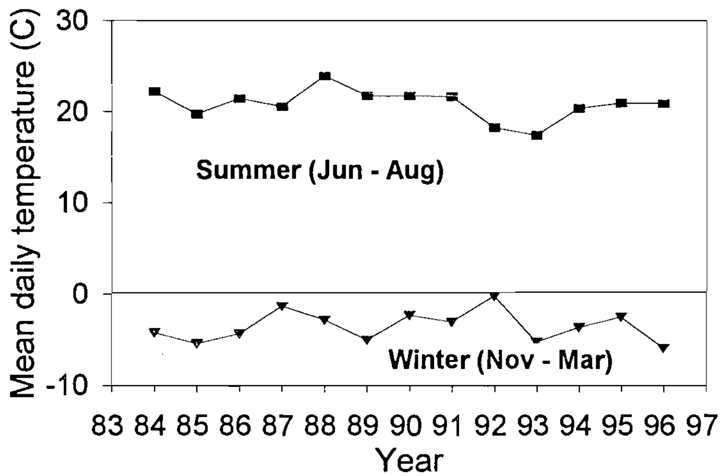

Figure 2. Mean temperatures for the summer (June - August) and winter (November - March) recorded at the South Unit of Theodore Roosevelt National Park, 1984 to 1996.

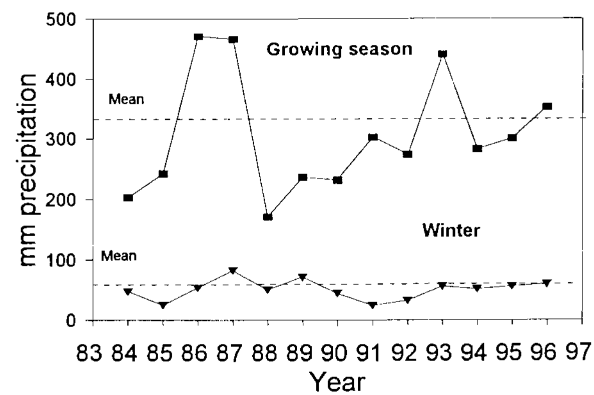

Figure 3. Precipitation during the growing season (March - September) and winter (November - March) recorded at the South Unit of Theodore Roosevelt National Park, 1984 to 1996. Means for 1950 to 1996 are displayed as dashed lines in the figure.

Table 2. Independent variables used in analyses of changes in green ash stands in Theodore Roosevelt National Park during 1985 to 1996.

Variable acronym	Definition
Short term effects	
Month	Month in which vegetation measurements were taken (> n = later phenology).
Pptmo	Precipitation (mm) in month vegetation measurements were taken
Tempmo	Mean temperature (°C) of month of vegetation measurement
One-year effects	
Pptgro	Precipitation (mm) in current growing season up to month of vegetation measurement
Snow	Total precipitation (mm) in winter (Nov - Mar) preceding vegetation measurement.
Temsum	Mean temperature (°C) for growing season up to month of vegetation measurement.
Temwin	Mean temperature (°C) for winter (Nov - Mar) preceding vegetation measurement.
Two-year effects	
Pptprev	Precipitation (mm) during growing season (Mar - Oct) one year before vegetation measurement.
Ppt2y	Precipitation in current and previous growing season.
Snow2y	Precipitation in past two winters.
Temsum2y	Sum of summer mean temperatures for current and previous year.
Temwin2y	Sum of winter mean temperatures for two winters prior to measurement.
Ungulate effects	
Elkpel	Mean ground cover (%) for elk pellets in 20 ground stratum plots/site.
Deerpel	Mean ground cover (%) for deer pellets in 20 ground stratum

Analysis

We used Wilcoxin's ranked sum tests to determine if values for individual vegetation categories (Table 1) changed across all sampled stands between 1985 and 1996 in directions consistent with deer population changes (a greater than 50% decline during 1985 to 1996) or cumulative weather trends (eight of the 12 years had below average growing season precipitation). If deer were negatively affecting vegetation in 1985, the population decline should have lead to increases in palatable shrubs and herbaceous plants by 1996. If below average precipitation negatively affected stands, we should have seen a decline in stem density of woody plants and/or canopy coverage of climax herbaceous species between 1985 and 1996.

We could not do a simple test of vegetation measurements in 1985 versus vegetation measurements in 1996 to identify changes that might be associated with elk impacts on green ash stands because the opportunity for elk to impact green ash communities varied among stands. Elk distribution within TRNP expanded from an area that included four of our sample sites in 1985 to 11 of the 12 sites by 1996. We hypothesized that changes in vegetation and ground cover associated with elk use of stands should increase with the number of years elk had access to a stand. We developed 18 vegetation and ground cover categories from our vegetation data that, based on food habits studies in TRNP (Sullivan 1988, Westfall 1989) and impacts on vegetation reported in other areas (Lyon and Ward 1982, Singer and Harter 1996, Singer et al. 1998, Wambolt 1998, White et al. 1998), we expected to decline following intensive use of a site by elk. Differences between values recorded for these categories in 1985 and 1996 were converted to percent change (V_{1996} - V_{1985} /V_{1985} x 100) and truncated to a range of -100% to +101% to normalize the data and decrease the influence of large proportionate changes in low absolute cover or density measurements. Truncation affected only 11% of the vegetation measurements but reduced the average skew of variables by 53% to -0.38 and the average kurtosis by 21% to 3.69. Truncated percent change between 1985 and 1996 was tested by using multiple t-tests on categories paired across sites. If elk did have impacts on green ash stands in TRNP, we expected to see significant differences in mean percent change among a set of stands with zero to 12 years of elk use, and we expected stands with the most years of elk use to have lower average values, i.e., greater negative changes between 1985 and 1996, than stands with the fewest years of elk use.

