ELK IN THE ROCKY MOUNTAIN NATIONAL PARK ECOSYSTEM - A MODEL-BASED ASSESSMENT

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EXECUTIVE SUMMARY

Rocky Mountain National Park (RMNP) was established after a period of substantial resource extraction by early settlers, including trappers, hunters, miners, loggers, and ranchers. A once abundant large herbivore, elk (*Cervus elaphus*) had by that time been extirpated from the region by a period of intensive market hunting in the 1860s and 1870s (Guse 1966). Mule deer (*Odocoileus hemionus*) were also much reduced. Elk were reintroduced in 1913-1914, and the population grew in size to approximately 900 animals in 1938-1939 (Packard 1947a). Elk were intensively managed from 1944-1968, due to early concerns that they were overabundant, and damaging the winter range. The herd was reduced by culling operations in 1944-1945 and 1949-1950, and generally kept in the 300-600 range through 1968. Public disapproval of elk culling in Yellowstone led to an experimental approach to management often referred to as natural regulation. The hypothesis was that elk would reach a natural food-limited carrying capacity, and population growth would be self-regulated through density-dependent competition for food. Since 1968, the elk herd in RMNP has been managed only by sport hunting outside of the park boundary, which has not controlled elk population growth. Furthermore, elk have been increasingly wintering outside the park boundaries in the town of Estes Park, where they also largely escape hunting.

Concerns about elk impacts on plants and other components of the ecosystem have heightened considerably during the last two decades (Olmsted 1977, 1979, 1997, Hess 1993, Wagner et al. 1995, Baker et al. 1997, Berry et al. 1997, Keigley and Wagner 1998). In particular, it has been suggested that elk are overabundant and present in unnatural densities due to lack of natural predators and Native American hunting. These authors felt that in pre-settlement times, elk were present at much lower densities, and they may not have wintered in the areas which now comprise RMNP. However, there appears to be no evidence that elk did not winter on the eastern slope of the park in historic times.

An effort was made to review the literature for prehistoric and historic elk presence. Prehistoric game drive systems discovered at high elevations within the park were most likely used to hunt elk (Benedict 1992, 1999). There was a considerable amount of historical evidence of elk presence prior to settlement (Sage 1846, Loring 1893, Sprague 1925, Fryxell 1928, Estes 1939).

Human impacts on the elk winter range prior to the creation of the national park provided an unnatural starting point for the elk reintroduction program, and likely exacerbated elk impacts on the range. Livestock grazing was widespread and apparently intense enough to cause significant changes in herbaceous vegetation cover (Mills 1924, McLaughlin 1931, Ratcliff 1941). Land had also been drained and willows cut to support haying operations (Gysel 1960).

A deer eruption in the 1930s, along with increased numbers of elk brought about declines in upland shrubs (Ratcliff 1941), willow cover (Dixon 1939, Gysel 1960), and barking and

suppression of regeneration in aspen (McLaughlin 1931, Ratcliff 1941, Packard 1942). Following the elk reduction programs of the 1940s, Buttery (1955) concluded that range condition had improved to fair condition, and was stable. After the cessation of elk reductions, Stevens (1980) found stable sagebrush grasslands, but increases in bare ground in grasslands between 1968-1979. Stohlgren et al. (1999) found grazing reduced herbaceous cover slightly, and increased diversity.

A greater level of concern has been recently expressed about elk impacts on riparian willow communities, beaver, and aspen. Aspen stands on the winter range have exhibited little or no regeneration, heavy bark scarring, and mortality (Olmsted 1979, 1997, Stevens 1980, Baker et al. 1997), all attributable to elk browsing. A recent analysis of historical aerial photography showed that over the last 50-59 years willow cover has declined by 19-21% (Peinetti 2000, Peinetti et al. 2002). These decreases were associated with 44-56% decreases in total stream channel density, which was believed to be a consequence of reduced beaver activity. Beavers have declined both on and off the winter range from high levels in 1925-1947 (Warren 1926, Packard 1947b) to current densities which are apparently 90% less than in 1940 (Hickman 1964, Stevens and Christianson 1980, Gense 1997, Zeigenfuss et al. 2002). Some authors have attributed the decline to elk, particularly their negative impacts on willow (Packard 1947b, Gysel 1960, Hess 1993). However, beaver numbers first declined when elk were being controlled below their food-limited carrying capacity.

These concerns led to the inception of several new studies of the elk winter range, including the present study. A three-year study of elk impacts on upland grasslands and shrublands has shown little impact of herbivory (Singer et al. 2001a). Few effects have been noted of elk on soil carbon and nitrogen or herbaceous root biomass (Binkley et al. 2002, Schoenecker et al. 2002), however, in willow communities Schoenecker et al. (2002) found markedly (5x) lower N mineralization outside short-term exclosures located in portions of the winter range judged to have high elk densities. All of the sites were in browsing-suppressed short willow communities. A five-year study of elk browsing impacts on willow (Peinetti 2000, Singer et al. 2001a,b; 2002; Zeigenfuss et .al. 2002) has shown large increases in willow growth when protected from elk herbivory. Zeigenfuss et al. (1999) found a continuation of some of the negative vegetation trends observed earlier by Stevens (1980). Olmsted (1997) found further evidence that aspen stands were degrading. Berry et al. (1997) examined whether vegetation on the elk winter range has deviated from pre-Columbian conditions due to elk overabundance. They concluded elk were responsible for aspen and willow declines and decreases in upland range condition, and suggested that the vegetation be protected from herbivory to facilitate recovery from past damage.

The present modeling study was initiated with the specific aims of estimating elk carrying capacity and elk impacts on riparian willow. The more general purpose of this research was to assess the role of elk in the RMNP ecosystem. Ecosystem modeling was used to assess the role of elk in the ecosystem, and the ways that ecosystem dynamics have been altered by interactions between elk, climate, and humans. Ecosystem modeling is a comprehensive approach to carrying capacity assessment. It simultaneously addresses different concepts of carrying capacity by

explaining ecosystem dynamics in terms of underlying ecosystem processes. The model was used to represent plant and soil responses to herbivory, food limitation of the herbivore population, and predation. It was used to project ecosystem dynamics under past, present, and future management scenarios.

Model Description and Data Inputs

SAVANNA is a spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems developed originally for studies in East Africa (Coughenour 1992, 1993). The model has also been applied to Elk Island National Park in Alberta (Buckley et al. 1995), Yellowstone National Park (Coughenour and Singer 1996), the Pryor Mountain Wild Horse Range, Montana (Coughenour 2000), northern Australia (Ludwig et al. 1999), South Africa (Kiker 1998), Tanzania (Boone et al. 2001), and Inner Mongolia (Christiansen 2001). SAVANNA simulates processes at landscape through regional spatial scales over annual to decadal time scales. The model is composed of site water balance, plant biomass production, plant population dynamics, litter decomposition and nitrogen cycling, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, and ungulate population dynamics submodels. Wolf predation and wolf population dynamics submodels are derived from a model used to assess wolf reintroduction into Yellowstone National Park (Boyce and Gaillard 1992, Boyce 1993).

The model was driven by weather data from weather stations in and surrounding the study area. Monthly precipitation and temperature maps were generated from spatial interpolation on elevation corrected data. Historical weather data since 1949 were readily available. Data for 1931-1948 were sparse, however there were key stations with data, including Estes Park, Grand Lake, and Fraser. Data for the period 1910-1930 were reconstructed based upon deviations from normal observed in the data from Fraser Colorado, which had the most reliable and longest record. Data for the period 1775-1911 were reconstructed from the tree-ring data base of Fritts (1991a,b).

SAVANNA requires a vegetation map for the initialization of plant biomass and population variables. A single-source vegetation map for the entire elk range did not exist, primarily because the elk range extends outside the park boundaries, and includes land from three administrative agencies, the U.S. National Park Service, the U.S. Forest Service (USFS), and the Town of Estes Park. Consequently, a vegetation map was constructed from multiple sources. Vegetation cover maps from RMNP and the Arapahoe-Roosevelt National Forest (ARNF) were combined into a single coverage (Ron Thomas RMNP GIS lab). Vegetation outside RMNP and ARNF, i.e., on private landholdings, was derived from a vegetation map of Larimer County Colorado that was developed at Colorado State University from a Landsat-TM scene (McCool 1995, Todd 1995). Disturbed areas, human land uses and areas subsidized by water, were delimited with the aid of satellite data of the normalized difference vegetation index (NDVI). An "undisturbed" vegetation map was created to represent the vegetation cover prior to the settlement of the Estes Valley. Vegetation and land covers of anthropogenic origin on the Larimer County vegetation map were restored to undisturbed conditions. All areas classified as disturbed, urban, golf course, etc., were reclassified as grassland. The Big Thompson river course was markedly altered by development, including the construction of a dam

and lake. Historical photographs of the valley prior to town and dam construction showed the former extent of the river course and riparian floodplain. These features were incorporated into the "undisturbed" vegetation map.

The model was configured to represent ten plant functional groups: upland grasses and forbs, riparian graminoids and forbs, upland shrubs, willow, aspen, ponderosa pine/Douglas fir, lodgepole pine, and subalpine conifers (spruce-fir). The area that was simulated was defined by the combined winter and summer ranges of the elk which winter on the east slope of RMNP, and in the town of Estes Park. Two subherds of elk were simulated, a park subherd and a town subherd, based on information that animals from these subherds exhibit fidelity to these ranges (Lubow et al. 2002). Mule deer were also simulated, primarily to represent their impacts on plants. Their range was assumed to be the elk-defined study area, but with different habitat preferences.

The plant growth model was parameterized from numerous data sources in the literature, and from recent field studies in RMNP. Then it was verified by comparing model outputs to observed biomass data from Hobbs (1979), Fisk et al. (1998), Singer et al. (2001a,2002), and Zeigenfuss et. al. (2002). Comparisons were made for several major vegetation types including: dry grasslands, mesic riparian herbaceous, upland shrubs, willow, low elevation woodlands dominated by ponderosa pine (montane woodland), high elevation woodland and forest dominated by lodgepole pine, Engelmann spruce and subalpine fir, and alpine tundra. Comparisons were made under grazed and ungrazed conditions. The comparisons proved to be generally favorable.

Model Verification – the Control Run for 1949-1998

A simulation was conducted to represent observed ecosystem dynamics for the period 1949-1998. This was referred to as the control run because it represented a set of standard conditions to which results from other model experiments could be compared. Control run output provided additional information for verifying the model's behavior by comparing simulation results to observations. The control run was a calibration run for animal submodels, because key model parameters for diet selection, forage intake, energy use, and population dynamics were calibrated so that model outputs most closely matched observed values.

The simulated elk population was reduced using observed rates of elk offtake by hunter harvest and management removals. The deer population was maintained within a range of 400-600 animals throughout the simulation by removals as necessary.

The snow submodel was verified by comparisons between observed and predicted data at seven SNOTEL stations 1979-1998. The snow model performed satisfactorily at most of the sites.

Water table depths in riparian willow stands (Singer et al. 1999, Zeigenfuss et al. 2002) were used to parameterize model relationships between water table depth and streamflow in the watershed. These relationships were then used in the model to estimate water table depths for different willow sites within each watershed.

The elk population model was calibrated to observed, sightability-corrected count data 1959-1998 (Lubow et al. 2002). The model was calibrated to pass through the higher of the reasonable data points, on the assumption that lower values were undercounts. The model simulated the correct rate of population increase, and most importantly, represented the leveling-off of the park population during 1980-1998. This indicates that the model was representing density dependent competition for food, and thus food-limited carrying capacity, correctly. There was a clear decline in the ratio of calves to cows over the period 1949-1998. This was consistent with data, and with the hypothesis that the elk population was exhibiting a density-dependent limitation on recruitment (Lubow et al 2001).

Simulated spatial distributions of elk were in agreement with observed data. High densities of up to 90 elk/km^2 were simulated in the Moraine Park area. High densities were also simulated in certain areas of Horseshoe Park, but overall density was less than in Moraine Park. These densities are consistent with the contour maps generated from aerial survey data (Singer et al. 2002), which show density contours of 12-16 elk/km^2 in Horseshoe Park and >90 elk/km^2 in Moraine Park.

Simulated elk diets were consistent with data of Riorden (1948), Hobbs (1979), Stevens (1980), Baker and Hobbs (1982), and Singer et al. (2001b).

The model predicted a reasonable spatial distribution of herbaceous biomass over the winter and summer ranges. Peak biomass generally ranged 40-150 g/m^2 on the winter range on grassland, shrubland, and ponderosa pine woodlands. Low production was simulated in the subalpine forests (20-40 g/m^2). Higher biomass levels were simulated on the alpine tundra and subalpine meadows. Aboveground net primary production was not much higher than peak standing crop.

Condition indices of elk reached maximum values each summer. End of winter minima declined over the period in response to increasing density and competition for limited forage. There was considerable variability among winters, reflecting differences in winter severity, and foraging conditions. Condition indices of the town population showed a similar pattern, but when densities were extremely low, winter minima were much higher than observed in the park population. As the town population increased, winter minima decreased markedly.

Model Experiments

Model experiments were conducted for three different time periods: 1775-1911, 1912-1948, and 1949-1998.

The period before the reintroduction of elk (1775-1911) included transitions from an ecosystem undisturbed by Euro-American colonists but possibly affected by Native Americans, to an ecosystem that was heavily exploited by early settlers. Beaver trapping occurred prior to 1850, market hunting and extirpation of elk occurred in the 1870s, followed by logging, and heavy livestock grazing throughout the Estes Valley and the elk winter range inside the current park boundaries.

Wolves were still present in 1894, but were extirpated well before 1917 (Stevens 1980). Simulation studies of this period were designed to examine the pre-settlement ecosystem, and the impacts of these initial disturbances.

The reconstructed undisturbed vegetation map was used in all of the 1775-1911 runs. Human impacts on ungulates were represented in the model through the imposition of prescribed hunting reductions. To reduce confounding effects, deer were kept at or below 600-700 throughout the entire simulation. Beavers on the elk winter range inside the park were held at 450 throughout. The control run for this period (a run to simulate actual conditions) examined the effects of the extirpation of elk by market hunting. Experimental runs were conducted to examine undisturbed conditions assuming one elk herd, undisturbed conditions assuming two elk subherds limited to the ranges now occupied by park and town subherds, respectively, and the effects of wolves.

When the historic pattern of hunting was imposed, elk were extirpated as specified, and in response deer numbers increased and wolves were eliminated due to lack of prey. With no elk hunting, and with wolves (undisturbed conditions), total elk numbers varied between 1,500-3,500 and gradually increased throughout the simulation. Distinguishing two subherds indicated the relative sizes of subherds that would be expected in the two ranges. The park subherd varied between 300-800 elk, while the town subherd varied between 1,400-1,500 elk at first, increasing to approximately 1,600-2,000 elk in later years. Deer numbers were kept to <200 by wolf predation. Without wolves, total elk numbers increased at first to about 3,800, then numbers exhibited a dynamic equilibrium at approximately 2,800 elk, but with a declining long-term trend due to deteriorating range conditions. Elk numbers ended at a similar point with or without wolves, but elk and vegetation conditions were substantially improved in the presence of wolves. Elk condition indices remained higher in winter when wolves were limiting the population compared to when food was limiting the population. Elk mortalities due to starvation were therefore likely to be far less with wolves present.

When elk were hunted to historic levels, dryland herbaceous biomass, i.e., herbaceous layer biomass everywhere on the park elk winter range except in riparian willow and wet meadows, increased. In undisturbed conditions (no market hunting and wolves present), dryland herbaceous biomass increased and then decreased slightly when elk were limited by wolves. Without wolves, dryland biomass declined gradually throughout the period. With historic elk hunting, willow cover increased to the maximum level, while with undisturbed conditions willow cover increased to near-maximal levels. In contrast, without wolves, willow cover declined. Aspen increased markedly following the extirpation of elk. With undisturbed conditions, aspen cover decreased even when wolves were present. The aspen decline was not accelerated by lack of wolves. This suggests that aspen cover at the inception of the park and elk reintroduction, could have been higher than if there were no elk extirpation.

To summarize the assessment of 1775-1911, it is very plausible for wolves and other predators to have maintained elk numbers below food limited carrying capacity, but still at moderately high numbers, maintained by increased productivity of the vegetation compared to current conditions. Increased cover of willow could be supported, but beaver activities would be critical to maintenance

of high water tables. Aspen would have had a difficult time becoming established or surviving the predator-limited densities of elk and mule deer on the core, lower elevation portions of the winter range. Purported evidence for aspen in those locations prior to 1870 should be carefully examined, since elk extirpation could have been a primary cause for the emergence of aspen stands in those locations. Localized effects of wolves and Native American hunters, effects of elk on beaver populations, and bison impacts on elk winter forage all require further consideration.

The period 1912-1948 included the inception of the park, the reintroduction of elk, and early conservation efforts. For most of the period, elk hunting was absent, or minimal. Hunting offtake was insignificant until 1941, and was 90-122 elk per year during the period 1941-1945 (Stevens 1980). The first significant management reduction did not occur until 1945, when 301 elk were removed (Stevens 1980). There were no reductions between 1946-1948, and hunting offtake was reduced to 20-80 per year. Thus, this was mainly a period of elk protection, with the first efforts of elk management occurring at the end of the period. Much of the elk winter range within the current park boundary was affected by human settlement, livestock grazing, haying, and resorts. Willow habitats were drained, and willow was removed to create pastures or hayfields. I assumed that between 1912-1931, the elk herd was mainly restricted to the area east of the current park boundary due to lack of access to the core grasslands in Moraine Park and Horseshoe Park, as these were grazed by domestic stock or hayed. Elk were introduced into the model in 1913 and 1914. Deer were kept at the 600-700 level until the period 1927-1942, when the population increased to 1,000-1,200 animals (Stevens 1980).

In the control run for this period, elk increased to about 800 animals by 1934, and then kept within a similar range to the estimated values. The undisturbed simulation began with the elk numbers simulated at the end of the undisturbed 1775-1911 run, and with wolves present. In this run, elk also had access to the full winter range, as opposed to being precluded from the core winter range inside the park. Wolves held the park subherd to 500-1,000 elk, while the town subherd increased to 2,500 and then declined to 1,200. Without wolves, the park subherd increased to 1,500, and the town subherd increased to about 2,700 before declining markedly to approximately 1,500.

There were few differences among dryland herbaceous biomass amounts in the different scenarios during this period. Willow cover increased to high levels in all runs where elk started out at zero, even with no elk reductions. The initial period when elk were absent or present at low numbers was sufficient for willow to reach tall stature. Once willow reached tall stature, it for the most part escaped herbivory. Subsequent conversion to short willow depended on the gradual mortality of old plants, and suppression of replacement plants. With the observed number of elk, and high water tables, the model did not simulate a decrease in willow during 1912-1948. In particular, the model could not explain willow declines under the number of elk present up until 1930. If water tables were high, the model only simulated willow declines during 1912-1930 if elk were assumed to be in the 500-1,000 range for the entire period, which was unrealistic. Willow declines were simulated during this period only when hydrology was altered. Humans likely played a significant role in these alterations.

In the control run, aspen increased at first but in about 1925-1930 began to decrease. In hypothetical runs with no elk or beaver present, the decrease did not occur. The results suggested that the combination of elk and beaver was responsible for the decline. In the undisturbed run with wolves, aspen remained steady at the low initial value, suggesting that aspen would be present at lower abundances in some locations on the core winter range.

The assessment of 1912-1948 revealed the importance of human disturbances both prior to and after 1912, in moving the system into what could be considered to be an alternate stable state. Livestock grazing, draining of wetlands, removal of elk and wolves, and compression of elevated numbers of beaver into reduced willow cover, all combined to reduce willow cover in Moraine and Horseshoe Parks further. Aspen declined as well, due to the combined effects of elk and beaver, but the initial presence of some of the aspen that declined in this period could have been a product of earlier elk extirpation.

Simulation experiments for 1949-1998 were intended to investigate the effects of elk, elk management, and wolves. In these runs, two elk populations and ranges were simulated, the park and the town populations. The first experiment was to allow elk populations to grow unchecked. The park population grew to a food limited carrying capacity earlier than in the control run, and food-limited population sizes were slightly higher in the 1960s and 1970s than in the 1980s and 1990s. Food-limited carrying capacity of the park subherd appeared to be in the range of 1,000-1,300 elk. The town population increased to a slightly higher level than in the control run (1,900 vs. 1,800) before declining. In the undisturbed run with wolves the park elk population was held to 300-500. The town population increased from 1,000 to 1,800, but then predation decreased the population to about 1,200. Wolf numbers varied between 14-17 throughout. Elk body condition in the run with no elk reductions was lower in winter than in the control run, throughout the simulation. In the undisturbed run, body condition was maintained at a higher level, with the exception of several severe winters.

When elk and deer were not reduced, there was about 10% less grass and 30% less forb biomass on drylands than in the control run by the end of the period. These results are consistent with Buttery's (1955) observations of modest increases in range conditions in some areas due to elk removals. In the undisturbed run, there was about 8% more grass and 5% more forb biomass than in the control run. Willow cover decreased with no elk reductions, while it remained constant in the control. In the undisturbed run, willow cover increased. All willow locations in the undisturbed run attained cover >60%. Reducing water tables had a negative effect on willow cover at three of the locations, but cover at those locations declined to lower values with elk than without elk. In additional experiments conducted to further examine the effects of water table levels, using undisturbed water tables led to an increase in willow compared to the control run which used current water table conditions. Conversely, switching to current water table conditions in the otherwise undisturbed run led to markedly lower willow covers. In the control simulation, aspen cover declined about 15%. With no elk reductions, the decline occurred earlier. In the undisturbed run with wolves, aspen cover also declined due to elk herbivory. In a hypothetical simulation with no elk present, aspen increased.

It seems likely, therefore, that the elk reductions in the 1940s-1950s brought about modest range improvement, and protected some, but not all willows and aspen. The reductions did not appear to have led to a restoration of willow to its former range, primarily because elk reductions do not address the problem of lowered water tables. While the elk reductions would have created opportunities for aspen recruitment in some areas, it seems unlikely that they would have promoted aspen regeneration on the primary elk concentration areas. While there is some evidence that elk reductions promoted aspen regeneration (Olmsted 1979, Baker et al. 1997), the spatial locations of such regeneration are critical to this interpretation. For example Stevens (1980) suggested that regeneration occurred in places where elk were shot and thus avoided using, and Olmsted (1979) showed that aspen only regenerated in areas with <50% utilization by elk.

A factorially designed experiment was conducted in which elk and beaver densities were varied in all possible combinations, to assess their relative effects on plants. A response surface of willow cover generated from the results showed that elk and beaver can both have negative effects, but beaver effects are negligible at low elk densities. Increasing beaver had little impact on willow below 400 elk. In the range of predator-limited elk carrying capacity (400-800 elk), less than 450 beavers had little impact on willow.

Alternative elk management and vegetation fencing scenarios were simulated by running the model for 50 years, starting in 1994, using weather randomly selected from data for the period 1949-1998. All runs began with current conditions, including current herbivore numbers, willow sizes and densities, and soil water table depths. There were three elk reduction scenarios. The park elk subherd either was never reduced, reduced to 600-800, or reduced to 200-400. In all elk reduction scenarios the town population was reduced to 1,000-1,200. Beavers were assumed to start at current levels, and then gradually be restored to historic levels (450) over a 25-year period. Aspen and willow within the park boundary were either unfenced, or fenced to exclude elk and deer, but not beaver herbivory.

With no reductions of the park or town elk subherds, the park elk population fluctuated between 800-1,100 animals, consistent with the range previously estimated to be the food-limited carrying capacity. The town population increased at first to 2,400, then varied between 1,400-2,000. Fencing all of the willow and aspen inside the park reduced the food-limited carrying capacity of the park population by approximately 30-40%. Elk body condition in the winter was low when elk were not reduced. Reducing elk to 600-800 raised winter body conditions moderately, while reductions to 200-400 raised body conditions markedly.

Dryland herbaceous biomass remained essentially constant when elk were not reduced. However, when elk were reduced to 600-800, biomass increased slowly, over the entire period. Reducing elk to 200-400 caused a faster rate of biomass increase, and biomass was still increasing after 50 years. Fencing had no discernable effects on dryland herbaceous biomass. Without fencing, aspen declined to similar levels irrespective of elk reductions. During the years when aspen were protected by fencing, cover increased markedly. However, when the fence was removed, aspen began to decline once again, in all elk reduction treatments. Willow continued to decline when elk were not reduced, increased slightly when elk were reduced to 600-800, and markedly increased when elk were reduced to 200-400. Fencing resulted in a large increase in willow cover irrespective of reductions. After the fence was removed, willow began to decline when elk were not reduced and when reduced to 600-800. In contrast, when elk were reduced to 200-400 willow cover remained at a high level after the fence was removed.

Increasing water table heights had little positive benefit when elk were not reduced and willow were unprotected by fencing. With fencing, the added water supported higher willow cover during the fenced period, which was sustained after the fences were removed, even with no elk reductions. With no fencing, higher water tables led to small increases in willow cover when elk were reduced to 600-800, and larger increases in willow cover when elk were reduced to 200-400. With fencing, high water tables led to further increases in willow cover when fences were removed, and elk were reduced. Increased water table depth had no effect on aspen, because it was assumed that elevated water tables only occurred in riparian willow and wet meadow habitats, and not in aspen habitats.

Beginning with current vegetation, soil water table depths, and elk numbers, a hypothesized wolf reintroduction quickly reduced elk numbers in both the town and park subherds. After 15 years, the system stabilized at 14 wolves, about 200 elk in the park population, and about 1,000 elk in the town population. Wolves held elk to lower levels in future vs. historic runs because of deteriorated range conditions. Deer were held to 200.

The assessment of alternative management scenarios showed that a marked elk reduction to levels which may be lower than those present in pre-settlement times, or fencing, would achieve a recovery of willow, but only in locations where water tables are still elevated. Reintroduction of beaver or other manipulations to raise water tables would be required to achieve complete recovery. Aspen cover could be increased by fencing or severe elk reductions, however, elk numbers would have to be maintained very low, or once fences are taken down, aspen cover on the core winter range would again decline.

Simulations were performed to examine sensitivity to the wolf submodel parameters. The model was particularly sensitive to the parameter which represents how wolves control their own density through territoriality, the fraction of prey mortality which is compensatory vs. additive, and the way predation is distributed among age/sex classes. It was possible to find plausible parameter values which resulted in diminished or no effects of predation on elk population size, as well as values which resulted in lower elk numbers than noted above.

The model showed that the situation in RMNP is more complex than the simple plant-herbivore equilibrium predicted by natural regulation theory. While the elk-grassland subsystem may reach an equilibrium, that equilibrium would probably not have developed in the presence of wolves and other predators. Instead, a different dynamic equilibrium would be expected, involving interactions among three trophic levels. It would not be totally accurate to refer to this as a predator-limited number of elk, because the productivity of the forage base also has an influence. In a more productive system, there would be more herbivores and more predators alike, up until a limit on predator and possible herbivore numbers imposed by other factors aside from food, such as behavioral spacing. Because the tri-trophic equilibrium involves fewer elk than the bi-trophic equilibrium, there could be ramifications for plant species which are not necessarily limiting the elk population in a bi-trophic system, in particular aspen and willow.

Management Implications

Management of ungulates in U.S. National Parks is directed by the enabling legislation of the U.S. Congress (the Organic Act of 1916) which states that National Parks are "to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for future generations." In this view, managers must conserve the vegetation structure that was a product of pre-settlement climate, soils, and ungulate herbivory. In Yellowstone and RMNP, this vegetation structure is thought to be characterized by greater abundances of aspen and willow than are present at the food limited carrying capacities of their elk populations. Another view places more emphasis on the conservation of natural processes, and recognizes that ecosystems are dynamic, not static entities (Houston 1982, McNaughton 1996, Boyce 1998, Sinclair 1998, Huff and Varley 1999). National Park Service Management Policies (NPS 2001) state that the Service will try to maintain all the components and processes of naturally evolving park ecosystems, and will rely on natural processes to maintain native species and natural fluctuations in populations whenever possible. Natural processes are those which characterize ecosystems in general, rather than a specific ecosystem at a certain point in time. Thus, there is a fundamental policy discord, between a strict reading of the NPS Organic Act, and what many believe is a more modern and scientifically informed view about ecosystem dynamics in nature.

Ultimately the choice of elk management tactics reduces to a decision between trying to reconstruct, and then maintain, the vegetation structure which is believed to have been characteristic of the pre-settlement ecosystem, or allowing ecosystem processes to unfold with a minimal amount of human intervention so long as indigenous species are conserved. The question of which would be more natural or desirable cannot be answered here. The model provided insight into how a pre-settlement ecosystem might have looked and functioned, but it did not consider whether or not such an ecosystem is natural in the present time, most appropriate to NPS policies, or acceptable to the public.

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INTRODUCTION

An objective of U.S. National Parks is to preserve naturally functioning ecosystems (Wagner et al. 1995). In order to accomplish this goal, it is necessary to understand how ecosystem processes interact to give rise to a natural abundance of large herbivores along with their natural effects on ecosystem structure and function. Large herbivores exert significant effects in ecosystems, altering the structure and function of vegetation (McNaughton 1983a,b, Milchuness et al. 1988, Archer and Smeins 1991, Frank and McNaughton 1992, Hobbs 1996, Singer et al. 2002), ecosystem energy flows and nutrient cycling (Ruess and McNaughton 1987, Detling 1988, Pastor et al. 1993, Hobbs 1996, McNaughton et al. 1997, Frank 1998), and habitats and populations of other wildlife species (Barnes et al. 1991, Melcher 1992, Berger et al. 2001). As a result of long co-evolutionary grazing histories (McNaughton 1984, Coughenour 1985, Milchunas et al. 1988), plants have acquired adaptions to tolerate, resist, or avoid herbivory (Caldwell et. al 1981, Owen-Smith and Novellie 1982, Briske 1991). Plants and herbivores can attain dynamic equilibria in which herbivore numbers are regulated by density-dependent competition for food (Caughley 1976, Houston 1982, Sinclair et al. 1985), or herbivore populations may be limited by density-independent fluctuations in climate or other factors (Ellis and Swift 1988, Illius and O'Conner 2000). Alternatively, herbivore populations may be limited by predation (Messier and Crete 1985, Carbyn et al. 1993, Peterson et al. 1998) or human hunting (Kay 1994). Humans have had pervasive effects on large herbivores since their arrival in N. America. Widespread Pleistocene extinctions have been linked to human hunting (Martin 1966, Alroy 2000), however, the effects of rapid climatic changes likely played an important role, particularly since there were also many extinctions among non-game species at the same time.

RMNP (Figure 1) was established in north central Colorado in 1915 after a period of substantial resource extraction by early settlers, including trappers, hunters, miners, loggers, and ranchers. A once abundant large herbivore, elk (*Cervus elaphus*) had by that time been extirpated from the region during a period of intensive market hunting in the 1860's and 1870's (Guse 1966). Mule deer (*Odocoileus hemionus*) were also much reduced. Elk were reintroduced in 1913-1914, and the population grew in size (Figure 2) to approximately 900 animals in 1938-1939 (Packard 1947a). Concerns about their impacts on plants and range condition were expressed as early as 1929 (Ratcliff 1941, Packard 1947a). By 1939, it was decided that the elk winter range within the park boundaries was seriously overpopulated. After an attempt to reduce the herd by hunting outside the park had failed, a direct reduction program was carried out in 1944 which reduced the population to 500. Concerns about poor range condition arose again by 1949, and another direct reduction of 340 elk brought the population back down to approximately 500 (Stevens 1980). Between 1944 and 1953, 1,045 elk and 318 deer were removed (Gysel 1960). Reductions continued through 1968 and the population was maintained at 350-800 elk.

Since 1968, the elk herd has been managed only by sport hunting outside of the park boundary. This has proven largely ineffective, as the population increased markedly to 1,000 or more animals by 1975 and recent counts put the population that winters inside park boundaries at about 1,200 (Figure 2). Furthermore, elk have been increasingly wintering outside the park boundaries, in the town of Estes Park, where they also largely escape hunting. The Estes Valley elk herd is now

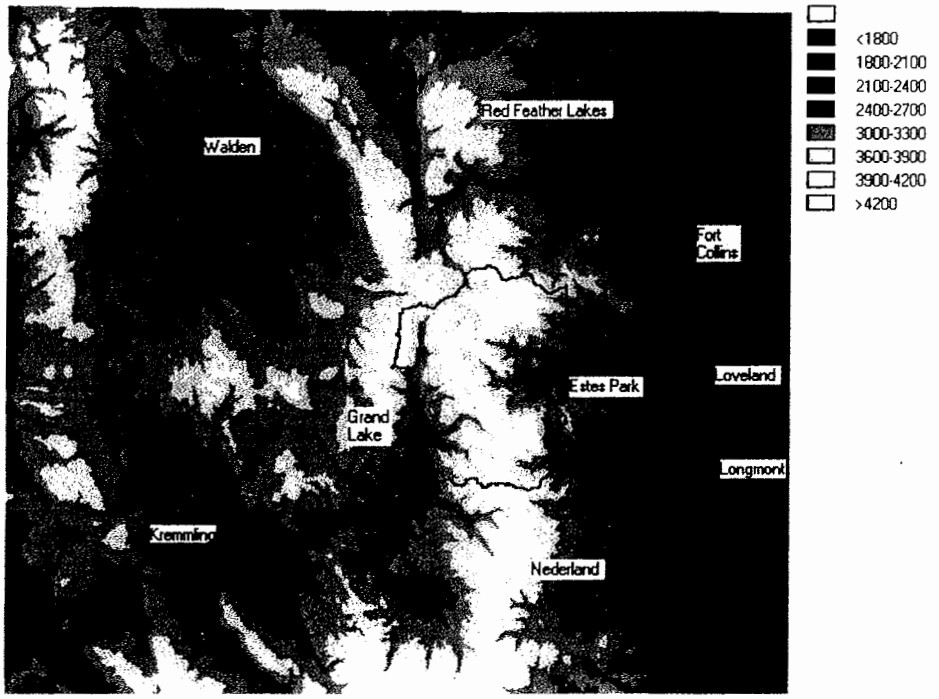


Figure 1. Location of Rocky Mountain National Park in north-central Colorado, in relation to surrounding population centers, and topography (elevation in meters).

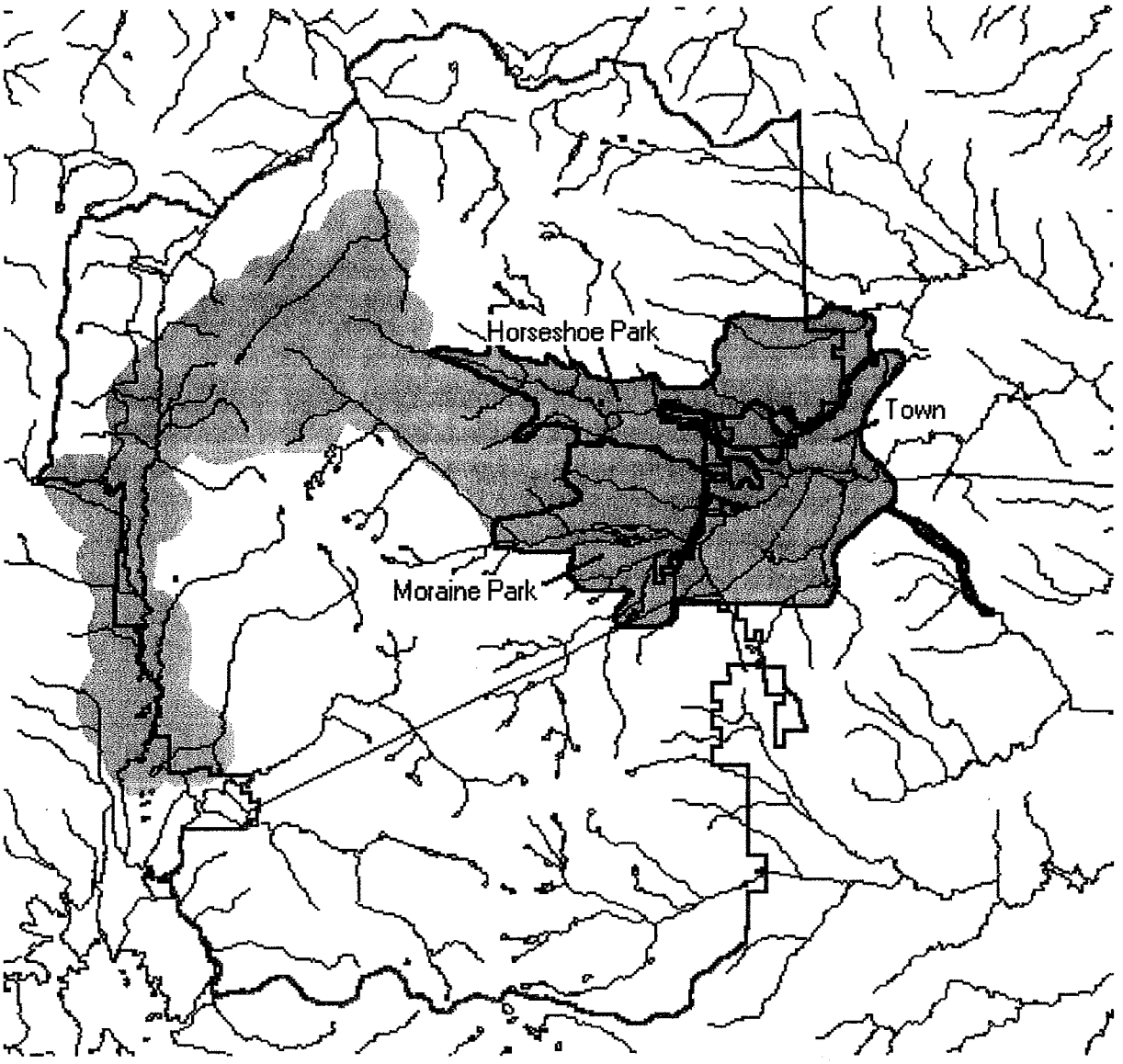


Figure 2. Elk ranges as delimited by drawing polygons around the majority radiolocations of Larkins (1997). Uncommon outlying locations were not included. The grey area is the combined summer and winter range. The winter ranges of three herd segments determined by Lubow et al. (2002) are shown in thick black lines. The town range corresponds to the area included in ground counts. Also shown are streams, and the Rocky Mountain National Park boundary.

consisting of three subherds with fidelities to their own winter ranges and to their own migration corridors to their combined summer range (Lubow et al. 2002, Figure 3). The town herd segment has been shown to be demographically distinct from the two herd segments which winter inside the park (Lubow et al. 2002), and has grown to nearly 2,400 animals (Figure 2).

Concerns about elk impacts on plants and other components of the ecosystem have heightened considerably during the last two decades (Olmsted 1977,1979, Stevens 1980, Hess 1993, Wagner et al. 1995, Berry et al. 1997, Baker et al. 1996, Keigley and Wagner 1998, Ripple and Larson 2000). Elk impacts on aspen and willow have been of particular concern. Although aspen were being damaged by elk as early as 1929 (Packard 1942, 1947a, Buttery 1955, Gysel 1960), more recent studies have shown than elk browsing is contributing to an aspen decline on the core (lowest elevation) elk winter range (Olmsted 1977,1979,1997, Stevens 1980, Baker et al. 1996, Suzuki et al. 1998). Heavy browsing of willow and declining willow abundance have also been observed since the 1930's (Ratcliff 1942, Gysel 1960, Stevens 1980, Peinetti 2000). These decreases have been linked to a marked decrease in beaver numbers since the 1940's (Packard 1947b, Hickman 1964, Stevens and Christianson 1980, Zeigenfuss et.al. 2002), since willow is a primary source of food and construction material for the beaver. The cause of the beaver decline has not been shown, but it has been suggested that it has in large part, been a result of increased competition from elk for willow (Packard 1947b, Hess 1993).

Decreases in willow, aspen, and beaver have likely also been influenced by humans, making it difficult to determine how much of the declines are solely attributable to elk. The first impacts of humans on vegetation were indirect. They were elicited through the responses of vegetation to the removals of elk and deer. During the period of elk absence (1875-1912) and low elk abundance (1913-1930), woody vegetation was largely released from herbivory. Browsers of woody vegetation (deer and elk) were replaced by cattle and horses, which primarily graze herbaceous vegetation. Herbaceous vegetation was heavily grazed by livestock on winter range that is now within the park boundary, as well as in the Estes Valley (Ratcliff 1941). It is quite possible that during this time, aspen and willow increased in abundance (e.g., Campbell et al. 1994). Wet meadows were drained and willow was cleared to provide hay fields and livestock pastures (Gysel 1960, Stevens 1980). Livestock were grazed on the park winter range until the 1930's. Water was diverted from streams and used for irrigation of the hay fields, and later, a golf course (Gysel 1960, Howe 1995). Numerous buildings were built on the winter range, including sizeable hotels, resorts, and homesteads. The last buildings, and the golf course, were only removed in the 1960s (Bucholtz 1983, Redente and McLendon 1992). The presence of humans could have altered elk behavioral patterns, particularly their use of space on the winter range. Later, the presence of park rangers involved in direct reductions of elk could have had similar effects, perhaps creating refugia for aspen recruitment.

As in Yellowstone National Park (Coughenour and Singer 1996), elk in RMNP have been managed in an experimental mode since 1968, with the hopes of learning how an ecosystem with abundant large herbivores could be sustained through the negative feedback limitations on herbivore populations arising from food limitation. In Yellowstone, the process has been referred to as natural regulation, based on the hypothesis that large herbivores are naturally regulated by food limitation.