The changes in vegetation we measured between the 1985 and 1996 sampling periods could also reflect the impacts of short-term (one month to two years) rather than long-term factors. We used two approaches to determine if recent weather patterns or recent ungulate use influenced the changes we observed from one sampling period to another. The strength of association between individual explanatory variables (weather indices and percent ground coverage of elk and deer fecal pellets in stands) and response variables (truncated percent change between vegetation measurements in vegetation/ground coverage categories taken at two-year intervals between 1986 and

1996) was determined by using Pearson's correlations. The second approach, multivariate analysis, was an attempt to develop a more realistic model for explaining changes in vegetation. Changes in vegetation are highly variable, usually not linear, seldom occur at consistent rates among different species, and frequently involve responses to multiple causative factors. Of the multivariate analytical methods available, we selected logistic regression as the most appropriate for our data based on guidelines presented by Morrison et al. (1998). We used logistic regression to determine if combinations of weather variables and ungulate fecal pellet indices would be useful in predicting the direction of change between sampling periods. Percent changes in vegetation categories between sampling periods were converted to class variables (1 = no change or increase, 2 = decline), and a step-up procedure ($P < 0.05$ to enter) was applied to identify the variable sets that could best distinguish between positive and negative changes. The MSUSTAT package (Lund 1989) was used for multiple t-tests and correlation analysis. SAS (1994) was used in the logistic regression analysis.

RESULTS

Overall changes

In 1985, the tree canopies in all of the sampled stands were dominated by green ash with choke cherry (*Prunus virginiana* L.) as the dominant understory tree. Saskatoon service-berry (*Amelanchier alnifolia* Nutt.) was the third most abundant species in the tree stratum. This pattern had not changed by 1996. Plots of mean stem counts for the tree stratum by year (Fig. 4) indicated little change occurred in green ash, but choke cherry declined through the sample period, and Saskatoon service-berry declined sharply between 1988 and 1992. Between 1985 and 1996, median stem density declined 53% for choke cherry and 71% for Saskatoon service-berry (Table 3). Plots of mean stem counts in the shrub stratum indicated increases through 1988 and declines or stability thereafter (Fig. 5). Median stem counts in 1985 and 1996 were not significantly different for any shrub species or height classes that we tested (Table 3).

Shrub canopy coverage in the ground stratum was highest in 1994 and lowest in 1992 and 1996 (Fig. 6). The relatively large changes between some consecutive sampling periods were due to high annual variability in choke cherry seedling numbers and/or annual differences in leaf volume on snowberry (*Symphoricarpos albus* L./*occidentalis* L.). If we had sampled only in 1985 and 1996, we would have seen no significant differences in median canopy coverage for shrubs less than 50 cm in height (Table 3).

The most striking change in canopy coverage of herbaceous plants was the increase in graminoids between 1985 and 1996 (Fig. 6). The increase was, however, not constant. A decline occurred in 1990, but coverage increased again in 1992.

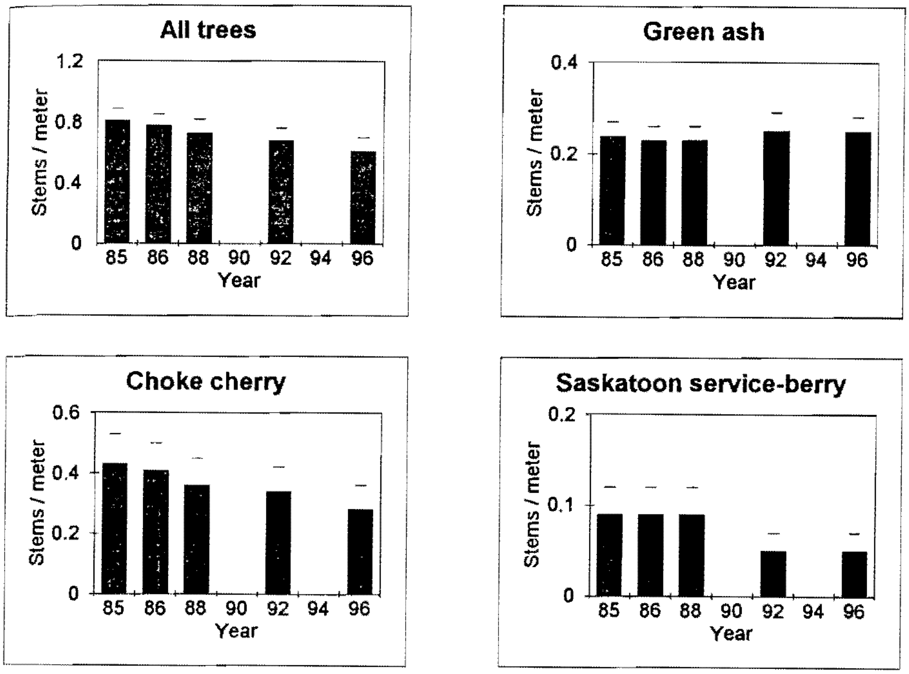

Figure 4. Mean stems per m^2 and standard errors (horizontal lines above bars) for four plant categories in the tree stratum recorded in 12 green ash stands in the South Unit of Theodore Roosevelt National Park, 1985 to1996.

Climax graminoids (Table 1) and exotic grasses increased over the 12-year period, but the ratio of climax to exotic species remained highly skewed in favor of native climax species. Bare ground and forb cover remained relatively low throughout the sampling period. Palatable forbs did not increase as much as invasive forbs, but invasive forb cover remained low in 1996. When medians for 1985 and 1996 were compared (Table 3), total graminoids, climax graminoids, total forbs, and invasive forbs showed significant increases.

Multiple t-tests of truncated percent change between 1985 and 1996 for 12 stands with zero to 12 years of access by elk (Table 4) indicated no overall difference among stands (Hotelling's $t^2 = 36.63$, $P = 0.35$) for the 18 vegetation/ground cover variables we included in the test. There were differences ($P < 0.05$) in 13 of 66 tests of stand pairs but no consistent pattern supporting a relationship between longer elk use of a site and greater declines in vegetation indices between 1985 and 1996. The mean percent

change over all variables for Site 6, the only stand with no elk use between 1985 and 1996, was +14%. This mean was significantly higher (P < 0.05) than means for two sites with 10 or more years of elk use (Site 9 = -20% and Site 13 = -9%), but it was not significantly different from means for six other sites with 10 or more years of elk use (range of means = -15% to +26%).

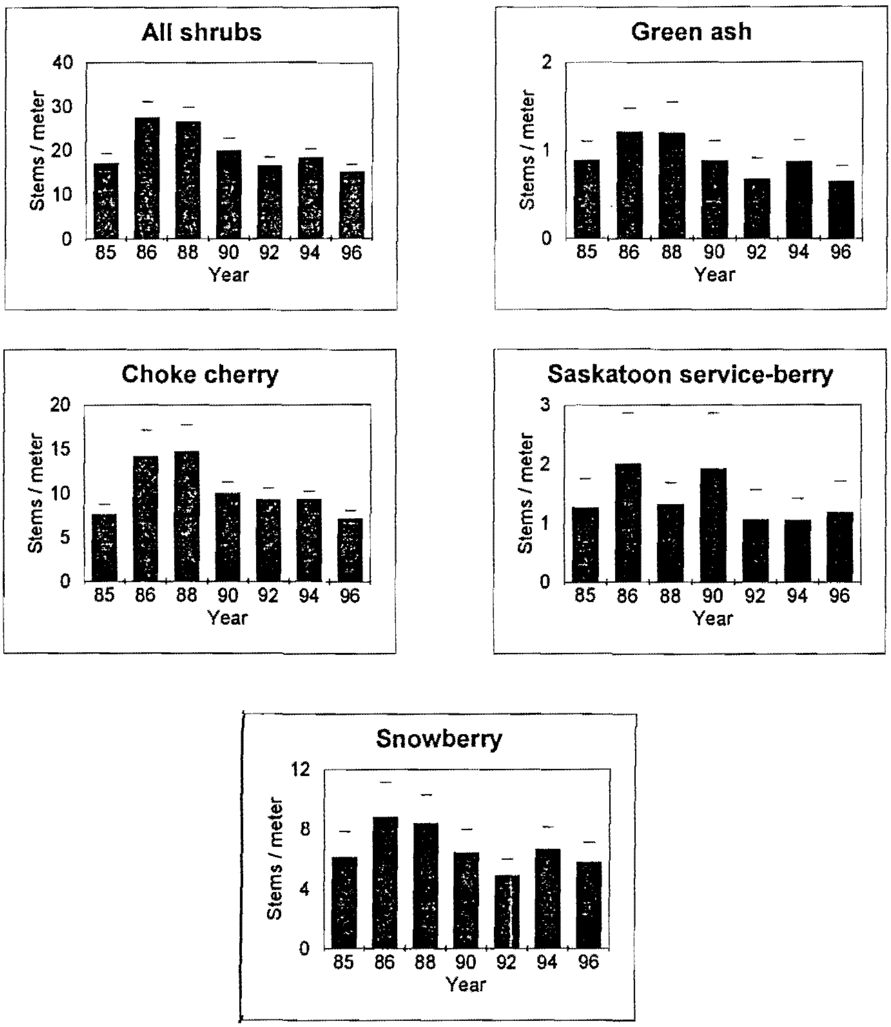

Figure 5. Mean stems per m^2 and standard errors (horizontal lines above bars) for five plant categories in the shrub stratum recorded in 12 green ash stands in the South Unit of Theodore Roosevelt National Park, 1985 to1996.