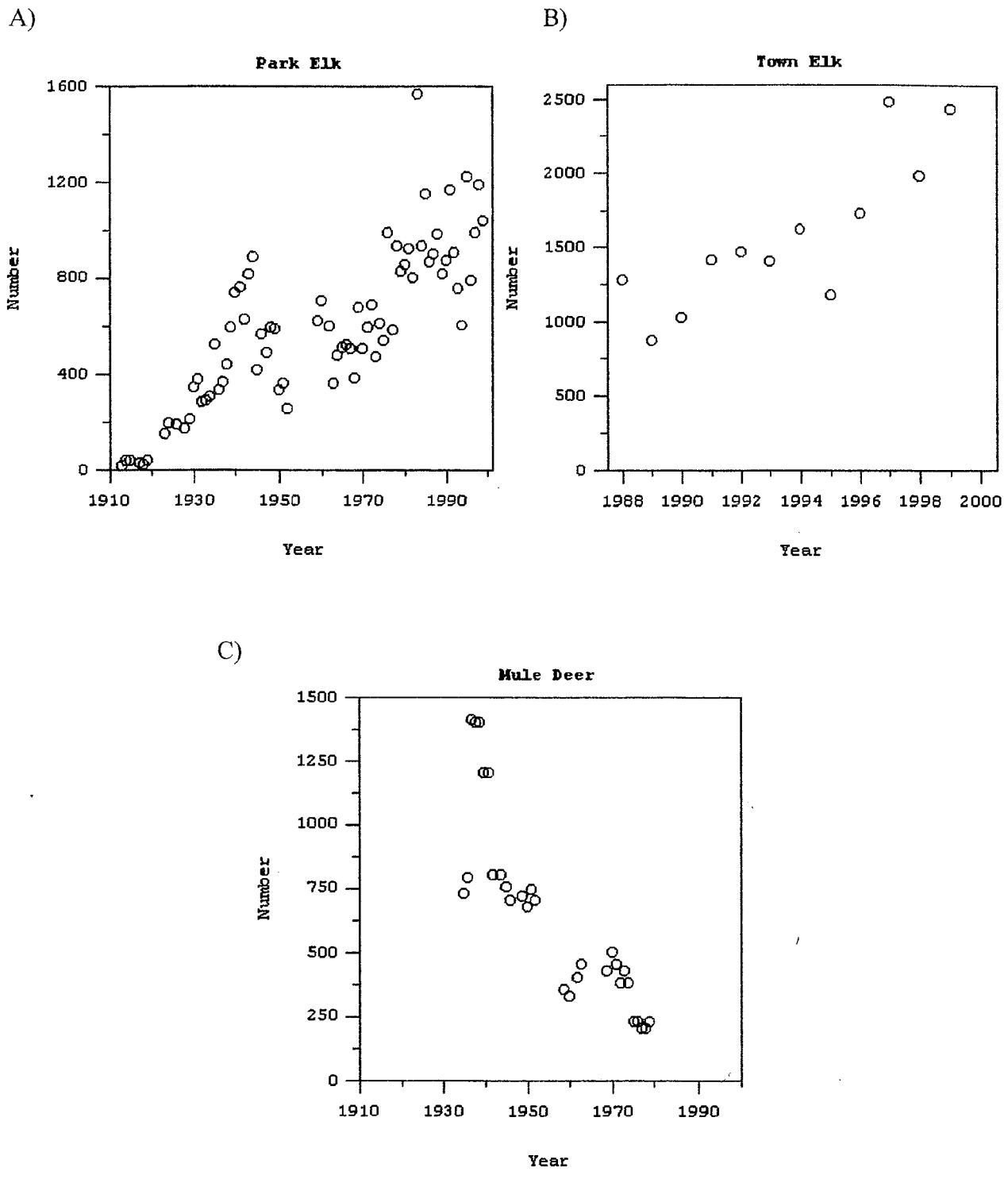


Figure 3. A) Size of the elk population wintering inside the park boundaries. 1915-1964 data are from Stevens (1980), "estimates" non-statistically corrected for sightablity. 1965-1998 are from Lubow et al. (2002) "estimates" statistically corrected for sightability. B) Size of the town population, as in Lubow et al. (2002) "estimates" statistically corrected for sightablity. C) Size of the deer herd, from Stevens (1980), "estimates" non-statistically corrected for sightablity.

National Parks in the U.S. have been directed to: conserve the scenery and the natural and historic objects and the wildlife therein" (NPS Organic Act 1916); "preserve vignettes of primitive America" (Leopold et al. 1963); provide the American people "with the opportunity to enjoy and benefit from natural environments evolving through natural processes minimally affected by human actions" (NPS 1988); and maintain all the components and processes of naturally evolving park ecosystems, and rely on natural processes to maintain native species and natural fluctuations in populations whenever possible (NPS 2001) (see also Kieter and Boyce 1991, Wagner et al. 1995). Human intervention is only warranted when it is necessary to prevent departures from natural conditions. National parks provide important ecological baselines for gauging human impacts in unprotected areas, as well as important information about natural ecosystem processes (Boyce 1998, Sinclair 1998). If herbivores are regulated by food limitation in natural ecosystems, then they should be allowed to do so in national parks. However, the premise of food limitation has been questioned by an increasing number of scientists and managers in recent years, who believe instead, that large herbivores populations are naturally controlled by predators and subsistence hunting by Native Americans rather than by forage limitation (Kay 1990,1994, Wagner et al. 1995, Hess 1993, White et al. 1998, Ripple and Larson 2000, White and Feller 2001). The effectiveness of predators in controlling elk populations is debatable, however. Only recently has there been an opportunity to observe the effects of wolf predation on Yellowstone elk, and their effects are still not easy to detect (USFWS 1999, 2000). In some ecosystems such as the Serengeti of Tanzania, herbivore populations are not limited by predators (Sinclair et al. 1985, Fryxell et al. 1988). Seasonal long-distance migrations of prey species are believed to hold sedentary predator populations to lower densities. Migratory elk in the Rockies could also benefit from this effect.

Past efforts to estimate elk carrying capacity have used a wide variety of assumptions and methods. The term "carrying capacity" is fraught with ambiguity, as it has been used to describe many different concepts (Caughley 1979, Peek 1980, McNab et al. 1983, Coughenour and Singer 1991, Coughenour 1996, McCullough 2000). In general, there are four different connotations, and associated methods of calculation. The first and most commonly applied is determined by resource limitation, particularly forage. Simply, it is the number of animals that can be nutritionally supported by the forage base. This approach has been used in Rocky Mountain N.P. as early as 1941, when a simple "forage-acre" method was used to calculate forage available to elk on the winter range (Ratcliff 1941). The calculation was dependent on the area of land that was assumed to be available to herbivores for foraging, as well as an estimate of forage production per unit land area. Thus, as the area of land increased due to land acquisitions by the National Park Service (NPS) and evacuation by humans and livestock, the calculated carrying capacity would have increased. The most sophisticated attempt to calculate food-limited carrying capacity was carried out by Hobbs (1979) and Hobbs et al. (1982), who also took into account the nutritional quality of the forage by removing forage items of low nutritional quality from the calculation.

A second method is based on population modeling. A population model is constructed for the herbivore population with a density-dependent term that slows population growth as the population increases, implicitly assuming that such would occur due to competition for increasingly limited forage, space, or some other limiting resource. The population model is then solved for the point of

zero population increase, or steady-state, at which the population is assumed to be at equilibrium with forage production (e.g., Noy-Meir 1975, Caughley and Lawton 1981). Alternatively, a population model driven by variable weather can be built to simulate a dynamic equilibrium (e.g., Caughley 1987, Coughenour and Singer 1996a). It is also possible to include predators in such a model, thereby relaxing the assumption that carrying capacity is determined by forage supply (e.g., Boyce 1990, 1993, Boyce and Gaillard 1992).

A third approach is to gauge an appropriate number of herbivores based on vegetation responses. The aim may be to prevent vegetation and soil degradation, or retrogressive succession of the vegetation community to a sub-climax species composition. This approach has been used for years by range scientists (Dyksterhuis 1949). Range condition and trend is assessed based on increases and decreases in palatable and unpalatable forage species. The goal of protecting vegetation is also implicit. Some food-limited carrying capacity calculations assume that only 50% of the available forage should be eaten (e.g., Hobbs et al. 1982). It is rarely recognized that Hobbs et al. (1982) made this important assumption in calculating the forage-limited carrying capacity of RMNP. Vegetation management may also be a goal when it is clear that herbivores are overabundant due to lack of predators, or where migratory dispersals have been impeded by humans (e.g., Berry et al.1997, Keigley and Wagner 1998).

A fourth approach is to determine the stocking rate which maximizes animal production. Animal production is highest when herbivore density is below food-limited carrying capacity. Ranchers would employ this approach as would big game managers trying to increase harvests or trophy sizes. This has been termed economic carrying capacity (Caughley 1979). Economic carrying capacity is not appropriate for use in national parks where the primary goal is to preserve natural processes, rather than maximize animal production (Coughenour and Singer 1991).

In a national park, carrying capacity might be defined as the number of animals that would be present in an undisturbed, naturally functioning ecosystem such as would have occurred prior to the arrival of Euro-American settlers. This definition would be consistent with the NPS Organic Act directive to conserve the natural and historic objects and the wildlife therein. It would also be consistent with the Leopold et al. (1963) recommendation that each park be maintained or recreated in the condition that prevailed when the area was first visited by white man (Leopold et al. 1963). This definition may or may not be in agreement with the philosophical and scientific needs for ecological baselines (Sinclair 1998, Boyce 1998). Human interventions that are required to preserve pre-settlement conditions could disrupt ecosystem processes and negatively affect our opportunities to see how ecosystems function "naturally" without humans. There is an important divergence of views about whether it is more appropriate or natural to preserve the vegetation conditions that prevailed at pre-settlement, or preserve processes that were present at pre-settlement but which might naturally give rise to different vegetation, or preserve processes that may or may not have functioned at pre-settlement, but which nevertheless give rise to a viable, albeit different ecosystem (Wagner et al. 1995, McNaughton 1996, Boyce 1998, Sinclair 1998, Keigley and Wagner 1998).

Some would argue that food-limited carrying capacity is not natural (Wagner et al. 1995). In

particular, it is hypothesized that ungulates are naturally regulated by predation as well as food, rather than food alone. Thus, self-regulation through food limitation is not the same as natural regulation (Wagner et al. 1995). To test the predation hypothesis, ungulate population dynamics would have to be observed with and without predators, in otherwise similar and natural conditions. Thus, predators would need to be reintroduced if they have been extirpated. This was possible in Yellowstone, but may not be possible in RMNP due to its much smaller size, and the fact that half of the former elk winter range is now occupied by the town of Estes Park. Making the problem even more difficult, is the possibility that herbivore migrations and dispersal movements may have been disrupted. In Yellowstone, it has been long argued that in winter, elk migrated out of the park and down the Paradise Valley to the plains more than 100 km north of the park boundary (Pengelly 1963, Kay 1990, Wagner et al. 1995, Keigley and Wagner 1998). This has been debated (Houston 1982, Schullery and Whittlesly 1992), and it would only shift the location of some form of population control, not the fact that food limitation or predator limitation would exist and that vegetation would respond accordingly (Coughenour and Singer 1991). There is also the question of why an apparently highly suitable winter range would be not be utilized by both elk and wolves.

Irrespective of which of these views is most appropriate, there is a need to understand pre-settlement baseline conditions, pre-settlement ecosystem processes, and the way the ecosystem functions without human intervention. Unfortunately, we usually have very little or no data from pre-settlement times. Ungulates could have been limited by forage, or they could have been limited by predators, or both. The only real-world experiment we can do to assess this, is to see if the ungulate populations can self-regulate by food limitation, and if so, whether the self-regulated populations would change the ecosystem to a condition or set of processes that was not present in pre-settlement time, or to an ecosystem that is different, but unsustainable. That was the essence of the natural regulation experiment in Yellowstone, which included a criterion of rejection of the hypothesis if elk caused retrogressive succession, high-lining of trees, or soil erosion (Houston 1971, Coughenour and Singer 1991). The northern Yellowstone herd population did in fact self-regulate by reaching it's food-limited carrying capacity (Houston 1982, Coughenour and Singer 1996a,b), as did the elk population which winters within RMNP (Hobbs et al. 1982, Lubow et al. 2002).

Understanding the causes of vegetation change is central to understanding ecosystem functioning and disentangling natural processes from the effects of human activities. The potential causes of vegetation change are many, and complex. Using vegetation changes to gauge appropriate herbivore numbers is complicated by the fact that changes could also have been affected by human activities and climate. If willow and aspen are decreasing, for example, we must determine whether or not this is due to Herbivory, humans, climate, or some combination of the three. Furthermore, some effects of herbivory are to be expected in a naturally functioning ecosystem, but herbivory may be modified by human activity and climate. A reasonable hypothesis might be that humans and/or climatic changes have amplified the effects of herbivory. We must also determine whether the vegetation that was present when a national park was designated was a product of earlier human activities. In RMNP, for example, elk were absent or present at low densities for 40 years due to intensive market hunting. Was the vegetation at RMNP designation an artificial by-product of that human impact? Were subsequent vegetation responses to elk reintroduction a manifestation of a shift

back to pre-settlement conditions as elk exert their expected effects on the ecosystem?

Water and nutrient fluxes through soils and plants are fundamental ecosystem processes, and they interact with vegetation responses to herbivory. Therefore, they must be considered. Grazing affects plant water relations by altering plant water use and vegetation cover, which in turn affect runoff and bare soil evaporation. These responses have subsequent effects on plant growth. Nitrogen is a primary limiting nutrient in most grazing and browsing ecosystems. Grazing may affect nitrogen cycling by removal of plant tissues and returning materials to the soil which have different nitrogen and carbon contents than dead plant tissues. Highly labile urea nitrogen is returned in urine (Detling 1988, Ruess and McNaughton 1988). Nitrogen is volatilized as ammonia when urea is converted to ammonium (Ruess and McNaughton 1988, Schimel et al. 1986). Herbivores respire carbon, so the overall nitrogen concentration (or equivalently, the N:C ratio) of the materials returned to the soil is higher than the plant material they are eating. This increases decomposition and nitrogen turnover rates in the soil. The overall effect of herbivory in many systems is to accelerate nitrogen cycling, which can then stimulate plant growth (Ruess and McNaughton 1987, Detling 1988). In contrast, herbivores can reduce the rate of nitrogen cycling by selecting forage that is high in nitrogen, which changes vegetation composition towards species which return low nitrogen plant material to the soil (McInnes et al. 1992, Pastor et al. 1993).

Ecosystem simulation models have been increasingly used to assess the responses of plant growth and ecosystem dynamics to herbivory (Coughenour 1984, Parsons et al. 1988, Seagle et al. 1992, Holland et al. 1992, Thornley 1998, Moen et al 1998). Some of these models represent plant ecophysiological processes and morphology in detail (Coughenour 1984, Thornley 1998), while others are more aggregated (Holland et al. 1992). Plant ecophysiological processes which determine plant responses to herbivory include photosynthesis, root-shoot allocation, water use, and nutrient uptake. It is possible to use models to explain from first principles how plants respond negatively, neutrally, and positively to herbivory under different conditions (Coughenour 1984, Thornley 1998, Mazancourt et al. 1998).

The spatial components of plant-herbivore interactions significantly affect ecosystem functioning (Coughenour 1991a, Hobbs 1999). In spatially extensive ecosystems with highly mobile herbivores and heterogeneous climate, vegetation, topography, and soils, a wide range of responses to herbivory are possible. The overall response of the ecosystem depends upon the behaviors of each of the spatial components across the landscape, and the manner in which the large herbivores forage at different spatial and temporal scales (Senft et al. 1987, Hobbs 1999). Few ecosystem models have included the spatial component, because it multiplies the complexity and computational requirements of the model. The SAVANNA model is a spatially explicit ecosystem model that has been developed over a number of years (Coughenour 1992, 1993) and applied to a wide range of ecosystems dominated by large herbivores (Buckley et al. 1995, Ludwig et al. 1999, Weisberg et al. 2002, Coughenour 2000, Boone et al. 2001). It was originally developed to examine a spatially extensive pastoral ecosystem in northwest Kenya (Coughenour 1992). SAVANNA includes submodels of plant growth, site water balance, soil decomposition and nitrogen cycling, herbivore foraging, energy balance, population dynamics, spatial distributions, and predators.

The purpose of this research is to assess the role of elk in the RMNP ecosystem. Ecosystem modeling is used to assess the role of elk in the ecosystem, and the way that ecosystem dynamics have been altered by interactions between elk, climate, and humans. Ecosystem modeling is a comprehensive approach to carrying capacity assessment. It simultaneously addresses different concepts of carrying capacity by explaining ecosystem dynamics in terms of underlying ecosystem processes. A process-based simulation model is used to represent plant and soil responses to herbivory, food limitation of the herbivore population, and predation. The model is used to project ecosystem dynamics under past, present, and future management scenarios. In contrast to other approaches which prescribe appropriate or proper use levels at the outset, the ecosystem modeling approach is neutral. The model only represents the consequences of different densities of herbivores and different modes of herbivore management. The compatibilities of the simulated responses with site-specific natural resource management objectives are evaluated separately.

SITE DESCRIPTION

Landscape

RMNP lies in the southern Rocky Mountains, straddling the continental divide in northern Colorado (Figure 4). Elevations in the park range from 2,339 m on the east side to 4,345 m on the summit of Longs Peak. The mountains are relatively young geologically, with the last stages of uplift occurring five to seven million years ago. The landscape has been heavily worked by glaciation in three different periods. The most recent of these was the Pinedale glaciation 10,000-25,000 years ago. The glaciers carved out cirques, and formed valleys which are sometimes separated by sharp ridgelines. East-west running lateral moraines, composed of glacial material deposited along the flanks of the Pinedale glaciers, separate different valleys on the elk winter range. The moraines rise as high as 250 m above the valley floors. The valley floors have been filled in with alluvial deposits, forming relatively flat mountain parks interspersed with rocky outcrops that resisted glacial erosion. The last 12,000 years have seen intermittent periods of remnant mountain glacial advance and retreat, in response to climatic variation.

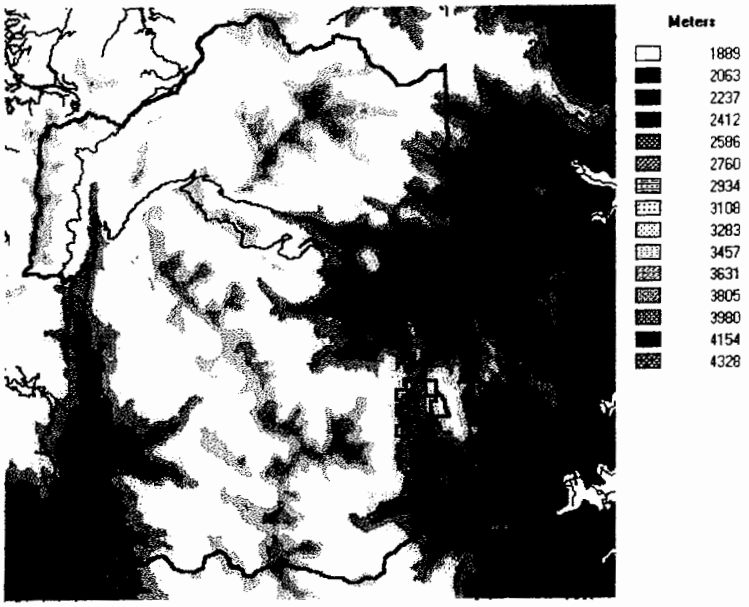
The elk winter range falls within the upper reaches of the Big Thompson watershed, which drains eastward onto the plains down a canyon between the cities of Estes Park and Loveland (Figure 5). Three lower order watersheds comprise the winter range. The Fall River watershed is northernmost, feeding into Horseshoe Park. To the south, the main fork of the Big Thompson River runs through Moraine Park. Between these is the small Beaver Brook drainage, which feeds into Beaver Meadows. South of Moraine Park is the Glacier Creek watershed (not shown), which subsumes the well-studied Loch-Vale watershed (Baron 1992). Between Glacier Creek and Moraine Park lies Mill Creek, which feeds into the smaller Hallowell Park. For the purposes of this report, the watersheds will be referred to by the names of the parks they feed into, i.e., Moraine, Horseshoe, and Beaver Meadows.

Climate

Climate is continental, characterized by wide variations and rapid changes. The climate is highly influenced by the mountainous topography. Temperatures fall with increasing elevation at average lapse rates of approximately 5.5 and 2.7° C per 1,000 m elevation in day and night, respectively. This pattern is modified by cold air drainage in valleys. Conversely, precipitation increases with elevation, so the combination of higher precipitation and cooler temperatures at higher elevations results in a steep elevational gradient in snowfall and snowpack.

Prevailing winds are from the west. The most important source of moisture during winter originates in the Pacific. As the Pacific air masses move east, successive mountains ranges experience orographic precipitation. In spring and fall, moist air from the Gulf of Mexico is pushed up against the eastern slope resulting in up-slope storms. This results in increased moisture on the east slope, while the west slope often remains dry. Moisture in late spring and summer is mostly a result of convective activity involving heating on the eastern plains, with upslope convective flow and cloud

A)



B)

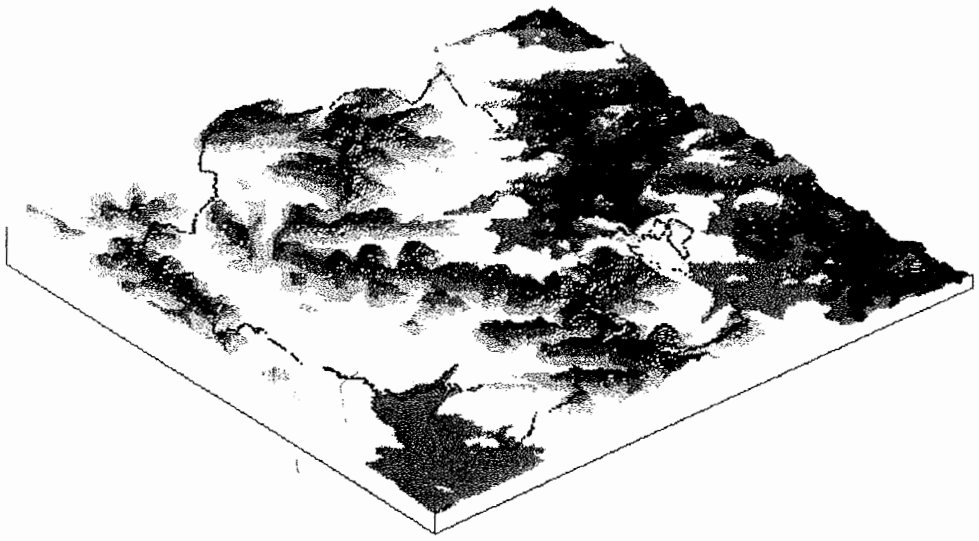


Figure 4. Topography of the Rocky Mountain National Park study area. A) Planar view with roads. B) Orthographic view from the southwest. The elk winter range lies in the valley on the eastern edge of the park.