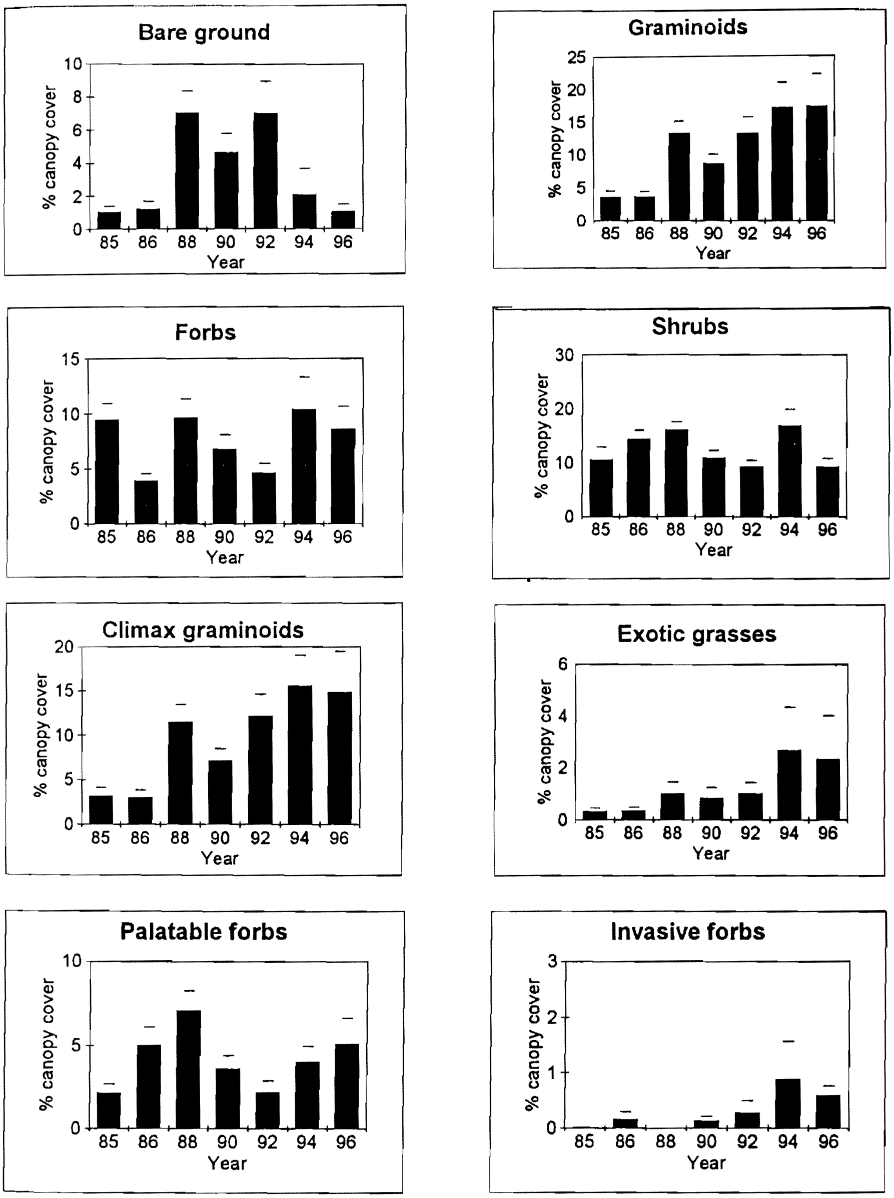

Figure 6. Mean percent cover and standard errors (horizontal lines above bars) for eight categories in the ground stratum recorded in 12 green ash stands in the South Unit of Theodore Roosevelt National Park, 1985 to1996.

Table 3. Wilcoxin's tests of changes in coverage (ground stratum categories) and density (shrub and tree strata) between 1985 and 1996 in 12 green ash stands monitored in Theodore Roosevelt National Park. Species or genera included in limited multi-species categories are identified in Table 1.

Category	Median		Summed ranks	P
	1985	1996	1985 positive	
Tree density (N/60 m², > 200 cm)				
All trees	64.5	56.5	62.0	0.08
Green ash	15.5	13.5	32.0	0.96
Choke cherry	21.5	10.0	64.0	0.05
Saskatoon service-berry	3.5	1.0	40.0	0.04
Shrub density (N/7 m², 0-200 cm)				
Green ash (0-200 cm)	4.5	3.0	45.0	0.08
Choke cherry (0-200 cm)	56.0	49.0	47.5	0.53
Saskatoon service-berry (0-200 cm)	4.0	2.5	24.5	0.86
Snowberry (0-200 cm)	27.5	39.5	34.0	0.97
All species 0-50 cm	80.0	75.0	41.0	0.50
All species > 50-100 cm	19.5	17.5	59.5	0.12
All species > 100-200 cm	18.0	12.0	53.5	0.27
Ground stratum canopy/ground cover (%)				
Bare ground	1.0	0.1	27.0	0.64
Litter	95.2	65.3	78.0	<0.01
Total shrubs	5.0	9.4	33.0	0.67
Total graminoids	3.3	11.7	6.0	0.01
Climax graminoids	2.8	11.3	6.0	0.01
Exotic grasses	<0.1	0.5	14.0	0.34
Total forbs	2.1	6.8	8.0	0.02
Palatable forbs	1.4	3.1	22.0	0.20
Invasive forbs	0.0	0.3	0.0	<0.01

Table 4. Percent change (truncated to -100% to +101%; changes > 100% = 101%) in 18 vegetation categories expected to decline under heavy grazing pressure from elk.

	Stand ID											
	6	4	5	14	13	15	2	7	1	3	8	9
Years elk use	0	4	6	6	10	10	11	11	12	12	12	12
Tree stratum												
Green ash tree stems (n > 2 m)	19	-18	26	0	36	50	10	-27	20	20	-16	-35
Choke cherry tree stems (n > 2 m)	-55	-52	-33	-25	-82	-29	-12	96	-25	-90	17	-100
Saskatoon service-berry tree stems (n > 2 m)	-62	-80	100	0	-100	-67	-71	101	-58	-67	0	0
All tree stems (n > 2 m)	-11	-33	27	-10	-39	-20	-13	25	-21	-75	-6	-37
Shrub stratum												
Green ash shrub stems (n < 2 m)	0	-23	-91	20	-29	0	100	-100	0	-50	101	-100
Choke cherry shrub stems (n < 2 m)	100	-37	79	60	-47	87	-13	-10	-33	-24	-22	13
Saskatoon service-berry shrub stems (n < 2 m)	101	-67	-25	0	60	100	15	0	-13	-100	-42	0
All shrub stems (0-50 cm)	9	-26	21	101	-14	101	-36	-7	-2	-66	-40	0
All shrub stems (51-100 cm)	-55	-19	-29	25	-39	-17	51	29	8	-26	-30	-54
All shrub stems (101-200 cm)	-33	-20	100	101	-88	15	-28	-52	-59	100	-83	-100

Table 4. Cont.

	Stand ID											
	6	4	5	14	13	15	2	7	1	3	8	9
Ground stratum												
Nonbare (100 - % bare ground)	<1	-1	<1	0	0	0	6	-1	<1	6	<1	-3
Litter (% ground cover)	-30	-28	-44	-22	-71	-34	-35	-8	-31	-14	-46	-62
Total low (< 50 cm) shrub (% canopy)	101	101	-36	101	55	101	-30	-93	-55	-80	-12	101
Climax graminoids (% canopy)	101	101	101	101	101	101	-74	101	19	101	101	101
Nonexotic grasses (% graminoids - % exotics)	0	0	-20	-2	0	<1	<1	0	<1	<-1	<-1	-3
Nonforb (100 - % forb canopy)	-3	-7	-2	-9	-2	-23	3	<-1	-7	-2	-5	2
Palatable forbs (% canopy)	66	101	-74	101	101	101	-19	-100	101	101	101	-74
Noninvasive forbs (100 - % invasive forbs)	0	0	-2	-1	-1	0	-2	<-1	0	<-1	0	<-1
Mean (of 18 vegetation categories)	14	-6	5	30	-9	26	-8	-3	-9	-15	1	-20
SD	56	54	58	49	61	58	40	61	37	64	52	59

Changes between individual sampling periods

Differences in density and canopy cover between individual sampling periods (Figs. 4 to 6) indicated that vegetation might be responding to short-term rather than long-term factors. We developed a matrix of 224 Pearson correlations (14 weather, phenology, and short-term ungulate use indices by 16 vegetation variables). The highest correlation coefficient (r) in the matrix was 0.55 indicating that no single weather or ungulate index provided a good explanation of changes in individual vegetation variables in the stands (Table 5). When we looked at the patterns of moderate ($P = 0.05$ to 0.10) and strong ($P < 0.05$) associations across all vegetation variables, one phenology index and two weather indices were significantly correlated with changes in half or more of the vegetation variables: 1) the month in which vegetation measurements were made (10 significant negative correlation coefficients indicating greater negative changes for late summer vegetation measurements than for early summer vegetation measurements); 2) precipitation in the growing season the year before vegetation measurements were made (nine significant positive associations indicating greater positive changes with greater precipitation); and 3) the sum of growing season precipitation in the year prior to and the year of vegetation measurement (eight of nine significant correlation coefficients suggested positive changes with higher precipitation). Only one significant association was indicated between vegetation variables and elk pellet cover and two between vegetation and deer pellet cover.

In our multivariate analysis, we used the same vegetation categories and independent variables used to develop the Pearson correlation matrix, but we created a separate logistic regression model for each vegetation variable (Table 6). Only five of the 14 independent variables (weather and ungulate indices) met the minimum criterion for entry into any model ($P < 0.05$). No models included more than two independent variables. The SAS (1994) Logistic Regression module created statistically significant models for predicting positive or negative changes in 12 of the 16 vegetation categories. Of the 12 models in which inclusion of independent variables was statistically justifiable, only eight could be considered biologically significant, i.e., the contribution of the selected model to prediction of positive or negative changes was greater than 25% more than that of the null, no variable, model. In seven of these eight models (models for prediction of change in choke cherry stems, snowberry stems, shrub stems greater than 100 to 200 cm, low shrub canopy cover, graminoid canopy cover, exotic grass canopy cover, and palatable forb canopy cover) precipitation in the growing season of the year prior to vegetation measurement, one of the variables with the highest number of significant associations in the univariate analysis, was the only variable in the model or the first variable to enter. Month of measurement and summed precipitation in the growing season the year before and the year of vegetation measurement, two other important variables identified in the univariate analysis, did not enter in any model.

Table 5. Correlations between independent variables and percent change (truncated Theodore Roosevelt National Park, 1986 to 1996.

	Month	Pptmo	Tempmo	Pptgro	Pptprev	Ppt2y
Shrub stratum (stem counts)						
Green ash	0.00	-0.21*	0.17	0.08	0.19	0.22*
Choke cherry	-0.36**	0.07	0.00	-0.25*	0.49**	0.29*
Saskatoon service-berry	-0.02	-0.20	0.25*	0.09	0.04	0.10
Snowberry	-0.23*	-0.23*	0.26**	-0.05	0.55**	
Tot 0-50	-0.32**	-0.11	0.17	-0.17	0.54**	
Tot 51-100	-0.13	-0.02	-0.06	0.04	0.08	0.10
Tot 101-200	-0.11	0.13	0.04	0.09	0.08	0.13
Ground stratum (% cover)						
Bare ground	-0.27**	0.32**	-0.07	-0.49**	0.10	-0.23*
Litter	0.16	0.08	0.34**	0.23*	-0.11	0.05
Low shrub canopy (0-50 cm)	-0.50**	-0.11	0.06	-0.26*	0.55**	
Total graminoids	-0.43**	0.24*	-0.04	-0.45**	0.55**	0.21
Climax graminoids	-0.38**	0.16	-0.07	-0.33**	0.42**	0.18
Exotic grasses	-0.36**	0.04	0.14	-0.27**	0.42**	0.22*
Total forbs	-0.36**	0.04	0.26**	-0.04	0.33**	
Palatable forbs	-0.24*	0.05	0.41**	-0.04	0.50**	
Invasive forbs	0.00	0.05	0.17	0.21	-0.16	-0.01