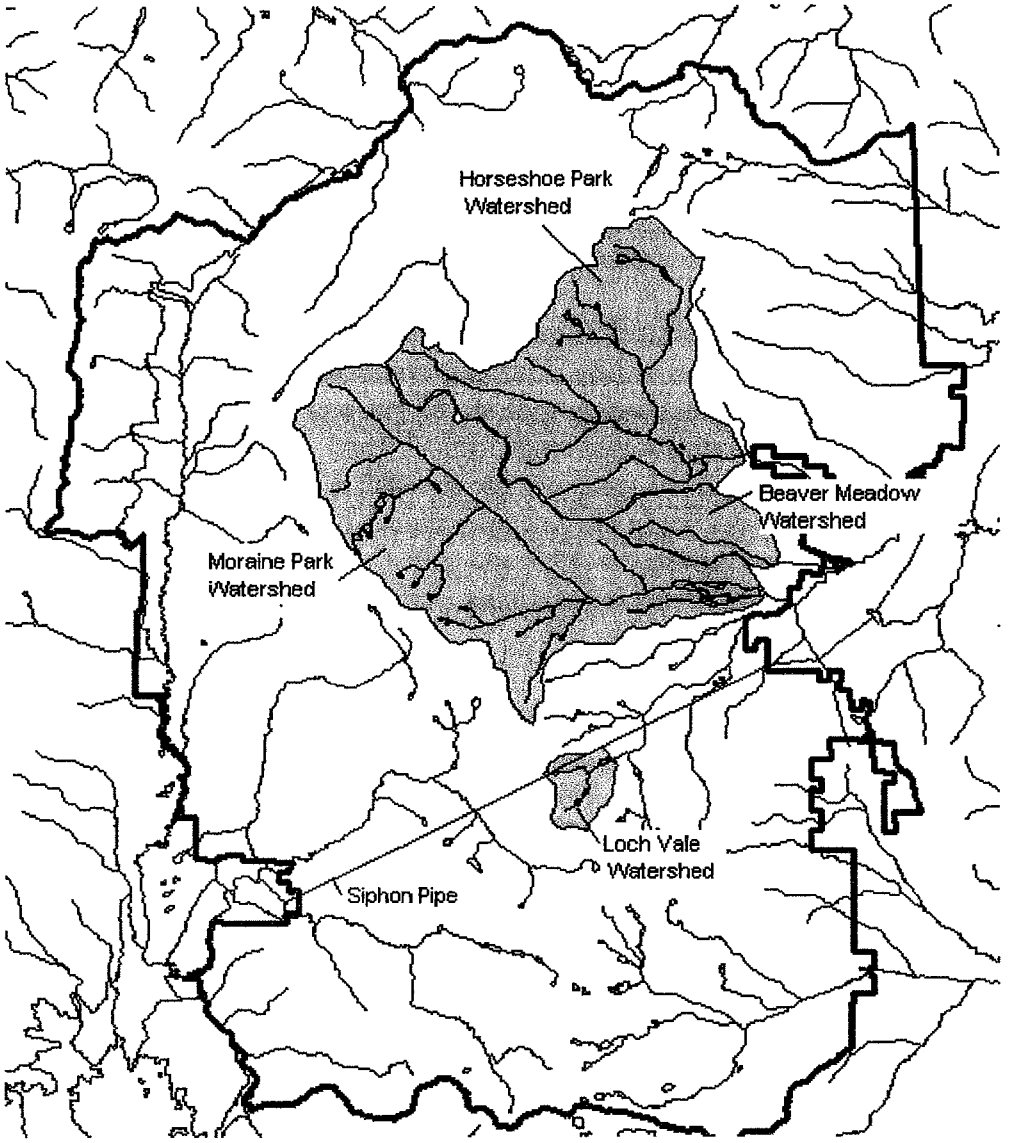


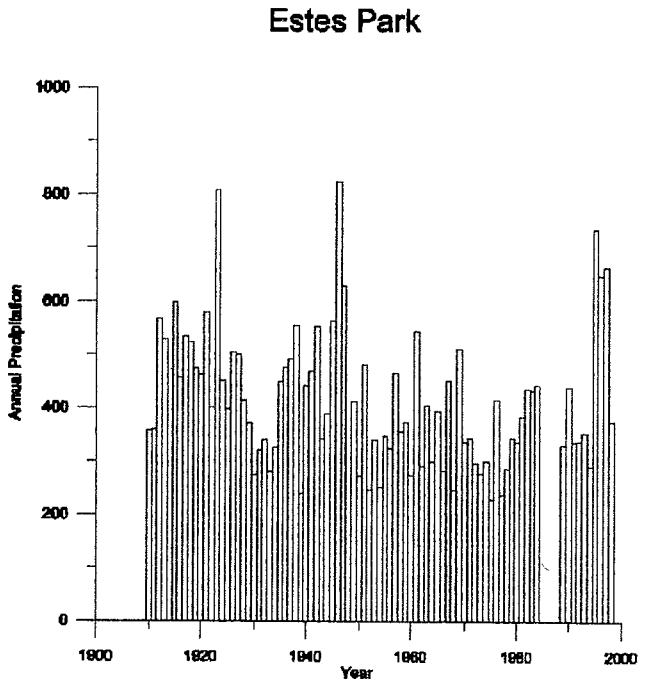
Figure 5. Hydrography of Rocky Mountain National Park, showing the three principle watersheds feeding into the elk winter range. Also shown are the well-studied Loch Vale Watershed (Baron et al. 1992), and the location of the Big Thompson siphon, which brings water from the west to the east slope.

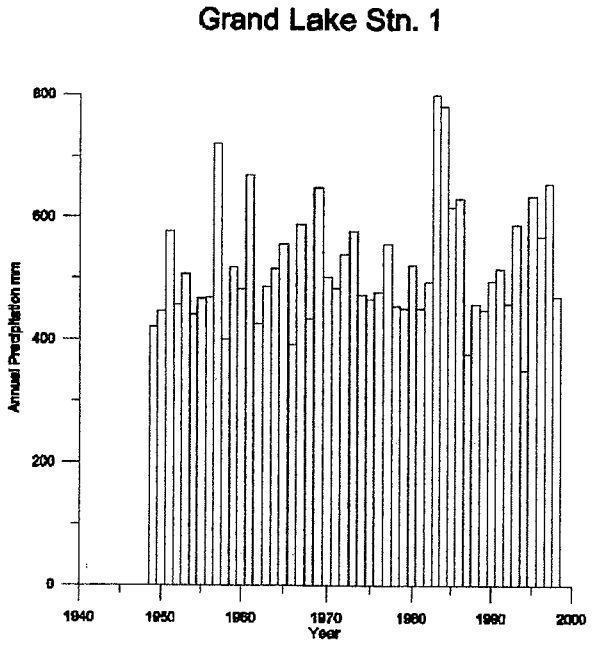
formation at higher elevations. The western slope is not influenced by this activity. As a result of these differences in precipitation, the east and west slopes have different seasonal precipitation patterns. Precipitation on the west slope is nearly uniform throughout the year while the east slope precipitation varies seasonally. At Estes park, maximum precipitation occurs in the spring and summer months. Higher up, at Loch Vale, maximum precipitation occurs in late fall and early spring (Baron and Mast 1992). At Grand Lake, precipitation is more uniform, but wettest months are in the summer.

At Estes Park (elevation 2,293 m), daily minimum and maximum temperatures vary from -8.7 and 3.6° C in January to 7.8 and 25.7° C in July. Average monthly precipitation ranges from 9 mm in January to 57 mm in July. Annual precipitation is 361 mm, and annual snowfall is 368 cm. Mean snow depths in March and April are 22 and 10 cm. At Grand Lake NW (elevation 2657 m), max and min temperatures range from -16.6 and -0.6° C in January to 24.0 and 3.1° C in July. Precipitation varies from 33 mm in October to 53 mm in July. Annual precipitation is 513 mm, annual snowfall is 368 cm and mean snow depths in March and April are 63 cm and 30 cm. At Grand Lake SSW (elevation 2,526 m), max and min temperatures range from -2.9 and -17.4° C in January to 23.5 and 5.4° C in July. Annual precipitation is 351 mm, average snowfall is 216 cm and average March and April snow depths are 51 and 20 cm. At Loch Vale (elevation 3,150 m) max and min temperatures range from -8.8 and -3.1° C in January to 19.7 and 1.0° C in July. Precipitation varies from approximately 50 mm in August to 140 mm in November. Annual precipitation is 1,134 mm of which 793 mm is snow (Baron and Denning 1992).

Annual variability in precipitation is relatively high at Estes Park (Figure 6), with a standard deviation that is 22% of the mean. At Grand Lake NW and SSW the ratios of standard deviations to means are only slightly less, at 0.19 and 0.20 respectively. The difference between wettest and driest years at Estes Park is 85% of the mean, while at Grand Lake it is 87 -88% of the mean. The years 1995-97 were wetter than normal in Estes Park (Figure 6).

Climate trends have been examined by Barnett and Singer (1999). They found significant warming rates of 0.011° C yr^{-1} at Estes Park 1909-97, and 0.023° C yr^{-1} at Grand Lake 1909-97. For Estes Park, they found significant trends of decreasing precipitation in fall/winter of -0.074 mm yr^{-1} and an annual trend of -1.15 mm yr^{-1}, but with a recent wetter trend since 1995. At Grand Lake, they found significant trends for increasing precipitation in spring and fall/winter of 0.46 mm yr^{-1} and 0.54 mm yr^{-1} respectively. In comparison, in Estes Park Stohlgren et al. (1998) found no significant changes in July temperature over the last 45 years, but found a -0.68 ° C cooling of July temperatures since 1980. At Grand Lake they found no long-term trends in temperature, but they found -0.10 and -0.08° C yr^{-1} cooling rates since 1980 at the two stations. They used a mesoscale atmospheric model to show that recent cooling could be caused by land use change along the front range, particularly the increase in irrigated agriculture and lawns, which results in a greater partitioning to latent as opposed to sensible heat flux regionally. Another analysis of a 100-year data set (Kittel et al. 1997) for the Rocky Mountain region showed no temperature or precipitation trends in western Colorado, while in NE Utah, a warming trend of 0.5° C yr^{-1} was detected (Reiners et al. 2000).





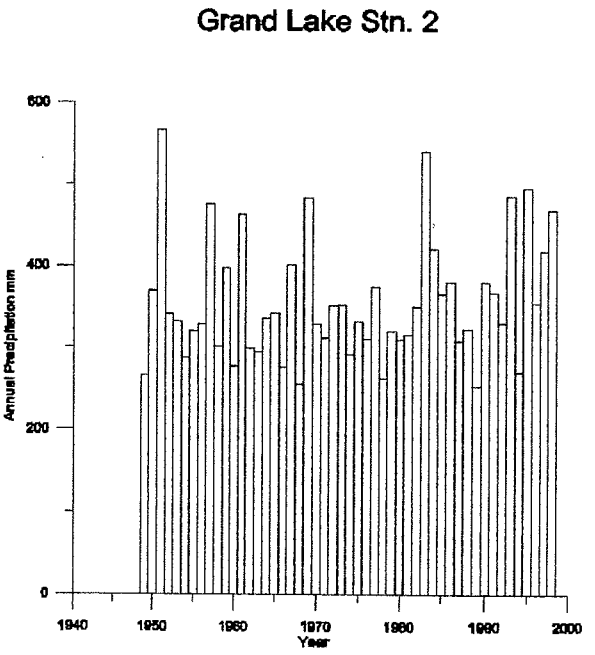


Figure 6. Annual precipitation recorded at Estes Park 1910-1998, and at Grand Lake 1949-1998. The two stations at Grand Lake are situated at different elevations.

Soils

Soils have been described as being generally infertile and sandy, with poor development from decomposed granitic substrate (Stevens 1980). However, swales and bottom lands have highly-developed soils, and mountain parks contain associations of brown regosol and lithosols. Forested areas contain gray wooded, podzolic, and rock land soils, and alpine tundra has alpine turf, bog, and meadow soils (Stevens 1980).

On the elk winter range, Leader (1995) found sandy loam soils at most sites, both in meadows and forests. Carbon contents were 3.7-3.9 kg C m^{-2} and nitrogen contents were 0.22 and 0.32 kg m^{-2} in forests and meadows respectively. Stohlgren et al. (1999) also found sandy loams at long-term exclosure sites, with 2.2-3.42% C and 0.14-0.22% N. Binkley et al. (2002) found no difference in soil C or N inside vs. outside of long-term (35 years) grazing exclosures, however bulk density was consistently greater outside the exclosure. Ca, Mg, K, and P were lower outside of the sagebrush grassland exclosure but not at meadow or aspen exclosures. Soil C contents were 4.8, 10.1 and 8.9 kg m^{-2} in the 0-30 cm layer at sagebrush, aspen, and meadow sites, respectively. N contents were 0.4, 0.78 and 0.74 kg m^{-2}, respectively. Menezes (1999) sampled soils of open riparian willow communities, and found 4.6% C and 3.15% N in a clay loam soil. Nitrogen limitation of plant growth was demonstrated by Binkley et al. (2002), who found a doubling of grass and shrub production after adding 10 g m^{-2} urea N on upland sagebrush, aspen and wet meadow sites.

Vegetation

Stevens (1980) provides a synthetic vegetation description organized following Daubenmire (1943) and Marr (1961). This description can be briefly summarized as follows.

The upper montane zone climax region occurs from 2,300-2,740 m elevation, comprising most of the elk winter range. Ponderosa pine (*Pinus ponderosa*) is the dominant tree species on xeric upland sites. The tree cover is typically open woodland or parkland, with an understory of bitterbrush (*Purshia tridenta*) and mountain muhly grass (*Muhlenbergia montana*). More open sites with deeper soils support big sagebrush (*Artemesia tridentata*), grassland, and sedge (*Carex rossii*). Disturbance or grazing cause a shift to grasslands dominated by mountain muhly or needle and thread (*Stipa comata*) if lightly grazed, and with increasing grazing pressure blue grama (*Bouteloua grama*), wheatgrass (*Agropyron spp.*), cheatgrass (*Bromus tectorum*), and June grass (*Koeleria macrantha*) become prevalent. On northern facing slopes and at slightly higher elevations, closed canopy forests dominated by Douglas fir (*Pseudotsuga menzesii*) and ponderosa pine occur, with a sparse understory of common juniper (*Juniperus communis*), ninebark (*Physocarpus monogynus*), and forbs such as heart-leaved arnica (*Arnica cordifolia*) and the grass spike fescue (*Leucopoa kingii*). Aspen (*Populus tremuloides*) occurs on upland seeps and swales but also occurs at lower elevations where there are good soils, and swales or high water tables. Understories are variable, but have a relatively high biomass of forbs such as alpine daisy (*Erigeron spp.*) and columbine (*Aquilegia spp.*), and shrubs such as wild rose (*Rosa spp.*) and chokecherry (*Prunus virginiana*). Willow communities occur on soils with higher water tables, with *Salix monticola, S. planifolia, S. bebbiana, and S. subcoerulea.*

In areas with incomplete willow cover, the herbaceous layer is dominated by Canadian reedgrass *(Calamagrostis canadensis)* and water sedge (*Carex aquatilis*).

The subalpine forest climax region occurs from 2,470-3,500 m elevation. The climax tree cover is composed of Engelman spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*). However, lodgepole pine (*Pinus contorta*) is a widespread seral stage for over one to three centuries after fire. The understory is sparse. Shrubs include kinnikinnik (*Arctostaphylus uva-ursi*) and huckleberry (*Vaccinium myrtillus and V. scoparium*), and common forbs include heart-leaved arnica (*Arnica cordifolia*) and goldenweed (*Haplopapus parryi*). Herbaceous parks are common, dominated by hairgrass (*Deschampsia ceaspitosa*), sedges, and numerous forb species. Alpine willows (*Salix planifolia and S. wolfii*) are found where there are higher water tables.

The alpine tundra climax region (>3500 m) is a mosaic of communities determined by microclimate and snow redistribution. Fellfield vegetation occurs on the windiest sites on coarse soils, and where snow cover is essentially absent. Vegetation is composed of low-growing life forms and cushion plants with communities dominated by moss campion (*Silene acaulis*), alpine clover (*Trifolium dasyphyllum*), and mountain dryad (*Dryas octopetala*). Snowbed vegetation occurs where snow accumulates for 60-90% of the year. Common plant species include tufted hairgrass (*Deschampsia ceaspitosa*) and rush (*Juncus drummondii*). Sites with high moisture levels are dominated by Rocky Mountain sedge (*Carex scopularum*), and on some sites, alpine willow species can be found.

ECOLOGICAL HISTORY

Evidence of Elk Prior to Euro-American Settlement

Prehistoric game drive systems discovered at high elevations within the park are suggested to have been predominantly used to hunt elk, mule deer, and bighorn sheep (Benedict 1992, 1999). Radiocarbon dates place these artifacts at 2,610-4,590 years before present (BP) at one site and 220-4,310 years BP at a second site. It is likely that elk were hunted during late summer and fall, especially during their migrations from their summer to their winter ranges. While bison were likely present (Fryxell 1928), Benedict (1992) felt that the configurations of the game drives, their topographic locations, and the absence of reworking tool flakes that would be expected to be present if animals as large as bison were butchered, indicate that the game drives would have been unlikely to have been used to hunt bison. These remarkable findings point towards elk hunting, and thus, the presence of elk in the area during late summer and fall. They do not address the question of whether elk wintered in the Estes Valley, however.

There is a considerable amount of historical evidence of elk presence prior to settlement. Loring (1893, cited in Guse 1966) observed - "That at one time elk were abundant is evident from the large number of horns that may be found in the timber." Two elderly Arapahoe men (ages 63 and 73) were brought to Estes Park in 1913 and were interviewed and accompanied on a tour by Superintendent Oliver W. Toll. The main purpose of the visit was to inquire whether bison formerly inhabited the park (Fryxell 1928). The Arapahoe men had many vivid recollections of hunting bison in the Estes Park Valley and RMNP area in their youth, which would have been between 1855-1870. Toll reported that the party found a large hunting camp with elk and bison bones at Tuxedo Park (Fryxell 1928). Tuxedo Park is only hundreds of meters east of Moraine Park on the current elk winter range. Fryxell (1928) compiled many sources of physical evidence of bison presence in the area. Many bison skulls were found throughout the park at an early date.

Rufus Sage visited North Park, an area just northwest of the current RMNP in 1842. He noted that "the entire country was crowded with game, in countless numbers, both of buffalo, elk, and deer" (Sage 1846, Benedict 1992). The first settlers of the Estes Valley were Joel and Milton Estes, who arrived in 1859. They found abundant elk and deer (Estes 1939).

> "The park was a paradise for the hunter... There was no end to the game, for great bands of elk, big flocks of mountain sheep and deer were everywhere..., so plentiful that we could not suffer for anything to eat or wear... Winter drove all the game down to the foothills except the elk, they would remain in the park until summer, then they went up over the range of mountains."

Heavy hunting occurred through the 1860s and early 1870s to provide meat to supply mining camps. Wagon-loads of elk and deer were delivered to markets in Denver. Milton Estes (1939) said:

> "One fall and winter the writer killed one hundred head of elk, besides other game, such as

mountain sheep, deer, and antelope. By this time (ca. 1862), we had made a trail to Denver where we sold many dressed skins and many hind-quarters of deer, elk, and sheep."

Elk must have been present and common, if not abundant, for this hunting to have occurred.

In 1875, elk came down from the mountains by the thousands and were met by hunters (Sprague 1925). In the winter of 1875-76 in Moraine Park, hunters continued to kill elk and deer by the thousands and carted them to markets in the valley towns (Sprague 1922). In 1876, few elk came down, and by 1877, very few were seen, and the last one was killed in 1878 (Sprague 1925).

Elk Carrying Capacity Estimates

After being reintroduced in 1913-1914, Superintendent Toll stated in 1925 that the present number of elk was as large as could be supported without supplemental feeding during winter (Guse 1966). The elk were raiding haystacks and crops in times of heavy snowfall. In 1925, there were at most 200 elk (Stevens 1980). By 1928 even more numerous reports were being made of elk damage (Guse 1966). Based on these low estimates of forage-based carrying capacity, it is clear that elk at that time did not have access to the land or the forage that is available to them now. In 1931, Dixon (1931) recommended that additional lands be purchased by the park to provide additional winter range, saying that "the present winter range is entirely inadequate for the elk and deer now on hand." There were 200-300 elk and 800 deer at that time. Later, Dixon (1939) stated that "now elk have reached and passed the carrying capacity of the winter range in the park and are destroying it through overbrowsing." In 1938-1939, elk reached an estimated peak of 1,100 (Stevens 1980).

Rutter (1937) estimated a carrying capacity of 500 elk. Ratcliff (1941) used the "forage-acre" method to estimate that 530 elk could be supported by the available forage. However, Gray (1943, cited in Guse 1966) estimated that 1,400 elk could be supported. He attributed damage to browse plants (trees and shrubs) to deer rather than elk. Grater (1945) estimated an elk carrying capacity of 673, based on an assumed 5,060 acres of winter range. Riordan et al. (1948, cited in Stevens 1980) calculated a carrying capacity of 620 elk, and attributed the range condition decline to overabundant deer. In 1954, after a period of elk reductions, George Cole judged that the range recovery was enough to cease further controls. Elk had been held at 500 for the previous several years. The formal management plan that was adopted in 1964 after the Cooperative Elk Study in 1962 called for 400 elk and 450 deer (Stevens 1980). There was no specific citation, or any basis for this estimate in Stevens (1980).

Hobbs (1979) conducted PhD. research in which he used a comprehensive ruminant nutrition model (Swift 1983) to estimate how many elk-days could be supported per hectare of land in eight different vegetation types for which he gathered data on forage biomass and nutritional quality. However, he did not attempt to multiply these numbers by the areas of each vegetation type on the winter range to estimate a winter range carrying capacity. Using a completely different elk nutritional model than he used in his PhD. research, but the same forage biomass and quality data to recalculate elk-days ha^{-1}, Hobbs et al. (1982) calculated how many elk-days could be supported for these

vegetation types. They then multiplied the new figures by land areas (ha) to derive estimates of total food-limited carrying capacity. An important assumption in both exercises was that elk *should* consume no more than 50% of the forage. It was not established that elk would actually follow this rule on their own accord. Carrying capacities of 1,481 elk in 1977 and 991 elk in 1978 were calculated, based on different forage productivities in the two different years.

Lubow et al. (2001) solved a density-dependent population model to estimate a carrying capacity (K) of 1,069+55 in the park subherd, and 2,869±415 in the town herd. Significant negative relationships were observed between calf recruitment rates and density in both subpopulations. When observed hunting offtakes were applied to the town population, the estimate of their equilibrial density was reduced to 3,530.

Singer et al. (2002) estimated carrying capacity for the town herd based on biomass sampling in different vegetation types including domestic lawns and golf courses and a GIS-based vegetation map (described below under Vegetation Map). With 50% utilization of forage, food-limited carrying capacity for the town herd segment was calculated at, 3,082 for 200 days of use in an average precipitation year. Estimates based on an hypothesized natural vegetation map (also described below) were only slightly higher (3,251±109) than with the current vegetation/land use map, suggesting that although high productivity lawns and golf courses would add forage, this would be more than offset by losses of forage to development, the creation of a water storage reservoir (Lake Estes), and the channelization of the Big Thompson River where there once was a lush alluvial floodplain covered by mesic meadows and willow (based on a historical photograph of the Estes Valley).

Elk Management

Early wildlife policy for the U.S. national parks was developed following the 1930-1932 field surveys in RMNP, when it was clearly stated that native ungulates on a deteriorated range should not be allowed to exceed the carrying capacity, and should preferably be kept below it to allow range recovery (Wright et al. 1933, Guse 1966). Given the date and size of the elk population, it is likely that this policy was aimed at repairing damage done by prior livestock grazing. Subsequently, as the elk population climbed, and repeated and consistent observations of range degradation rather than recovery continued from 1925-1941, the decision was made to control the elk population. Cahalane (1943) commented that "most of the elk and deer remain within the park and are not subject to hunting," thus justifying the need for direct reductions within the park. The first big direct elk reduction followed in 1944-1945 when 301 elk were removed. Subsequently, there was little management until after World War II, when 350 elk were removed in 1949-1950. By 1950, a program of annual herd reductions was in place and during 1950-1959, 507 elk were removed. Lethal reductions within the park ended in 1960. Colorado Game and Fish and Parks (CGFP) called a meeting with park officials in early 1961 to discuss the possibility of hunting in the park, which was denied, but a decision was reached to undertake a cooperative elk study program (Guse 1966). According to Gill (1968), the direct reduction programs were discontinued in response to the large public outcry against the direct elk reductions (shooting) in Yellowstone National Park in winter of 1961-62. This backlash contributed to the inception of natural regulation policy in Yellowstone (Kay

1990, Coughenour and Singer 1996). The reaction to events in Yellowstone could have markedly catalyzed action on the prior agreement for cooperative management. In December 1962, the CGFP, the NPS, and the USFS signed a Memorandum of Understanding to begin cooperative investigations to determine if ways could be found to control elk by methods other than direct reductions (Guse et al. 1965, Guse 1966). A winter hunting season east of the park was initiated in January 1963, with the hopes that hunting outside the park boundary would be sufficient to keep the elk population in check. Subsequent studies documented elk movement in and out of the park (Gill 1966, 1967), so expectations of success remained high.

Data provided by the Colorado Division of Wildlife show that hunting offtake from Game Management Unit 20 has varied between 250-500 elk per year since 1983. This game management unit is large, and includes many additional elk besides the elk which winter in the Estes Valley. Lubow et al. (unpubl., 2002) found that their best population model fits to data were obtained by assuming 35% of the total harvest in the unit was taken from the town segment of the Estes Valley herd. Harvests from the unit seem to have declined since 1986, possibly as a result of increased number of elk taking refuge in town, or reductions in hunting opportunities due to increased human development. Elk population data from both the park and town herd segments (Figure 2), indicate that these harvests have had little impact on the combined Estes Valley elk population.

Upland Herbaceous and Shrub Communities

The first human impacts on vegetation pre-dated the creation of the national park. Livestock grazing was widespread, and apparently intense enough to cause significant changes in herbaceous vegetation cover. Abner Sprague settled in Moraine Park in 1875, and had 200 head of cattle by 1876. By 1900 it was evident that chronic overgrazing had mowed valley vegetation to the ground and left wet areas trampled and barren (Mills 1924, cited by Hess 1993). McLaughlin (1931) stated that the range was overgrazed to the extent that in many places the original ground cover had been destroyed and mineral soil was exposed to erosion (Steven 1980). Part of the poor range condition was attributed to past severe livestock grazing during summer, which left little forage for elk during winter (Guse 1966). In 1931, Moraine Park was grazed year-long by domestic livestock and was badly overgrazed, Deer Mountain was overgrazed by livestock, and Beaver Meadows was a hay meadow, so was not overgrazed (McLaughlin 1931, cited by Stevens 1980). Haying took place between the 1880s and the 1930s in Moraine Park, as well as Beaver Meadows.

Range condition continued to deteriorate (McLaughlin 1932, 1933, Ratcliff 1934). The primary blame shifted to deer, however. Bitterbrush, the primary winter forage for deer was so heavily overbrowsed that much of it was dead and remaining plants were reduced to about half of their normal forage production (Thompson 1933, cited by Buttery 1955). Ratcliff (1941) observed that 75-90% of upland shrub growth was eaten by deer, causing significant plant mortality. Moraine Park still showed the effects of heavy livestock grazing prior to 1932. Grasses elsewhere seemed to be holding up, but Ratcliff expressed concern about the future effects of increasing elk utilization.

Buttery (1955) conducted a study of seven 20x20 foot exclosures that were established in the

1930s. In the sagebrush area he found that: a) bitterbrush was largely replaced by rabbitbrush and sagebrush outside the exclosures; b) mountain muhley (grass) was the same inside and out; c) *Danthonia* (grass) was lacking outside and had been replaced by blue grama (grass); and d) grass vigor was similar in and out. In the mesic meadow area he found vegetation was little damaged, except for willow: a) grass cover was similar inside and out; b) willow was severely damaged in the past, but seemed fairly vigorous and showed signs of recovery. In the bitterbrush area there were: a) signs of past damage including a lower density and vigor of browse outside; b) more mountain muhly inside; and c) more *Stipa* (grass) outside. In the willow area: a) grass was higher inside; b) there was relatively more sedge inside; and c) there was lots of fringed sage outside but absent inside. Despite these differences, he concluded that the elk reduction program had resulted in an upward trend in condition, and the range was in fair condition.

Gysel (1960) reported that the former distribution of sagebrush was probably much greater, as there were many stems of dead plants. He attributed this to deer, since elk eat little sagebrush. Bitterbrush was actually less abundant inside than outside exclosures, due to an outbreak of field mice in 1957-1958 which preferentially girdled bitterbrush stems inside the exclosures.

Stevens (1980) found that sagebrush and bitterbrush communities were stable between 1968 and 1978. Zeigenfuss et al. (1999) analyzed data collected by Stevens on the same transects for the period 1968-1992 and found that after 24 years bitterbrush cover increased by 36%, and height increased by 14%. In sagebrush grassland, Stevens found sagebrush cover declined from 26% in 1968 to 19% in 1978, but the herbaceous community was stable. After 24 years, Zeigenfuss et al. (1999) found a height increase on these transects of 56%, and an increase in grass cover of 32%. In grassland, Stevens found bare ground cover increased from 15% in 1968 to 20% in 1979. Zeigenfuss et al. (1999) found a consistent continuation of this trend after 20 years. Zeigenfuss et al. (1999) observed small, but significant increases in forb and moss/lichen cover over the whole time span.

Singer et al. (2001a) sampled bitterbrush and associated herbaceous vegetation inside and outside exclosures over a three-year period, with and without a controlled burning treatment. They found only an 11% utilization of bitterbrush growth, and although utilization of the herbaceous layer was 50%, there was no effect of grazing on production. Fire had the expected negative impacts on shrub canopy cover, reducing it by approximately 50%, but had no effect on herbaceous productivity.

Stohlgren et al. (1999) sampled herbaceous communities inside and outside long-term (35-year) grazing exclosures. They found that species diversity was slightly greater outside the exclosures, and that grass cover and forb foliar covers were 66% and 63% lower outside exclosures than inside. However, no precautions were taken to correct for grazing offtake, so the measures are not accurate indices of total plant growth. Schoenecker et al. (2002) sampled root biomass inside and outside of long-term (35-year) exclosures and found no differences due to grazing in willow/wet meadow, aspen, or upland bitterbrush/sagebrush. However, the level of sampling was very limited relative to the size and heterogeneity of the winter range. They sampled two exclosures and took 15 root samples inside and 15 outside both of the exclosures combined.

Aspen

The first reports of aspen damage occurred when it was observed that: "Last winter, for the first time, the elk began tearing bark off aspen trees," (McLaughlin 1931, cited by Guse 1966). Buttery (1955) cited a memo from Thompson (1933) which stated that aspen throughout the winter range was heavily utilized by deer and elk and that aspen production was eaten each winter until much of it died, and the rest was malformed. Ratcliff (1941) observed that there was no aspen reproduction, and smaller aspen groves were dead. Packard (1942) stated that "the trunk of every aspen tree in this meadow (Beaver Meadow) is heavily scarred as high as the elk can reach, and no branches survive below that height. There is almost no reproduction. The trees bordering the meadows are dead or dying by the hundreds." Gysel (1960) found that even after the big elk reduction programs in 1944-1945 and 1949-1950, aspen suckers in many parts of the winter range had a difficult time getting above two feet.

Stevens (1980) stated that it was clear that aspen covered more area in 1930 than it did in 1979, based on examination of historic photos and decadent stands. He established transects in 1968 and reread them in 1978 finding three to four of the stands showed a reduction in mature trees and decreases in young trees and sprouts. Zeigenfuss et al. (1999) analyzed the trend on these transects for 1968-1988, and found no significant changes in basal area, density, or heights, but variances were large.

Olmsted (1979) found that all of the aspen stands he examined regenerated during 1860-1930. There were no trees older than 1860. The biggest regeneration pulse occurred in 1890-1910 when elk were absent. A large pulse also occurred in 1950-1955, but only in lightly browsed stands. Nearly all of the heavily browsed stands (in the highest concentration areas for elk) regenerated before 1925. Recently, Olmsted reexamined his earlier study sites and found no evidence of tree replacement in any stand, due to heavy browsing (Olmsted 1997).

Baker et al. (1997) compared the timing of aspen regeneration to climatic fluctuations and elk density. They found no evidence that regeneration pulses were related to climate, but believed they found a correlation between regeneration events and periods of low elk abundance. They also examined historical photographs of aspen which showed mature aspen present in 1900-1914, which they believed regenerated prior to elk extirpation, based on tree size and an empirical relationship between size and age. The trees in the photos lacked elk-induced bark scars which would have persisted from the period prior to elk extirpation. Thus, they surmised that elk were present at low densities prior to their extirpation. However, the locations of the photos were not reported, and the single photo which appeared in their publication was clearly well above the primary elk winter range. Furthermore, the form of the relationship between elk density and aspen bark utilization is not known, so it would be difficult to infer what elk densities might have actually been. Since aspen barking was reported when there were only 312 elk (McLaughlin 1931), the inference would be that there would have been even fewer than that number.

Suzuki et al. (1998) found that only 20% of aspen stands in the Estes Valley contained a

cohort of regenerating stems, but 45% of the stands on the winter range outside the Estes Valley were regenerating, and 75% of aspen stands in the Roosevelt National Forest on the east side of RMNP were regenerating. They concluded that while aspen was declining in localized areas on the primary elk winter range, it was not declining at landscape and regional scales.

Willow

The grassy areas with few willows in Horseshoe Park and Beaver Meadows were reportedly once largely covered by willow. High water tables were prevalent, probably due to beaver dams, but the willow were cut as the land was drained by early ranchers to grow hay (Gysel 1960). Packard (1947b) referred to a "wide willow swamp" in Moraine Park, which absorbs the river as it exits the valley upstream. He noted that beaver flourished as a result of predator control and removal of ranching operations in the 1930s, which then overall, improved willow habitat. Yet he also said "In many places the carrying capacity (for beaver) has been overreached and the crowding (of beaver) is detrimental to the beavers as well as to private property." J.S Dixon reported vigorous willow growth in 1933-1934, but he also noted that willow was heavily browsed by elk, and by 1939 he reported willow deterioration and many clumps broken down and dying (Dixon 1939, Gysel 1960, Stevens 1980). Ratcliff (1941) noted an increase in deer and elk utilization of willow between 1936-1940, from 23% to 50% of current growth. Gysel (1960) reported that most of the remaining willows were growing along streambanks, and a large proportion of those were tall willows which were apparently not cut during the early haying operations.

Gysel (1960) resampled two exclosures that were erected in 1939 by Dixon at the borders of clumps or bands of willow and grasslands. In 1939 cover was similar inside and outside of the exclosures, but in 1959 cover had declined outside the exclosures but not inside. Gysel thus concluded that willow were declining in the grass-willow transition zones due to elk browsing.

Stevens (1980) established and sampled transects in willow in 1968, and reread them in 1978. He concluded that willow cover declined in five of six transects by a mean of 14%. Leader use averaged 69%. However, Zeigenfuss et al. (1999) reanalyzed the data, and concluded that while leader use was >80%, there was no statistical change in cover overall. Decreases on at least two of the transects were offset by increases on four other transects.

A recent analysis of historical aerial photography showed that over the last 50-59 years willow cover has declined by 19-21% (Peinetti 2000, Peinetti et al. 2002). These decreases were associated with 44-56% decreases in total stream channel density, which was believed to be a consequence of reduced beaver activity and an unnatural flood event. Tall willow communities still remained in the upper reaches of the valleys, but short willow communities were prevalent in the mid and lower reaches, particularly in the areas where channel density had declined. The combination of reduced channel density, lower water tables, and elk herbivory likely caused a loss of willow cover and a transition to short willow.

The conversion to short willow in Horseshoe Park was also believed to have been accelerated

by the Lawn Lake flood of 1982, when an earthen dam broke far upstream. Willow cover in Horseshoe park was significantly affected by the flood (McCutchen et al. 1993). The flood had a considerable amount of energy, moving large boulders, destroying willow as well as mature trees, and depositing a layer of fresh alluvium over the existing vegetation. It is likely that this fresh alluvial deposit provided a favorable environment for the establishment of a new willow cohort. Subsequent elk herbivory has suppressed height growth of the new willow (Peinetti 2000).

Beaver

Trapping of beaver and trading of their pelts was widespread in North America during 1800-1850. Trappers were present in Colorado well before 1850, and beaver were severely depleted by the late 1850s. Trappers were present in the region of RMNP as early as 1841, and by 1890, trappers, people and cattle had virtually eliminated beaver from Estes Park (Mills 1913). According to Jacobs (1968), the Saint Vrain River was prime beaver habitat, extensively used by trappers. A beaver pelt trading post was established at the mouth of the Saint Vrain River as early as 1837. The Saint Vrain was the most probable first access to the Estes Park area, since the Big Thompson Canyon would have been too difficult to negotiate (Jacobs 1868). Trapping success declined by 60% in 1850 compared to earlier days (Audubon and Bachman 1850, cited by Walters 1996).

Beaver apparently rebounded between 1890 and 1925. Warren (1925) found abundant beaver at several sites on the eastern side of the park, but none of these sites were located on the elk winter range of the Estes Valley. Packard (1947b) later surveyed the same area and found that conditions had changed. The colonies were less extensive, many ponds had been drained or dried up, and the number of beavers had decreased. Most of the abandoned sites were turning into meadow. In this general area, Warren estimated 160 beaver while Packard estimated 68.

Packard (1947b) also surveyed sites on the elk winter range. He found an abundance of beaver to the point of overpopulation. He stated that "there is an abundance of food and building material on many of the important streams, and almost every stream that can support beavers is stocked to capacity or is overpopulated." However, he noted that elk and deer were negatively affecting beaver food supplies.

> "A serious problem especially on streams in the vicinity of Estes Park, is the competitive effect of deer and elk on their winter range upon the supply of aspen and willow... Together these animals produce a noticeable decrease in the beaver's food supply, which is especially conspicuous in Moraine Park."

Overall, Packard estimated there were 447 beaver in the Fall River, Big Thompson River, and Beaver Creek (Brook) portions of the elk winter range (Horseshoe Park, Moraine Park, and Beaver Meadows). On all the drainages where he mentioned elk presence and negative effects on willow and aspen, there were 547 beavers. On all drainages where wintering elk could occur there were 816 beavers. It is possible that these are overestimates, because estimates were based on lodge numbers, and he did not distinguish between active and inactive lodges (Stevens and Christianson 1980).

Packard (1947b) noted that irrigation ditches were decreasing the amount of water in Beaver Creek (Brook), and that the 200 elk which overwintered there had killed much of the aspen and willow and were probably having a detrimental effect on beaver food supplies. He noted negative elk effects on willow at Cow Creek, Horseshoe Park, Hidden Valley, Beaver Meadow, and Moraine Park.

Packard counted 52 lodges and estimated 315 beavers at the site he called Thompson River. Packards's description indicates that he was referring to Moraine Park. He described Moraine Park as a wide willow swamp through which several channels crossed. The channels then merged below the timothy meadows to reform the Thompson River. He felt that beavers were very overcrowded there, and that the willow supply was insufficient to maintain the large number of beavers and was suffering from competitive use by elk and deer. Furthermore, livestock grazing appeared to have reduced the amount of grass available to elk, possibly causing increased elk herbivory on willow.

There is evidence that beavers declined by 1964. A survey of Moraine Park by Hickman (1964) only found 17 lodges and 23 food caches. Based on an assumed four beavers per cache, Hickman estimated there were 92 beavers. Assuming six beavers per lodge, there would have been 102 beavers (Stevens and Christianson 1980). Earlier in the same area, Packard (1940) found 52 lodges and 315 beavers.

Stevens and Christianson (1980) conducted a survey in response to an apparent sudden decline in beavers that occurred about 1976. They only found two active lodges in Moraine Park, five food caches, and estimated twelve beavers. They attributed the decline to a reduced habitat, particularly a reduction in tall willow. At Horseshoe Park, they found five lodges and estimated 30 beavers. They felt that lower Moraine Park and Horseshoe Park, because of severe competition with elk and an apparent drop in the water table as a result of earlier beaver dams collapsing, may never develop a sufficient forage supply for beaver reestablishment.

Recent surveys found two active lodges in Moraine Park, and one in Horseshoe Park (Gense 1998, Zeigenfuss et.al. 2002).

VEGETATION MAP

The model requires a vegetation map for the initialization of plant biomass and population variables. A single-source vegetation map for the entire elk range did not exist, primarily because the elk range extends outside the park boundaries, and includes land from three administrative agencies, the U.S. National Park Service, the USFS, and the Town of Estes Park. Consequently, a vegetation map was constructed from multiple sources.

Vegetation cover maps from RMNP and the Arapaho National Forest (ARNF) were combined into a single coverage (Ron Thomas RMNP GIS lab). The RMNP "Cover Types" map was based on aerial photography taken in 1987 and was estimated to be 80-85% accurate. Attributes included canopy cover and tree diameter. The ARNF cover map was obtained from the ARNF Resource Information System, and is also based on aerial photography. Crown cover and stand structural stage were included as attributes. Data in the RMNP "Cover Types" map were reclassified to classes used in the ARNF map. Polygon maps were rasterized to a 100m grid. Vegetation classes were aggregated into 23 vegetation types to produce the map shown in Figure 7.

Vegetation outside RMNP and ARNF, i.e., on private landholdings, was derived from a vegetation map of Larimer County Colorado that was developed at Colorado State University from a Landsat-TM scene (Todd 1995, McCool 1995). There were no cover or tree size attributes for this map. The 30 m Larimer County map was resampled to a 100m grid, and overlain on the RMNP-ARNF map (Figure 8).

Additional detail was needed in areas in and around the town of Estes Park, where humans have increased and decreased herbaceous vegetation biomass in different areas. Herbaceous biomass and cover have been decreased by disturbance, buildings, roads, and other paved areas. Biomass production has been increased by irrigation, fertilization, and replacement of native grasses by domesticated turfgrasses.

The basis for reclassification of vegetation in Estes Park, was a remote sensing-based map of vegetation greenness. A SPOT image from July of 1996 (20 m pixel width) was used to compute a map of normalized difference vegetation index (NDVI), as the ratio

$$NDVI = (Band\ 3 - Band\ 2) / (Band\ 3 + Band\ 2) = (NIR-IR)/(NIR+IR)$$

where NIR is reflectance in the near infrared and IR is reflectance in the infrared band (Tucker 198). The NDVI map of the entire winter range is shown in Figure 9. There were no marked differences between NDVI inside and outside of the RMNP boundary. Areas of human influence, both positive and negative, were readily discernable.