* $p < 0.10$
** $p < 0.05$

to -100% to +101%) in 16 vegetation variables measured at two-year intervals in

Snow	Snow2y	Temsum	Temsum2y	Wintem	Wintem2y	Elkpel	Deerpel
0.01	0.15	0.06	-0.16	-0.14	-0.25*	0.06	-0.17
-0.05	0.05	0.11	-0.14	0.08	0.15	-0.08	0.25**
0.15	0.22*	0.13	0.00	-0.23*	-0.27**	0.09	0.01
0.06	0.25*	0.17	-0.26**	-0.18	-0.2*	0.02	-0.15
0.05	0.20	0.19	-0.18	-0.07	-0.06	-0.13	-0.09
-0.10	-0.10	-0.13	-0.21	0.05	-0.07	0.13	-0.02
0.10	-0.09	-0.13	-0.13	-0.08	-0.02	0.04	0.04
0.25*	0.10	0.34**	0.51**	0.12	0.56**	-0.10	0.34**
0.18	0.21	0.11	0.16	-0.39**	-0.21*	-0.03	-0.08
0.00	0.10	0.12	-0.25*	0.04	0.00	0.02	-0.03
0.04	0.06	0.23*	0.07	0.13	0.42**	-0.24*	0.21
-0.02	0.00	0.12	-0.02	0.14	0.29**	-0.06	0.17
0.06	0.18	0.23*	0.02	-0.07	0.10	-0.04	0.00
0.12	0.21	0.16	-0.07	-0.22*	-0.13	0.08	-0.14
0.08	0.33**	0.27**	-0.04	-0.35**	-0.15	0.02	-0.12
0.14	0.05	-0.04	0.02	-0.23*	-0.20	0.12	-0.05

Table 6. Summary of stepwise logistic regression analysis of changes in vegetation Roosevelt National Park at two-year intervals from 1986 through 1996. A positive an increase in that independent variable would predict an increase in the associated included more than two of the set of 16 independent variables in the analysis.

Category	Changes (n) + (or 0)	Changes (n) -	Significant First variable to enter	Significant Standardized coefficient
Shrub stratum (stem counts)				
Green ash	33	27	None	
Choke cherry	25	35	Pptprev	0.666
Saskatoon service-berry	34	26	None	
Snowberry	25	35	Pptprev	0.785
All species 0-50 cm	30	30	None	
All species 51-100 cm	26	34	Temsum	-0.385
All species 101-200 cm	21	39	Pptprev	0.600
Ground stratum (% cover)				
Bare ground	32	28	Pptmo	0.714
Litter	17	43	Temwin2y	-0.494
Shrubs 0-50 cm	24	36	Pptprev	0.758
Graminoids	39	21	Pptprev	0.525
Climax graminoids	35	25	Pptprev	0.422
Exotic grasses	43	17	Pptprev	0.654
All forbs	27	33	Snow	0.360
Palatable forbs	28	32	Pptprev	0.584
Invasive forbs	53	7	None	

[a] AIC = Akaike Information Content is a relative measure of the efficiency of the model. The lower the model with independent variables added, the full model is significantly ($P < 0.05$) better than the null model.

categories in the shrub and ground strata for vegetation measurements in Theodore value for the standardized coefficient of individual variables to the logit indicates that vegetation category. A negative value would predict an inverse relationship. No model

($P < 0.05$) variables		AIC[a]			
Second variable to enter	Standardized coefficient	Intercept only	Full model	Model R^2	Hosmeyer-Lemeshow test of P-value
		85.5	69.3	0.32	0.75
Temwin2y	-0.415	83.5	63.4	0.45	0.96
		84.1	79.9	0.13	0.61
		79.7	69.0	0.26	0.53
Temsum2y	0.927	84.9	63.2	0.46	0.09
		73.5	68.0	0.17	0.42
		82.8	65.3	0.37	0.62
Temwin2y	0.409	79.7	68.2	0.31	0.69
Temwin2y	0.345	83.5	75.6	0.24	1.00
		73.5	62.6	0.28	0.58
		84.6	81.2	0.10	0.67
		84.9	73.4	0.27	0.43

value, the more efficient the model. If the AIC for the null model (intercept only) is ≥ 2 units more than the

DISCUSSION

Vegetation in green ash stands in TRNP varied substantially within stands, among stands, and among years. The only directional changes for the sample of stands as a whole that we identified during 12 years of monitoring were a decrease in mature choke cherry and Saskatoon service-berry plants and an increase in plant cover in the ground stratum. Recruitment of green ash and choke cherry seemed adequate to maintain the stands given the low mortality in mature trees. Recruitment of Saskatoon service-berry was low, but may have been adequate to maintain the low density of this species in the stands we measured. Changes in canopy cover in low shrubs and forbs was loosely linked to wet (increases) and dry (decreases) years. The directional changes we observed did not appear to be due to the cumulative effects of the numerous dry years during our sample period nor were they consistent with overuse by native ungulates. The changes were consistent with stand succession.

The protection afforded stands after the creation of TRNP and the absence of fires in stands we sampled would have allowed ash plants alive in the early 1950's to continue growth and maturation. Green ash and choke cherry trees are relatively short-lived, and, in stands we sampled, many of the larger plants of both species were nearing the ends of their lifespans. As old plants die, sunlight at ground level increases, which stimulates plant growth in the ground stratum until new green ash or choke cherry plants mature. This process presumably occurs on a patch by patch basis in uneven aged stands. In even aged stands, whether the evenness was created by grazing, fire, or tree harvest, these normal stand dynamics may result in waves of maturation and decay.