Herbaceous biomass was sampled in the town area in 1997 and 1998 in a variety of vegetation types (Figure 10). There were significant positive relationships between NDVI values and the total biomass densities measured on the ground (Figure 11). The golf-course values in 1997 were excluded

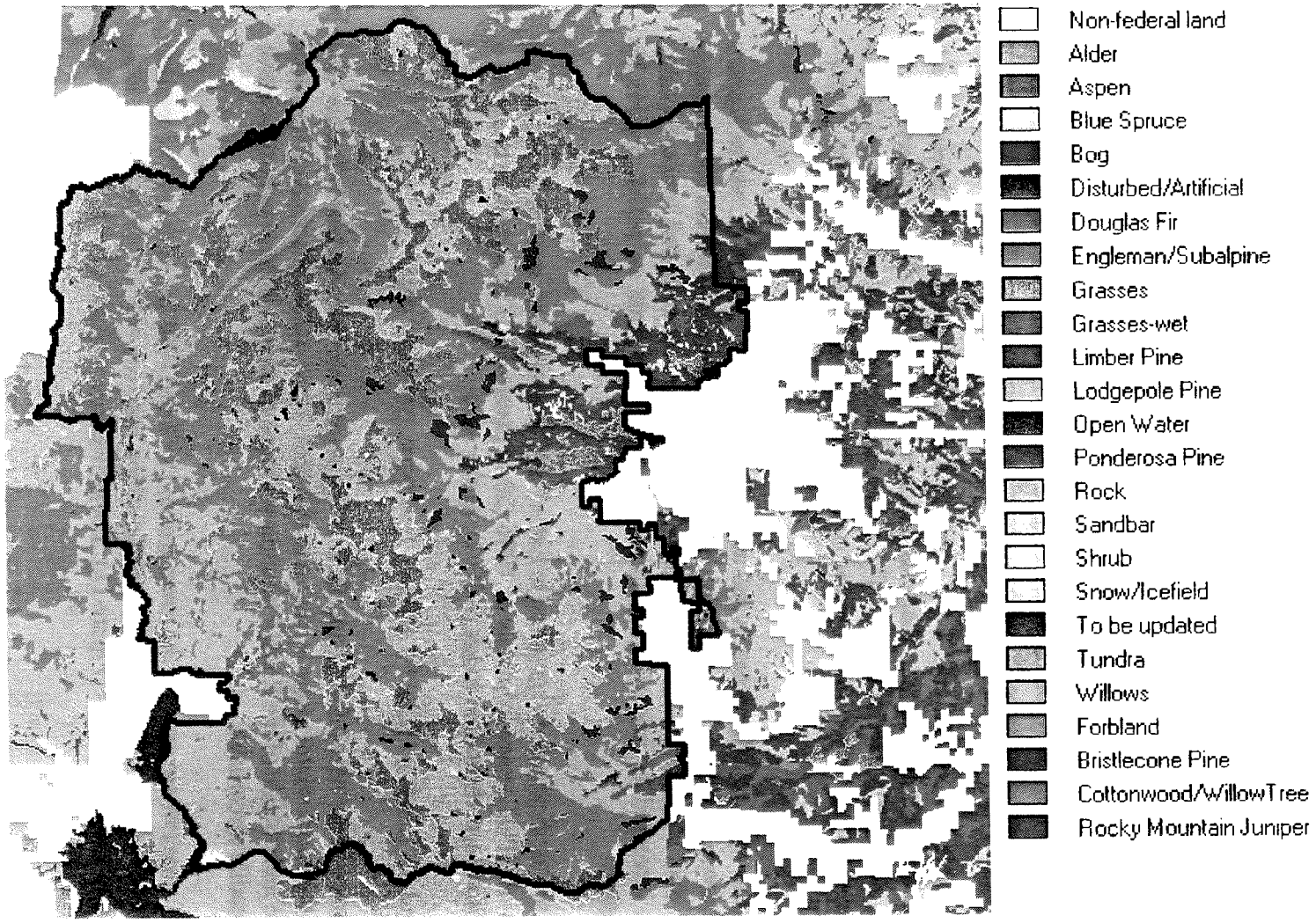


Figure 7. Vegetation map resulting from combining the Rocky Mountain National Park vegetation map (boundary is the thick black line), and the Arapaho-Roosevelt National Forest vegetation map (outside park boundary).

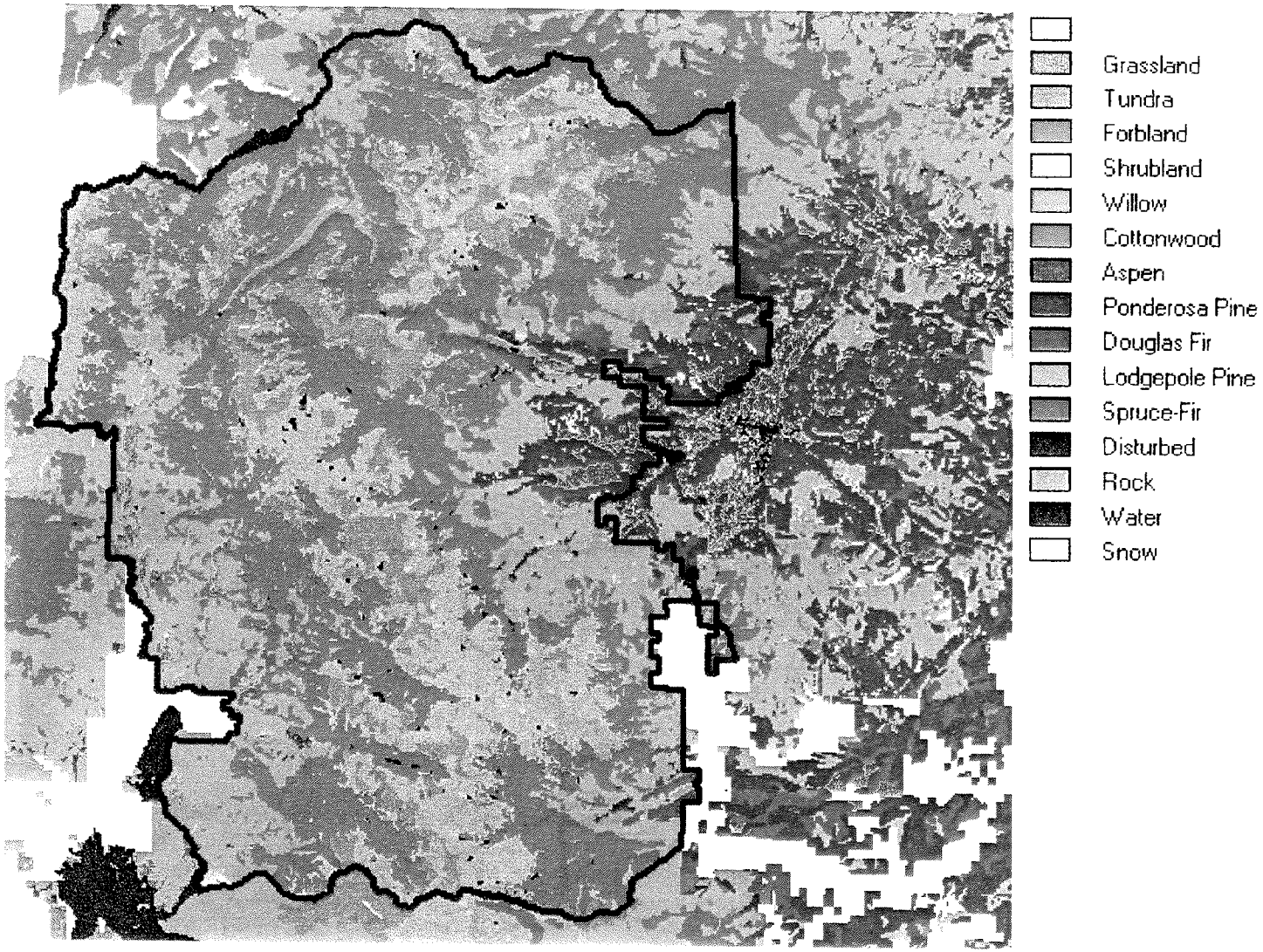


Figure 8. Vegetation map with missing areas in the RMNP/USFS map filled in with data from a Landsat-based vegetation map of Larimer County, Colorado. High elevation grasslands have been reclassified as tundra. Original classes simplified to 15.

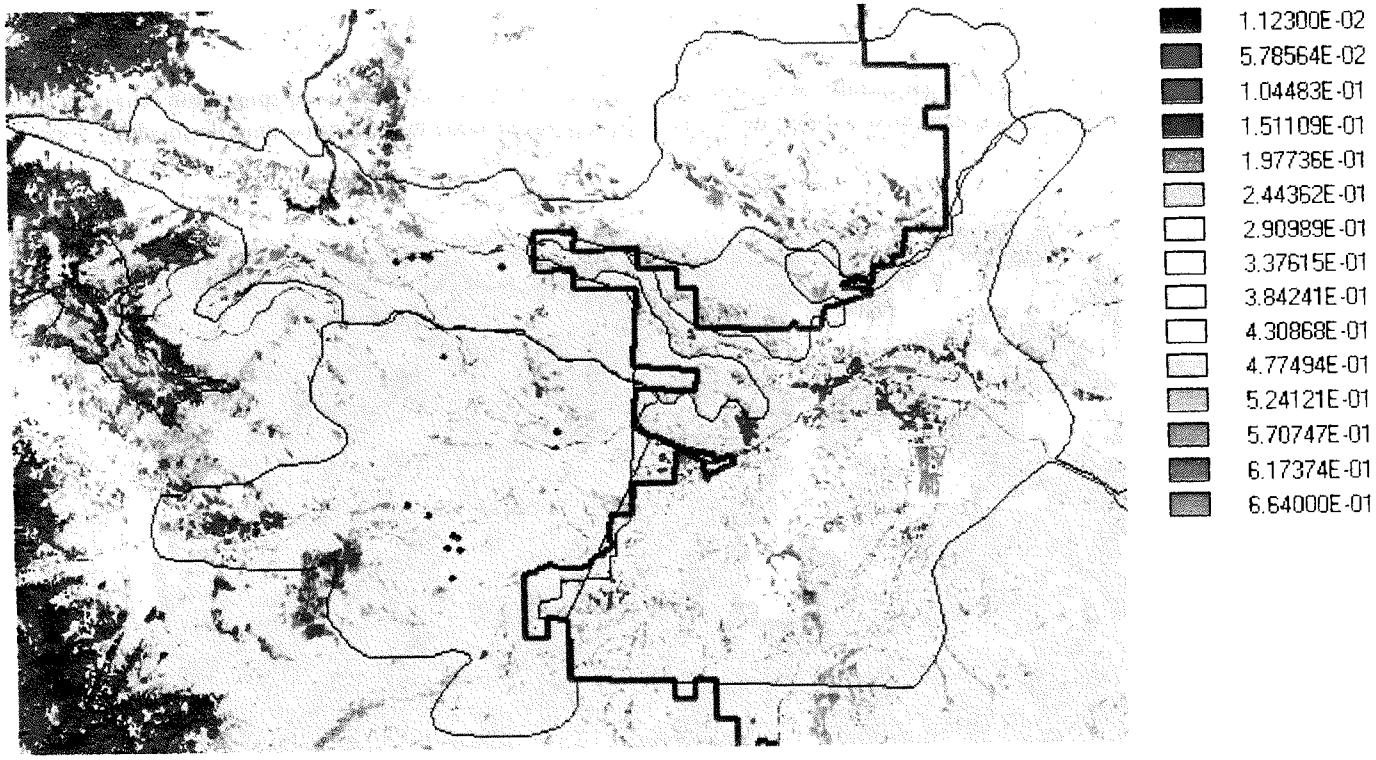


Figure 9. Normalized difference vegetation index (NDVI) of the principle winter range areas of the 2 park herd segments and the town segment ground count area (thin black lines). The boundary of Rocky Mountain National Park is shown a thick black line. Exclosure study sites appear as small black rectangles. The NDVI value does not have any units but is an index that generally ranges from 0 to 1. The units are given here in scientific notation where for example 1.12E-02 means 0.0112 and 3.37E-01 means 0.337.

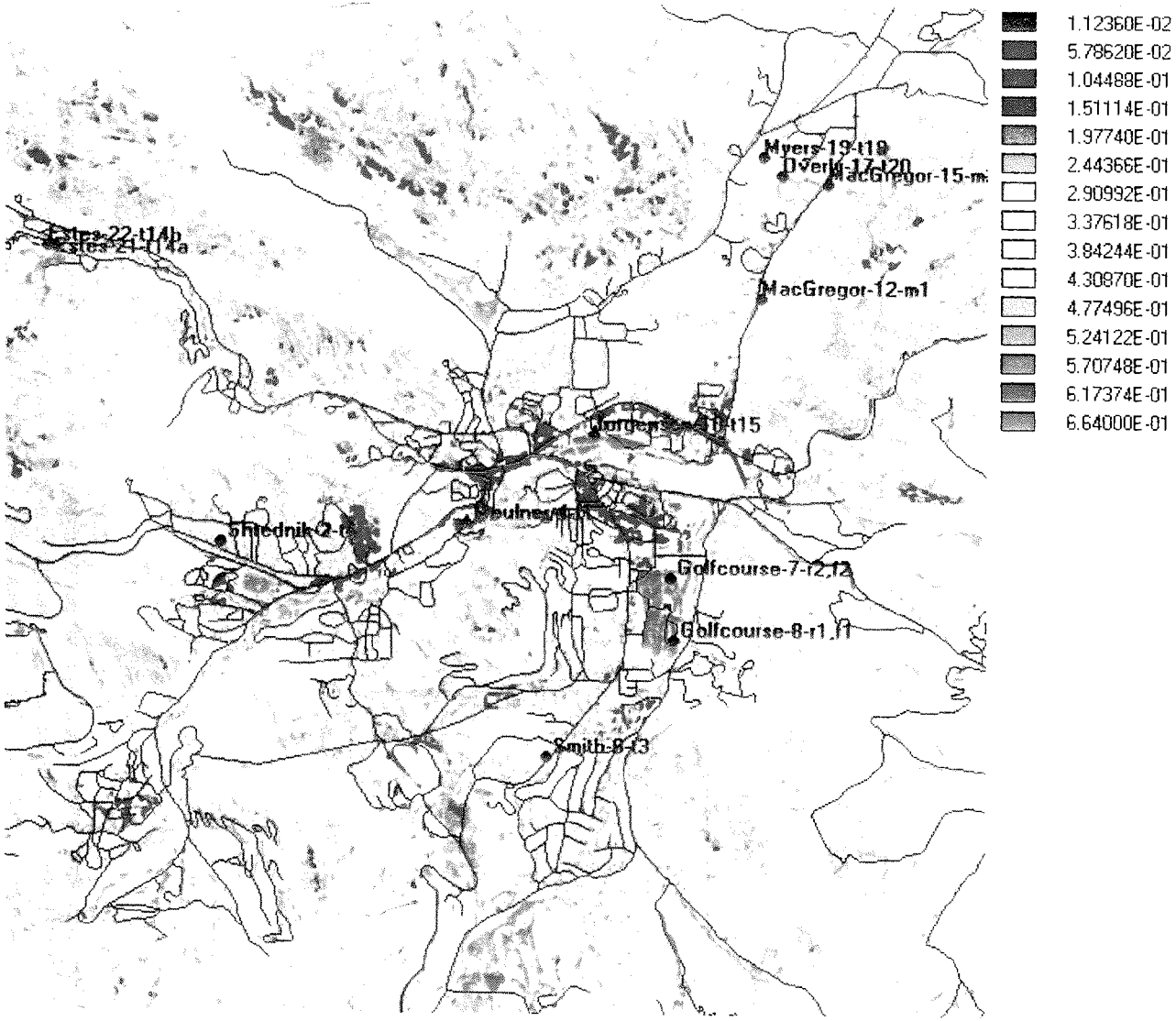


Figure 10. NDVI in the town of Estes Park, showing roads, and biomass sampling sites. The NDVI value does not have any units but is an index that generally ranges from 0 to 1. The units are given here in scientific notation where for example 1.12E-02 means 0.0112 and 3.37E-01 means 0.337.

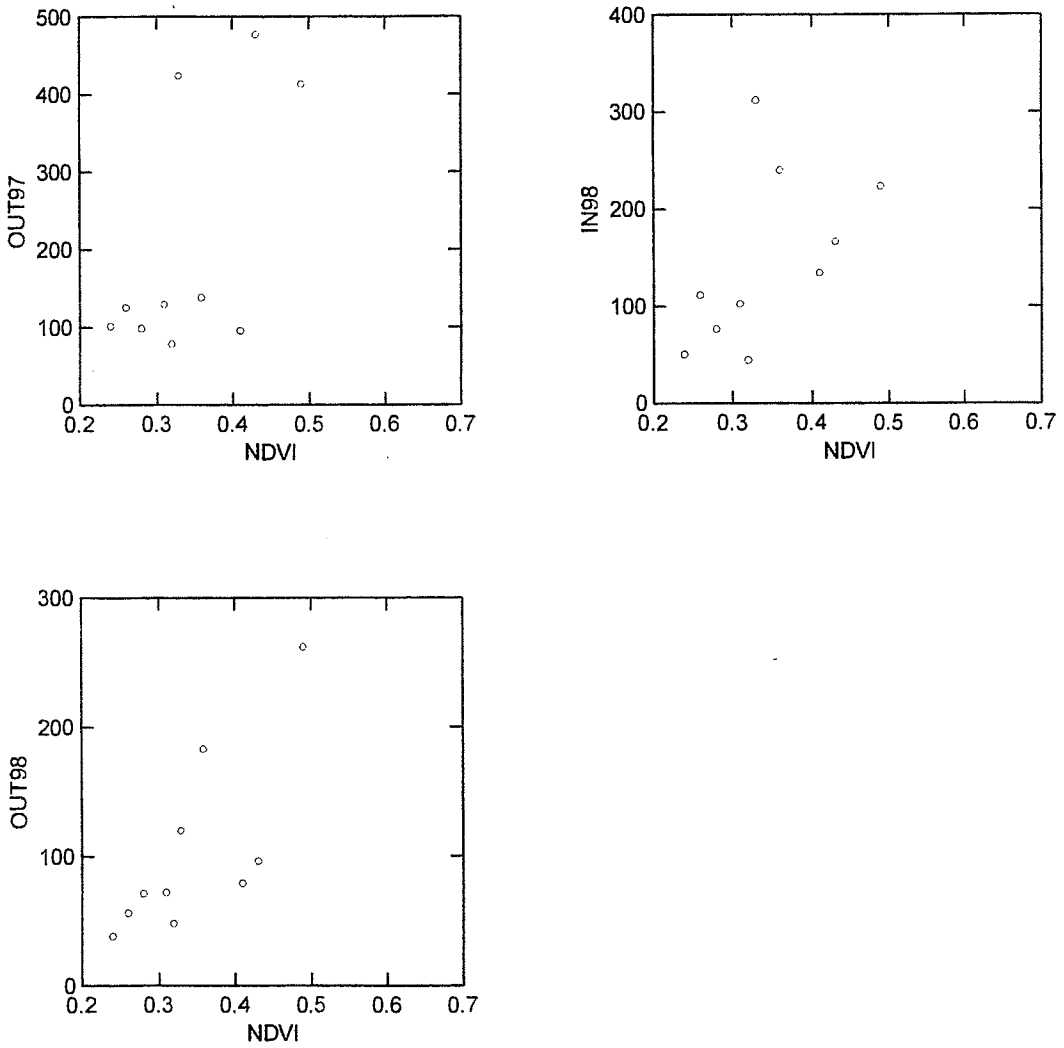


Figure 11. Plots of total green plus brown biomass (grams per square meter dry weight) measured at sampling sites in Estes Park town vs. NDVI values at those locations on the NDVI map: A) unexclosed plots in 1997 (r2=0.62, p=0.05); B) exclosed plots in 1998 (r2=0.27, p=0.13); C) unexclosed plots in 1998 (r2=0.55, p=0.014).

from the 1997 regression. High values of NDVI occurred (0.57-0.61) while relatively low biomass was measured (104-177 g m-2), due to exceptional greenness. The slope of the line varied among years, probably due to variations in the fraction of biomass that was green vs. brown.

The frequency distributions of NDVI for each vegetation class were computed to determine modal, high, and low values for each vegetation type. By examining this output for unusually low or high NDVI values for a vegetation type, a new set of vegetation classes was derived. The most common occurrence of unusually low NDVIs clearly occurred where there were roads and buildings in the town (Figure 12). Unusually low NDVIs also appeared to be related to less intensive human development, e.g., areas with high housing density. Vegetation was accordingly reclassified into two classes corresponding to complete or partial presence of roads and buildings where the NDVI for the pixel was markedly less than those typically found for the vegetation type. Areas of bare rocks that naturally occur in mountainous terrain were not reclassified.

A minor correction to the town vegetation map was required in the McGregor Ranch area. This area was scrutinized on the ground because of its potential importance as an elk grazing resource (F. Singer, unpublished data). On the Larimer County vegetation map, much of it was classified as riparian deciduous (cottonwood), when in fact it was grassland with higher than normal productivity due to anthropogenic irrigation, and natural subirrigation. This area was reclassified as grassland, and this was subsequently reclassified as partly or heavily subirrigated runoff or runon using NDVI values as described above.

An "undisturbed" vegetation map was created to represent the vegetation cover prior to the settlement of the Estes Valley. Vegetation and land covers of anthropogenic origin on the Larimer County vegetation map were restored to undisturbed conditions. All areas classified as disturbed, urban, golf course, etc., were reclassified as grassland. The Big Thompson River course was markedly altered by development, including the construction of a dam and lake. Historical photographs of the valley prior to town and dam construction showed the former extent of the river course and riparian floodplain. This area was digitized and reclassified as heavily subirrigated meadow. The extent of willow communities within RMNP and on the east slope elk winter range in 1937-1946 was delimited from historical air photography (Peinetti et al. 2002). Although willow was possibly more extensive before 1937-1946, no maps or quantitative data existed, so the 1937-1946 data were used as the closest available approximation. This procedure delimited the grid-cells on the model input vegetation map which were classified as willow. Willow canopy cover in the grid-cells classified as willow was initialized at 40% in all runs. During the course of the simulation cover in those grid-cells could vary between 0-70% according to simulated plant growth. Willow in early times was assumed to be primarily tall willow, but with a significant component of younger/smaller plants.

The final vegetation maps at 100 m resolution (Figures 13,14) were aggregated to produce maps at 500 m resolution for modeling purposes, using the pixel thinning procedure in IDRISI.