Snowberry, which is likely to increase under heavy grazing by livestock (Girard et al. 1987), did not increase significantly between the 1985 and 1996 in green ash stands while climax graminoids did. Invasive forbs and exotic grasses also increased but did not appear to be replacing native species in the interiors of green ash stands. Leafy spurge (*Euphorbia esula*) occurred in only two stands we measured and was not recorded in any stands in 1994 and 1996. Exotic plants, especially leafy spurge, increased in grass communities and riparian forest communities in TRNP during 1985 to 1996 despite an aggressive biological and chemical control program (Leafy Spurge Scientific Advisory Panel 1994, Trammel and Butler 1995 and Irby, unpubl. data.).

Deer and elk were the only ungulates that made any use of the interiors of green ash stands that we sampled. Signs of browsing by deer were observed in all of the stands, but the intensity of use of stand interiors was low. Forb and climax graminoid canopy did increase as deer density declined, but densities of palatable shrubs decreased or remained relatively stable. Neither the increases nor decreases were likely to be attributable to ungulate browsing. Over all transects and years, only 8% of shrub stems counted in 1-m^2 plots showed evidence of more than 10% removal of current year's growth. Median use for most shrub species counted in 1-m^2 plots was zero in all

years (Irby, unpubl. data.).

Elk have been identified as a factor in degradation of deciduous tree communities in the Rocky Mountains (Singer et al.1998, White et al. 1998) and probably had negative impacts on deciduous tree stands in Wind Cave National Park (R. Klukas, National Park Service, Omaha, pers. comm.). When we examined vegetation in green ash stands with zero to 12 years of elk use in TRNP, we did not find any consistent patterns of negative changes in vegetation categories expected to be susceptible to overuse by elk.

The lack of detectable elk effects on vegetation in TRNP can be explained by four factors. First, elk numbers have been regulated in TRNP. The herd is reduced to approximately 200 when it exceeds 400 individuals (based on aerial counts). Linear models developed by Westfall et al. (1993) predicted possible deleterious effects on vegetation when elk numbers exceed 400 for long time periods in a system with approximately 400 bison, 150 horses, and 800 deer. TRNP staff have used this numerical guideline in managing populations of all four species. Second, initial ungulate impacts on mature green ash stands are likely to occur in stand edges rather than stand interiors. All of our sample sites were placed in the middle of draws to avoid edge effects in vegetation measurement. Third, change takes time under any stocking rates (Laurenroth et al. 1994, Hobbs 1996, Biondini et al. 1998). We measured changes in stands over only approximately 10% of the lifespan of the trees dominating the canopy in mature stands during one regeneration cycle. Ultimate effects of ungulate herbivory could take longer to be expressed or could vary significantly with the successional status of a stand. Fourth, ungulates are only one of several environmental factors that affect plant species. An increase in ungulate use of plants could have been effectively masked at any point over the sample period by an increase in ground moisture or seasonal variation in temperature (Olson et al. 1985, Hart et al. 1988, Biondini and Manske 1996, Biondini et al. 1998).

Results of logistic regression and correlation analysis suggested that precipitation during the growing season one year before vegetation measurements were taken was an important determinant of change in vegetation. Two other factors, the month in which vegetation measurements were taken and the sum of growing season precipitation one year before vegetation measurement and in the year of measurement, were identified as important in correlation analysis. Vegetation measurements taken after mid-August were likely to show lower canopy coverage in ground stratum vegetation than vegetation measurements taken in mid-July in most years as a result of late summer desiccation. Shrub counts also tended to decline over the growing season as young shrubs died due to browsing, crowding, or desiccation. The importance of precipitation a year before vegetation measurement may be an artifact of the pattern of wet and dry years we sampled or it may reflect the two-year interval in vegetation measurement. In all of our analyses of short term effects, plants had two growing seasons in which to change. Above average rainfall during the growing season of years in which we did not

sample stands could stimulate increased growth in the non-measurement year, and movement of water retained in upland soils to adjacent drainages could contribute to plant growth in the drainages at the beginning of the growing season in which the next round of vegetation measurements were made. A wet season in the year of vegetation measurement, would reinforce positive changes that occurred in the previous non-measurement year. Drought would have an inverse effect and reinforce negative changes.

Our results indicate that researchers planning tests of grazing systems designed to decrease negative effects of livestock on green ash communities need not exclude native ungulates (as long as the ungulates occur in low to moderate densities) but should concentrate on sample timing and should add covariates to account for precipitation differences between sampling periods. Researchers should attempt to sample in a relatively narrow time period and to adjust this period for phenological variability associated with variability in precipitation during the growing season. We attempted to concentrate our sampling in a four-week period in July and August with samples collected early in the sampling window in dry years and later in the window in wet years. This was not precise enough to avoid differences in growth stage in perennial species and presence of annual species that may affect interpretation of experimental results. The standard deviations we calculated (16% to greater than 200% of associated means) demonstrated the high variability among green ash stands for vegetation categories that researchers would be likely to measure in tests of grazing systems. The lowest variability occurred in the tree stratum and the highest in the ground stratum.

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LITERATURE CITED

Biondini, M. E., and L. L. Manske. 1996. Grazing frequency and ecosystem processes in a northern mixed prairie, USA. Ecol. Applic. 6:239-256.

Biondini, M. E., B. D. Patton, and P. E. Nyren. 1998. Grazing intensity and ecosystem processes in a northern mixed-grass prairie, USA. Ecol. Applic. 8:496-479.