The model required woody cover and tree size maps for initialization. Maps of woody canopy cover and tree size for the study area were developed by combining data from the USFS and RMNP

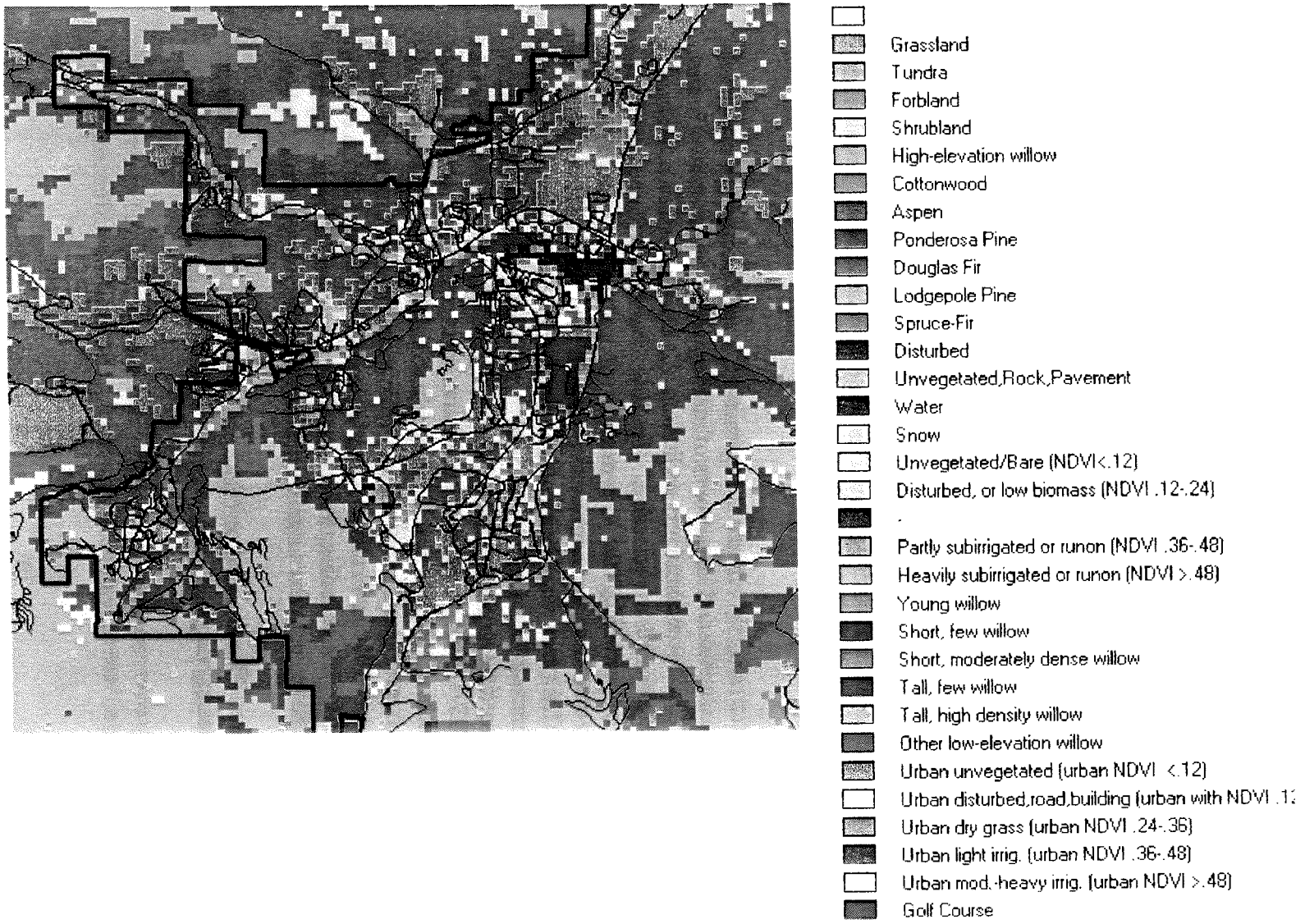


Figure 12. Vegetation classification of Estes Park, with human-influenced vegetation types, at 100m resolution. Also shown are roads and the park boundary.

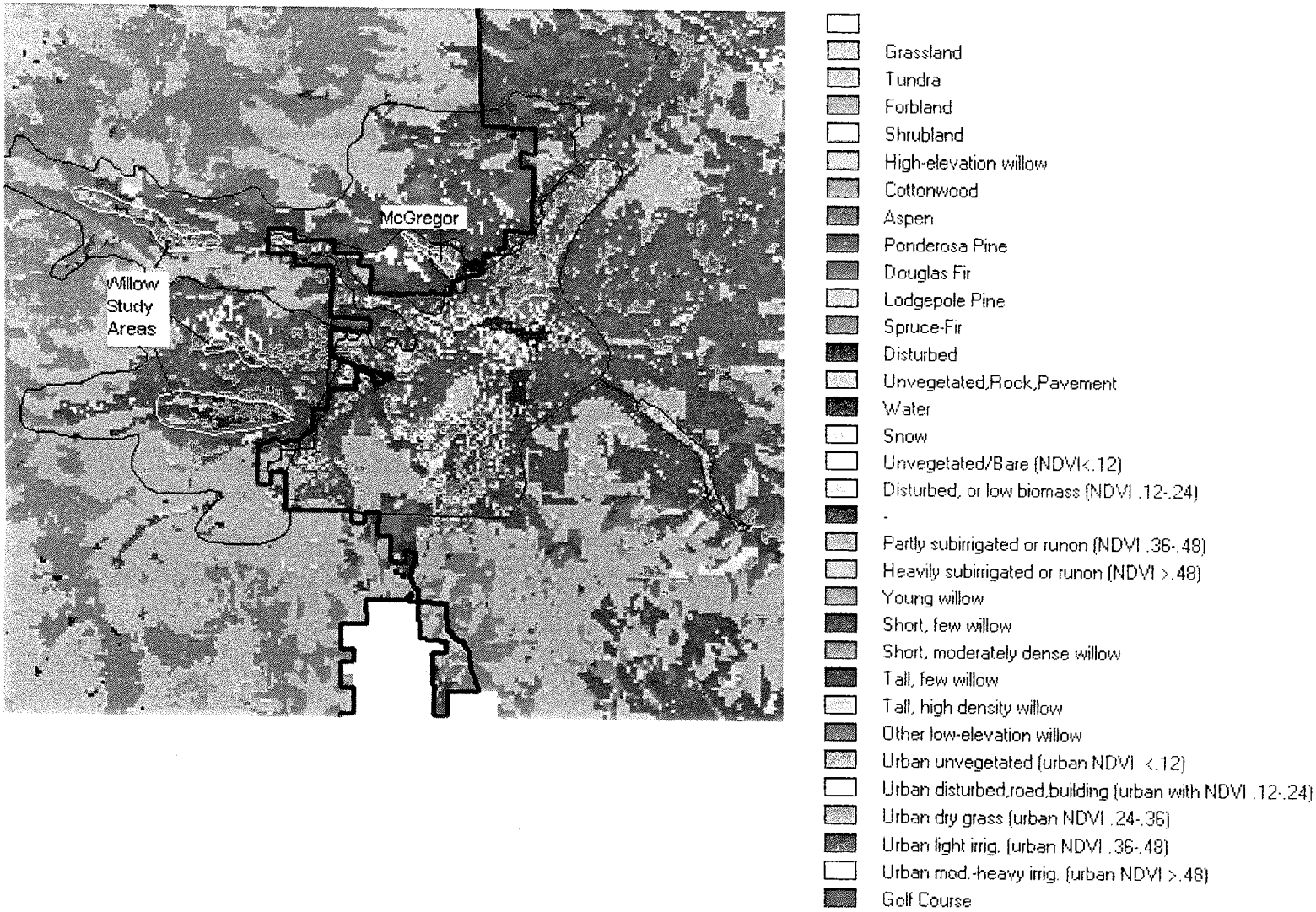


Figure 13. Portion of final vegetation map used in the model representing current conditions, focusing on the elk winter range. Also shown are willow stands that have been reclassified using data from Peinetti (2000), the 3 herd segment winter ranges, the park boundary, and the McGregor Ranch.

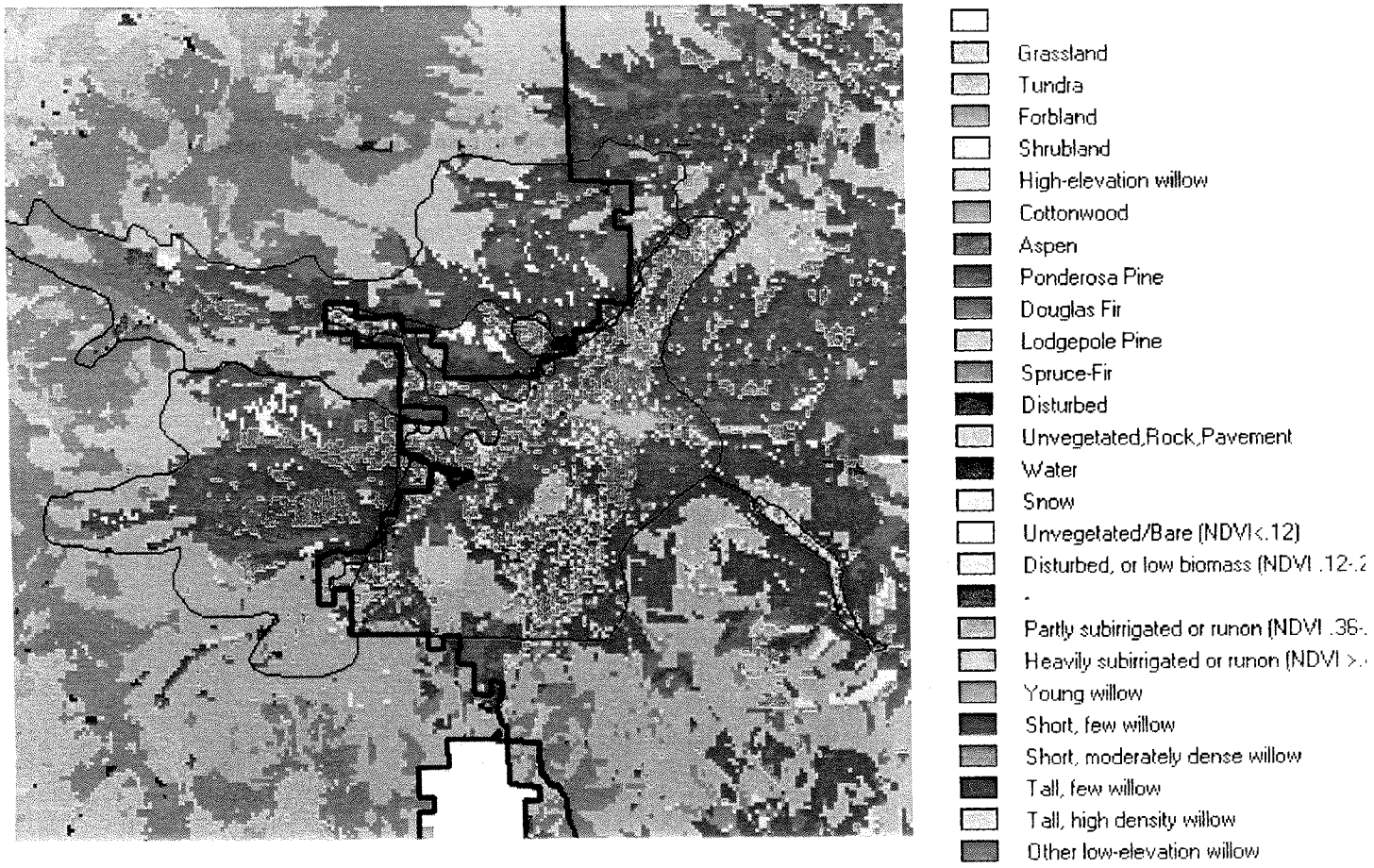


Figure 14. Reconstructed natural vegetation in the Estes Valley and elk winter range, for use in model scenarios. The 2 park elk ranges, Moraine Park and Horseshoe Park, and the Town count unit, are shown in thin black lines.

maps. The RMNP map had attribute data for canopy cover and diameter at breast height for each polygon. The ARNF database contained information on canopy cover, and structural stage. Typical values of diameter at breast height for each stage were used to create a coverage that could be merged with the RMNP tree diameter map. Unfortunately, there was substantial discrepancy between the woody cover values of the RMNP and ARNF maps, resulting in a large discontinuity at the park boundary. An effort was made to reclassify both the RMNP and ARNF maps in such a way as to make them consistent, and retain the best values of each. This was accomplished by examining digital ortho-photographs along the NE boundary. Visual estimates of cover were compared with values on the RMNP and ARNF maps. I decided the most realistic values would be achieved by reclassifying RMNP cover values of 100, 80, and 60% to 80, 60 and 35% respectively. ARNF cover values of 55 and 20% were reclassified to 80 and 65%. Finally, the area not covered by RMNP or ARNF maps, but only by the Larimer County map, was filled in using the most common cover and diameter values for each vegetation type elsewhere on the map. The resulting tree cover and tree diameter maps are shown in Figures 15 and 16.

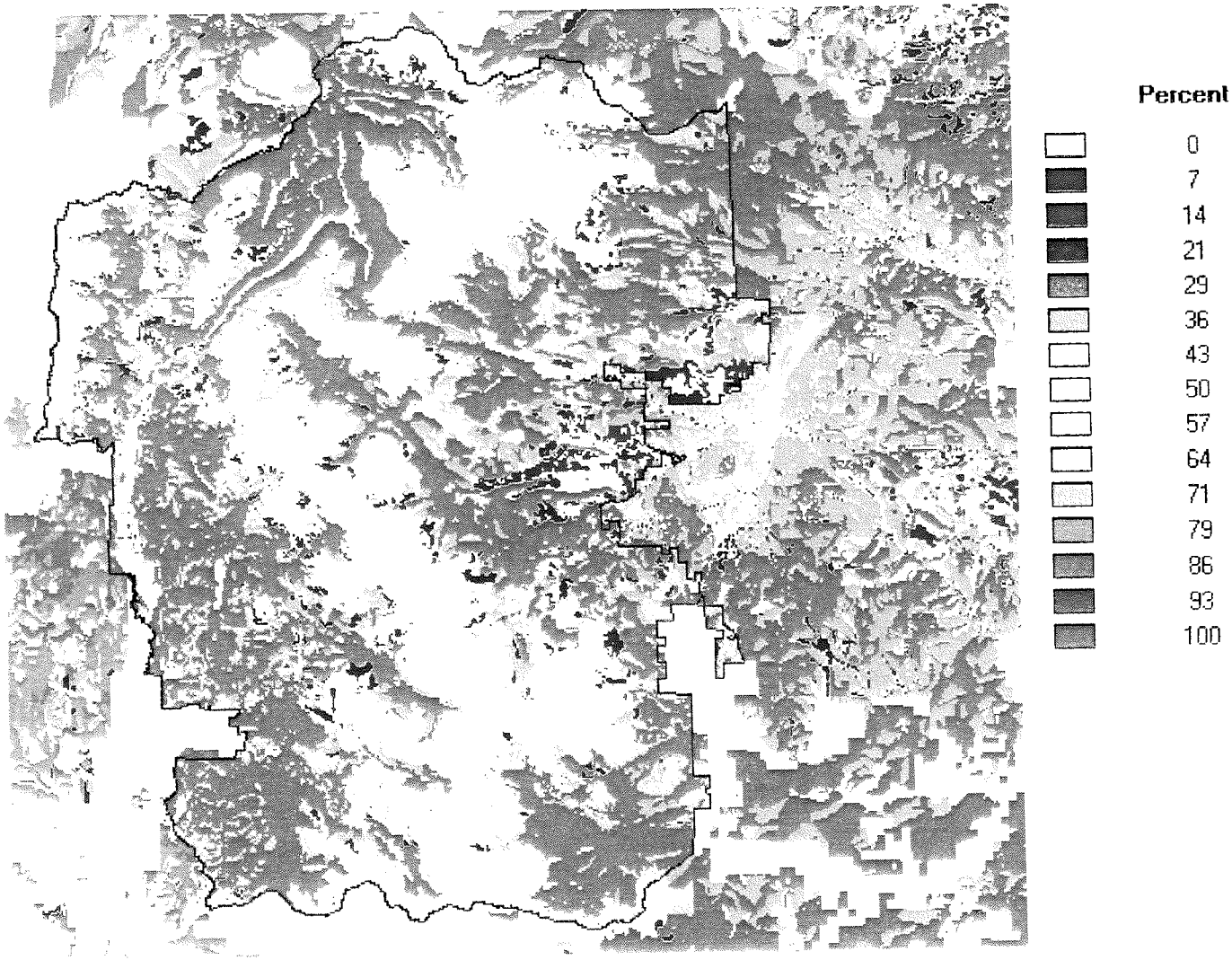


Figure 15. Tree canopy cover (percent) map resulting from combining RMNP and ARNF maps, reclassifying values for compatibility, and filling in missing values in town with typical values for vegetation types on the Larimer County vegetation map.

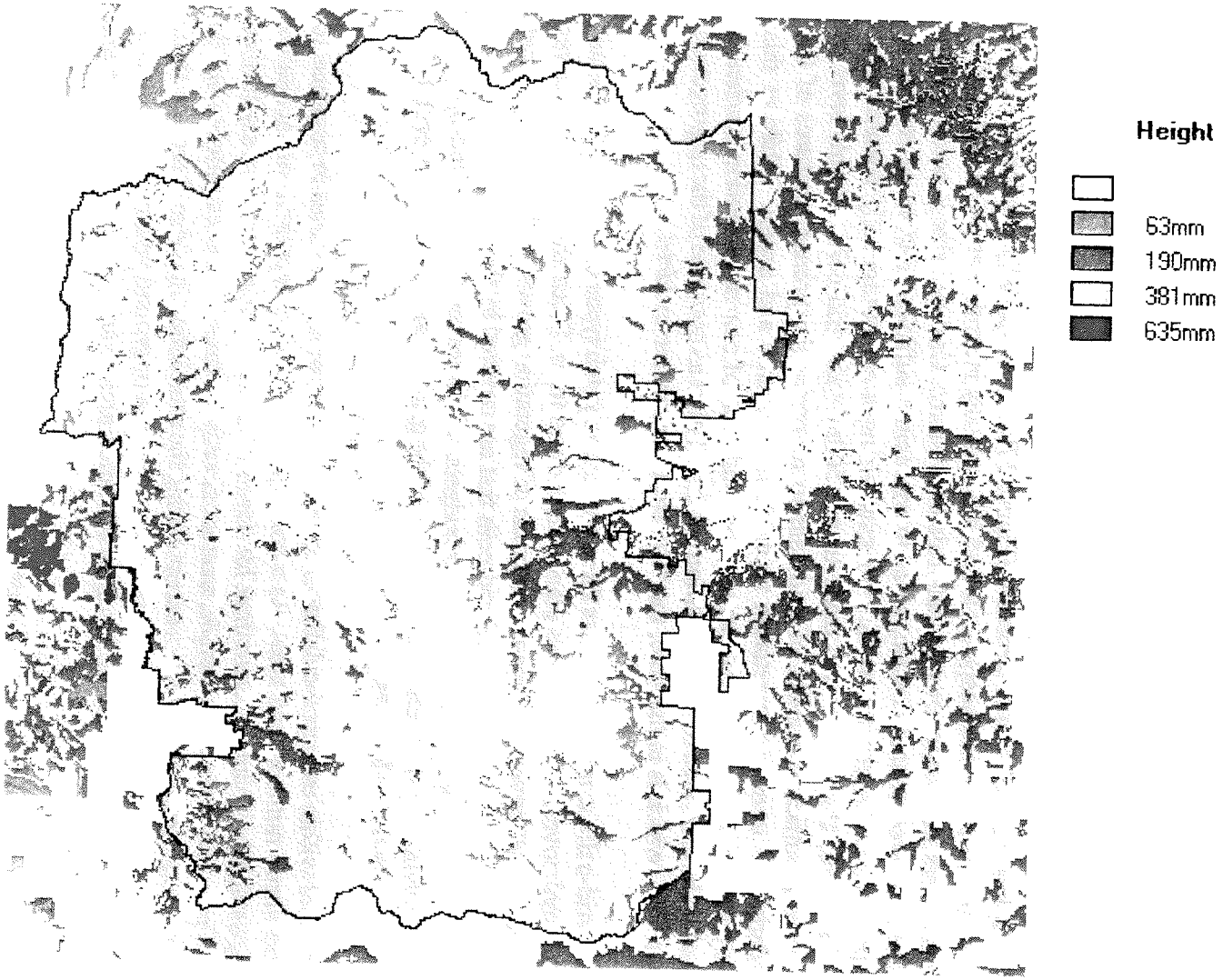


Figure 16. Tree size map, in diameter at breast height, using combined data of RMNP and ARNF. The area occupied by the town of Estes Park was classified based on modal values for similar vegetation types in RMNP and ARNF.

MODEL DESCRIPTION AND DATA INPUTS

Ecosystem Model Structure

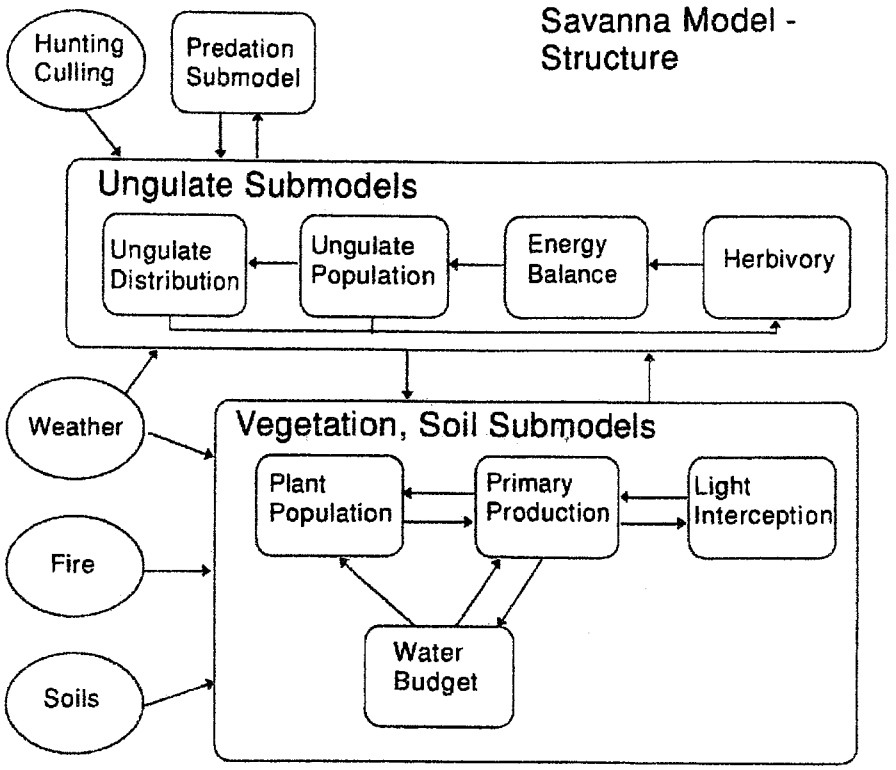
SAVANNA is a spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems. Version 5 of SAVANNA was used here. Versions 1 and 2 were developed to study a nomadic pastoral ecosystem in Kenya (Coughenour 1992). Version 3 was developed for Elk Island National Park in Alberta (Buckley et al. 1995), and Version 4 was applied to the Pryor Mountain Wild Horse Range (Coughenour 2000), northern Colorado (Weisberg et al. 2002), northern Australia (Ludwig et al. 1999), South Africa (Kiker 1998), Tanzania (Boone et al. 2001), and Inner Mongolia (Christensen 2001). SAVANNA simulates processes at landscape through regional spatial scales over annual to decadal time scales. The model is composed of site water balance, plant biomass production, plant population dynamics, litter decomposition and nitrogen cycling, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, and ungulate population dynamics submodels (Figure 17a). The time-step of the model is one week.