Boldt, C. E., D. W. Uresk, and K. E. Severson. 1978. Riparian woodlands in jeopardy on the northern High Plains, Pp. 184-189 *in* Proceedings of a national symposium on strategies for protection and management of floodplain wetlands and other riparian ecosystems (R. R. Johnson and J. F. McCormick, eds.), USDA Gen. Tech. Rep. WO-12.

Butler, J. L. 1983. Green ash communities in the North Dakota Badlands. M.S. Thesis. North Dakota State University, Fargo.

Daubenmire, R. F. 1959. A canopy coverage method of vegetational analysis. Northwest Sci. 33:33-64.

Girard, M. M., H. Goetz, and A. J. Bjugstad. 1987. Factors influencing woodlands of southwestern North Dakota. Prairie Nat. 19:189-198.

Girard, M. M., H. Goetz, and A. J. Bjugstad. 1989. Native woodland habitat types of southwestern North Dakota. USDA For. Serv. Rocky Mount. For. Range Exper. Sta. Res. Pap. RM-281, Fort Collins, CO.

Great Plains Flora Association. 1986. Flora of the Great Plains. Univ. Press of Kansas, Lawrence, KS.

Hansen, P. L., G. R. Hoffman, and A. J. Bjugstad. 1984. The vegetation of Theodore Roosevelt National Park, North Dakota: a habitat type classification. USDA For. Serv. Gen. Tech. Rep. RM-113, Washington, D.C.

Hansen, P. L., R. D. Pfister, K. Boggs, B. J. Cook, J. Joy, and D. K. Hinckley. 1995. Classification and management of Montana's riparian and wetland sites. Montana Forest and Conservation Exper. Sta., Univ. of Montana, Missoula. Misc. Publ. 54.

Hart, R .H., M. J. Samuel, P. S. Test, and M. A. Smith. 1988. Cattle, vegetation, and economic responses to grazing systems and grazing pressure. J. Range Manage. 41:282-286.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. J. Wildl. Manage. 60:695-713.

Hopkins, R. B. 1983. Woodland bird ecology - southwestern North Dakota. Ph.D. Dissertation. North Dakota State University, Fargo.

Laurenroth, W. K., D. G. Milchunas, J. L. Dodd, R. H. Hart, R. K. Heitschmidt, and L. R. Rittenhouse. 1994. Effects of grazing on ecosystems of the Great Plains. Pp. 69-100 *in* Ecological implications of livestock herbivory and the West (M. Vavra, W. A. Laycock, and R. D. Piper, eds.). Society for Range Management, Denver, CO.

Lèafy Spurge Scientific Advisory Panel. 1994. Recommendations for the management of leafy spurge in Theodore Roosevelt National Park. Theodore Roosevelt National Park, Medora, ND.

Lund, R. E. 1989. MSUSTAT statistical analysis package. Version 4.12. Montana State Univ., Bozeman.

Lyon L. J., and A. L. Ward. 1982. Elk and land management. Pp. 443-477 *in* Elk of North America, ecology and management (J. W. Thomas and D. E. Toweill, eds.). Stackpole Books, Harrisburg, PA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. Wildlife - habitat relationships, concepts and applications. 2nd ed. Univ. of Wisconsin Press, Madison, WI.

Olson, K.C., R.S. White, and B.W. Sindelar. 1985. Responses of vegetation of the northern great plains to precipitation amount and grazing intensity. J. Range Manage. 38:357-361.

SAS. 1994. Version 6.10. SAS Inst. Cary, NC.

Severson, K. E. 1981. Plains habitats, Pp. 459-485 *in* Mule and black-tailed deer of North America (O. C. Wallmo, ed.). Univ. of Nebraska Press, Lincoln, NE.

Singer, F. E., and M. K. Harter. 1996. Comparative effects of elk herbivory and 1988 fires on northern Yellowstone National Park grasslands. Ecol. Applic. 6:195-199.

Singer, F. J., L. G. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998. Elk, multiple factors, and persistence of willows in national parks. Wildl. Soc. Bull. 26:419-428.

Sullivan, M. G. 1988. Distribution, movements, habitat use, and food habits of reintroduced elk in Theodore Roosevelt National Park. M.S. Thesis. Montana State University, Bozeman.

Theodore Roosevelt National Park. 1984. Natural resource management plan and environmental assessment. Theodore Roosevelt National Park, Medora, ND.

Trammel, M. A., and J. L. Butler. 1995. Effects of exotic plants on native ungulate use of habitat. J. Wildl. Manage. 59:808-816.

Uresk, D. W., and C. E. Boldt. 1986. Effect of cultural treatments on regeneration of native woodlands on the northern Great Plains. Prairie Nat. 18:193-202.

Wasser, C. H. 1982. Ecology and culture of selected species useful in revegetating disturbed lands in the West. US Fish Wildl. Serv. Rep. OBS-82/56, Washington, D.C.

Westfall, J. A., Jr. 1989. The ecology of reintroduced elk in Theodore Roosevlet National Park, North Dakota. M. S. Thesis. Montana State University, Bozeman.

Westfall, J. A., Jr., L. R. Irby, and J. E. Norland. 1993. A forage allocation model for four ungulate species in Theodore Roosevelt National Park. Final Report to Theodore Roosevelt National Park, Medora, ND.

White, C. A., C. E. Olmsted, and C. E. Kay. 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Wildl. Soc. Bull. 26:449-462.

Wood, A. K., R. J. Mackie, and K. L. Hamlin. 1989. Ecology of sympatric populations of mule deer and white-tailed deer in a prairie environment. Montana Department of Fish, Wildlife, and Parks, Helena, MT.

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