Savanna has a hierarchical spatial structure (Figure 17b). It is spatially explicit (i.e., it is sensitive to spatial position) at the landscape scale and it is spatially inexplicit at patch scales. The mosaic of grid-cells covers landscapes or regional-scale ecosystems. Grid-cell size is scaled to the spatial extent of the simulated spatial domain, so as to maintain a sufficient degree of realism in capturing landscape-scale heterogeneity, while also maintaining a computationally feasible total number of grid-cells. Here, the choice was made to use 500m wide grid-cells. At this level of resolution, there were a sufficient number of grid-cells to represent the primary features of the landscape, particularly less common vegetation types such as willow and aspen. While at this resolution not every vegetation patch is represented, the total area of coarse resolution patches is approximately equal to the total area of fine-resolution patches. This is an outcome of the aggregation procedure used in a GIS, which is in this case, the "Contract" procedure in *Idrisi*.

Within each grid-cell the model simulates three vegetation patch types or "facets." These are defined by the fractional covers of herbaceous plants, shrubs and trees. Since shrub and tree cover are simulated variables, facet cover is a dynamic outcome of vegetation growth and mortality. Facet locations are not modeled, only the fractions of grid-cells that are covered by the facets. Within each facet, the model simulates plant growth and soil water budgets. Variables results are scaled-up to the grid-cell level by multiplying the variables by the fractions of the grid-cell area covered by each facet, and summing the products over all facets.

The area of land within each grid-cell that is covered by trees or shrubs varies in response to changes in tree and shrub numbers and sizes. As a consequence, direct competitive or facilitative interactions among established plants of these three life-forms are limited to patches where established plants are rooted. Trees and herbs, for example, interact directly on tree-dominated patches but do not interact on herbaceous-dominated patches except during the establishment phase. Tree and shrub vegetation covers are defined in terms of rooted area, i.e., the area of ground which corresponds to the exploited soil volume. Cover is defined in terms of rooted area mainly because soil water and

A)



B)

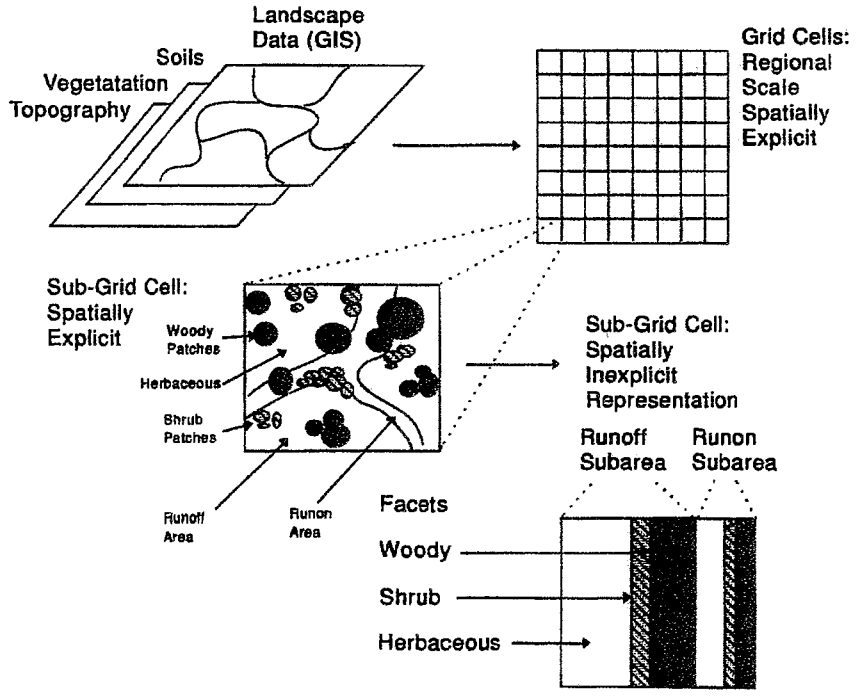


Figure 17. A) Primary components of the SAVANNA model. B) Spatial structure of the model.

nutrient budgets are computed on a soil volume basis.

The vertical spatial structure of the model is defined by soil and plant canopy layers. The soil is divided into three layers. The top soil layer is a zone of potential bare soil evaporation as well as root uptake. The second layer is generally the deepest layer that is exploited by herbaceous roots. The bottom layer is generally occupied only by shrub and tree roots. Plant canopies are organized into herb, shrub and tree strata. In turn, each of these are divided into three substrata to compute light intensity.

Weather

Savanna is driven by monthly weather data. Each month, a regression is performed between precipitation and elevation using data from all weather stations in the study area. If the correlation coefficient (r^2) is >0.2, the slope of the line (i.e., the rate of increase in precipitation with elevation) and the elevation difference is used to estimate precipitation for the weather station as if it were at the same elevation as the point in question. The elevation-corrected weather station data are then spatially interpolated using inverse distance weighting on the six nearest stations with data. This procedure is followed for each point on the landscape. Temperature for each point on the landscape is similarly estimated from the temperatures at the nearest weather stations by applying adiabatic lapse rates to the station temperatures to estimate temperature at the same elevation as the point in question. The corrected temperature data are spatially interpolated using inverse distance weighting.

Stochastic weather data are created by random sampling of years from the weather files. Each year, a random year of data is drawn from the files, and an additional amount of random variation is added to the data. The sampling and addition of variance are done in such a way that data from all weather stations are affected together, thus preserving the spatial pattern in the original data.

Atmospheric water vapor content is calculated from relative humidity and temperature of the main base station. Relative humidity is calculated from the water vapor concentration, and the temperature at each landscape location. Solar radiation is calculated from monthly cloud cover, latitude, and day of year, correcting for slope and aspect using the methods described by Nikolov and Zeller (1992). Cloud cover is estimated from monthly precipitation and water vapor content.

The weather input file was derived from the weather stations and SNOTEL stations shown in Figure 18. Precipitation was recorded in Estes Park beginning in 1910, and it was recorded in Grand Lake beginning in 1940. Temperature was recorded in Estes Park starting in 1931. Weather stations came on line for the most part beginning in 1949 and into the early 1950s. Older weather stations include Fort Collins (1900-present), and Fraser (1910-present). SNOTEL stations are remote recording devices that recorded precipitation and snow water equivalents beginning in 1981. Temperature data became available from SNOTEL stations in 1990. Weather data since 1948 were obtained from the EarthInfo Inc. NCDC (National Climate Data Center) Summary of the Day CD ROM data bases. Earlier data were obtained from the Colorado Climate Data Center. SNOTEL data

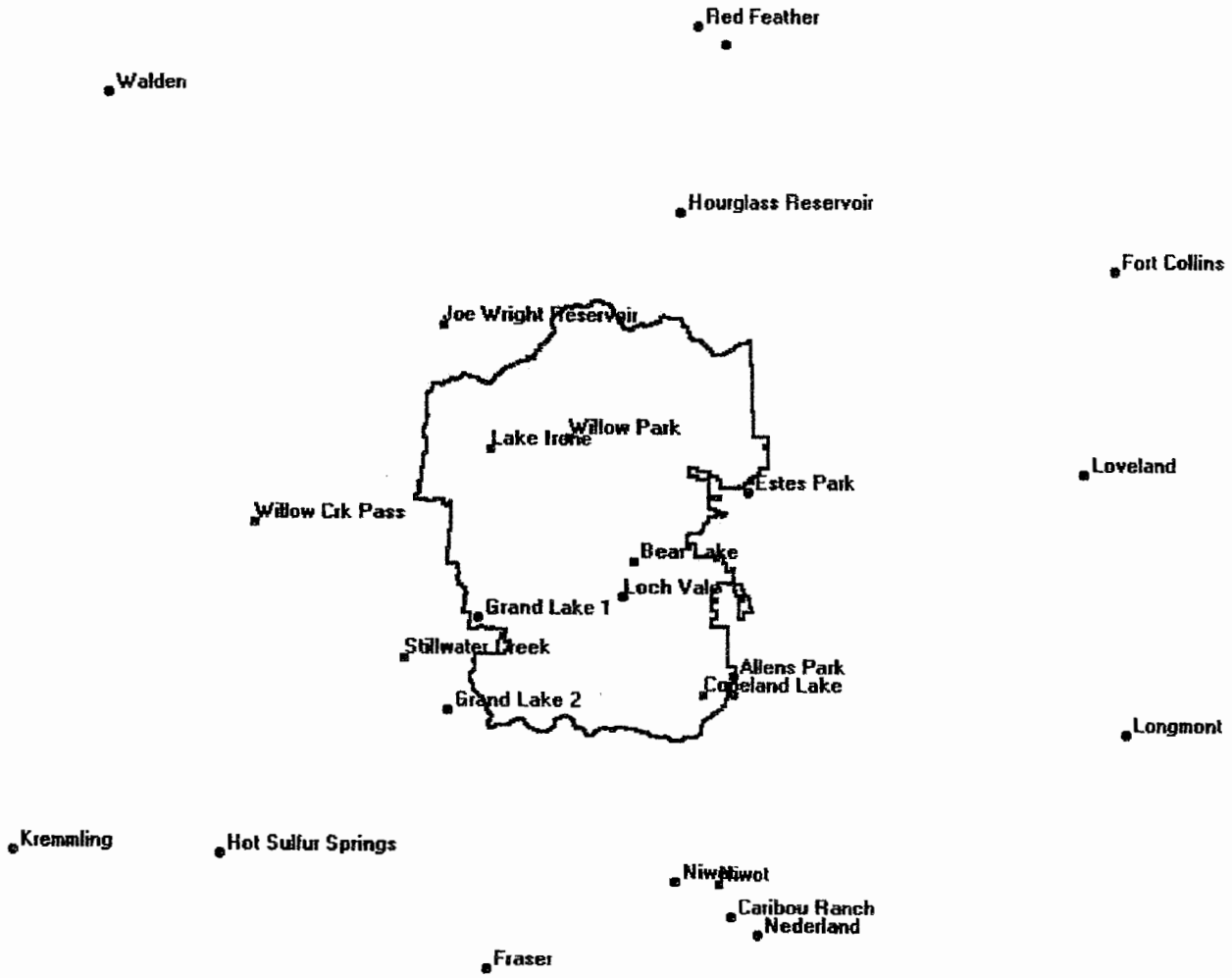


Figure 18. Weather station (circles) and SNOTEL station (squares) locations.

were obtained from USDA NRCS (National Resource Conservation Service) via the internet site of Chris Pacheco of the National Weather and Climate Center, Portland, Oregon.

SAVANNA reconstructs missing weather data while it is running based upon regression equations between data from the primary weather station (Estes Park in this case), and the other weather stations. The parameters from the equations are used in the model to estimate missing data from the main base station data, which are assumed to be complete and continuous. The results are then based on empirical correlations between the main base and the other weather station data. This captures the primary temporal patterns in the region, as well as the main patterns of difference between stations. Although not exact, this provides a realistic representation of climate patterns at the monthly time scale. This procedure was followed for the period 1931-1998. Weather data since 1949 are relatively complete. While data for 1931-1948 were sparse, there were key stations with data, including Estes Park, Grand Lake, and Fraser.

Data for the period 1910-1930 was reconstructed from the deviations from normal observed in the Fraser data. The normals were computed for the period 1949-1998. Then the deviations for 1910-1930 were estimated, in terms of degrees for temperature, and percent of seasonal precipitation. Four seasons were recognized: winter, spring, summer, and fall (months as in tree-ring data below). The deviations were then applied to 1949-1998 normals from other stations to fill in missing values for each of the other stations.

Data for the period 1775-1911 were reconstructed from the tree-ring data base of Fritts (1991a,b). The Fritts data base included reconstructions of temperature for Cheyenne, Wyoming, and precipitation for Fort Collins, Colorado. Data are by season: winter (December-February), spring (March-June), summer (July-August), and fall (September-November). Tree ring data were calibrated against data from weather data from 1901-1963. The method here was to use the reconstructed data of Fritts, along with the actual weather data from Cheyenne and Fort Collins for 1901-1963, to calculate deviations from normal in degrees or percent of normal precipitation, by season. The seasonal deviations were then applied to monthly means from the actual weather station data for 1949-1998, to construct weather data set for 1775-1911.

Water Submodels and Soil Properties

The water budget submodel simulates soil moisture dynamics and use on each patch type on each grid-cell. A soil map is used in conjunction with soil properties for each soil type, to determine soil water holding capacities of each subarea on each grid-cell. Water is routed to three soil layers using a simple "tipping bucket" approach that drains water in excess of field capacity to subsequently deeper layers. The water budget includes terms for precipitation, interception, runoff, runon, infiltration, deep drainage, bare soil evaporation, and transpiration.

The runoff curve number method of the U.S. Soil Conservation Service is used to calculate runoff (Wight and Skiles 1987). Runoff depends on daily rainfall, the quantity and distribution of water in the soil relative to water holding capacity, and the condition curve number for the soil.

Runoff curve numbers are based on range site classifications and range condition such that runoff increases under low plant and litter cover. The curve number for good condition is given in Table 1, A higher runoff curve number is specified for fair range condition. Bare soil evaporation is simulated using the Ritchie (1972) model (Wight and Skiles 1987). Evaporation also increases under low plant and litter cover.

A soils map and soil survey data did not exist for RMNP, nor for the area outside of the park in Larimer County. Instead, the vegetation/cover map was used as a surrogate for soil types, assuming that vegetation/cover types were correlated to soil types. Soil properties for each vegetation type were derived from available sources describing soils in the relevant vegetation types. Baron (1992) was a source of soil texture data for tundra and subalpine forests. Stohlgren (1999) and Binkley et al. (2002) reported soil texture, %N, and %C in soils of grazing exclosures on the elk winter range. Leader (1995) reported soil texture, %N, and %C in soils from montane forests, meadows, and transition areas on the elk winter range. Menezes (2000) reported values of soil texture, %N, and %C in riparian willow communities on the elk winter range. Soil data from other vegetation types was derived from the Larimer County Soil Survey (Moreland 1980). Texture data (percent sand, silt, clay) were the bases for calculating field capacity and wilting points. The resultant soil parameters are shown in Table 1.

The snow submodel adds water to the snowpack if temperature is below freezing. Melting during night and day are modeled individually. The rate of snowmelt is proportional to the difference in temperature above 0° C at night and -1° C in the day. The fraction of melt due to short vs. longwave radiation is calculated based on incoming short and longwave radiation and emmissivities of the surface. The fraction is used to correct snow melt rate for differences in incoming shortwave radiation due to slope and aspect. Water may also be lost from the snowpack through sublimation.

Precipitation is redistributed on the landscape using a topographic similarity index (TSI) (Beven and Kikby 1979, Band et al. 1993, Hartman 1999). Grid-cells in topographic positions with large contributing areas above them are more likely to receive water through runoff, baseflow, or wind redistribution of snow. For each grid-cell, the TSI is calculated as the log of the contributing area above the cell divided by the tangent of the slope. The contributing area map is calculated using the FLOWACCUM procedure in ARC/INFO. The ratio of the TSI at a point to the average TSI for a watershed gives a basis for redistribution of precipitation. A map is calculated that is the ratio of net water input to the water input from precipitation (Figure 19). The map is computed in such a way as to ensure that the total water input to watersheds, or 1 km blocks, equals actual precipitation. The map is contracted to a 500 m resolution by averaging of contiguous cells. During a model run, the map value is multiplied by the precipitation value to compute net precipitation input to a cell.

A simple hydrology model simulates streamflow in a watershed. A watershed map is read into the model. For each watershed, the model tracks the amount of water in a baseflow pool, which is derived from deep drainage (the amount of water draining from the bottom soil layer when it is in excess of field capacity). The baseflow water flows into the stream at a rate calibrated to match general streamflow patterns. Surface runoff, computed as described above, also flows into the stream.

Table 1. Soil parameters. Runoff curve number is a parameter in the SCS runoff curve number approach, with higher values producing more runoff.

Vegetation Type	Herbaceous Rooting Depth - mm	Total Depth - mm	Wilting Point - Vol. H2O % 3 Layers, Top to Bottom	Field Capacity - Vol. H2O % 3 Layers, Top to Bottom	Runoff Curve Number-Good Condi-tion	Soil C - g m^{-2}	Soil N - g m^{-2}
Grassland	1000	2000	8.1,4.3,2.0	12.7,8.4,6.0	50	3950	320
Tundra	500	1000	6.4,6.4,2.0	10.2,10.2,6.0	70	7560	700
Forbland	1000	2000	6.4,6.4,6.4	10.2,10.2,10.2	60	8880	740
Shrubland	1000	2000	8.1,4.3,2.0	12.7,8.4,6.0	50	4800	400
Willow	1000	2000	12.0,11.6,9.0	16.0,24.6,14.0	55	11,300	790
Cotton-wood	1000	2000	12.0,12.0,12.0	26.0,26.0,26.0	85	11,300	790
Aspen	1000	2000	8.1,8.1,8.1	12.7,12.7,12.7	60	10,100	780
Pond. Pine	1000	2000	8.1,4.3,2.0	12.7,8.4,6.0	50	3700	220
Doug. Fir	1000	2000	8.1,4.3,2.0	12.7,8.4,6.0	50	3700	220
Lodgepole Pine	500	1000	8.1,8.0,2.0	12.7,12.5,6.0	65	3700	220
Spruce-Fir	500	1000	8.1,8.0,2.0	12.7,12.5,6.0	65	3700	220
Disturbed	1000	2000	8.1,8.1,8.1	12.7,12.7,12.7	55	2000	160
Unvegetated, Rocks	23	24	0.5,0.5,0.5	1.5,1.5,1.5	95	0	0
Subirrigated	1000	2000	12.0,11.6,9.0	16.0,24.6,14.0	55	4000	350

A)



B)



Figure 19. Topographic precipitation redistribution map. There are no units, as this is a 0-1 scalar. Net precipitation input is the value of this map times actual precipitation. Units are in scientific notation, for example 1.60E-01 means 0.16 and 1.125E-00 means 1.125. A) *Original resolution of 100m.* B) Resolution used in modeling, 500m.

The output is total streamflow volume for that watershed over time. Watersheds for the streams flowing into Moraine Park and Horseshoe Park (Figure 6) were used in model runs, in order to affect riparian zone water tables on the winter range. A map for the entire Big Thompson watershed was used in separate runs to compare model output to streamflow data.

Water table depth is specified by either month for each soil type, or it is tied to streamflow in the watershed using an empirical function. In this application, water table depth is tied to streamflow in two watersheds on the elk winter range - the Moraine Park watershed and the Horseshoe Park watershed. Thus, water table depth in riparian willow habitats in those to parks are affected by streamflow. A summary of the data for water table depths in short and tall willow communities at these two locations is shown in Figure 20. These data are from the recent study of Singer et al. (Singer et al. 1999, 2001a, 2002; Zeigenfuss et.al. 2002). Artificial dams were constructed in some treatments, to examine potential effects of beaver. In Moraine Park, water tables were deepest in tall willow, followed by shallower depths in short willow with dammed streams, and short willow with undammed streams. In Horseshoe Park, the reverse pattern was observed, with deepest water tables in short willow.

In riparian willow and subirrigated vegetation elsewhere, water table depth is specified by month of year, with shallower depths occurring during times of spring runoff. There is a relatively shallow water table in willow and subirrigated habitats on the vegetation map. For "other low elevation willow," I use the mean monthly water table depths observed in Horseshoe Park tall willow (Figure 20b). For "heavily subirrigated" I use the depths observed in Moraine Park short willow (Figure 20a). "Partly subirrigated" water tables are 1 m deep in August-February, decreasing to 0.3-0.5 m deep in spring. Water tables in aspen are assumed to be 1.1 m deep in September-February, decreasing to 0.65 m deep in the spring. Cottonwood water tables decrease from 0.6 m in fall-winter to 0.4 m in spring. In all other vegetation types, the water table is assumed to be too deep to be of any use to plants.

Microclimate and Light

The microclimate submodel simulates windspeed profiles and aerodynamic resistances to water vapor diffusion. These depend upon canopy height, and reference height windspeed. Potential evapotranspiration (PET) and transpiration are calculated using the Penman-Monteith formula (Monteith 1973). PET is derived using Penman-Monteith with zero stomatal conductance. Transpiration is calculated from canopy-scale stomatal conductance. PET and transpiration are affected by radiation, temperature, humidity, and windspeed.

The light submodel simulates shading within and among plant canopies. On tree-covered facets, incident radiation first passes through the tree canopy, then the shrub understory and finally the herbaceous understory. Light extinction follows an exponential decay function (Beer's Law) which is dependent on leaf area index and a light extinction coefficient. The model tracks the relative heights of woody plants in different size/age classes, so for example small or young shrubs and trees will be more shaded than large or old shrubs and trees.

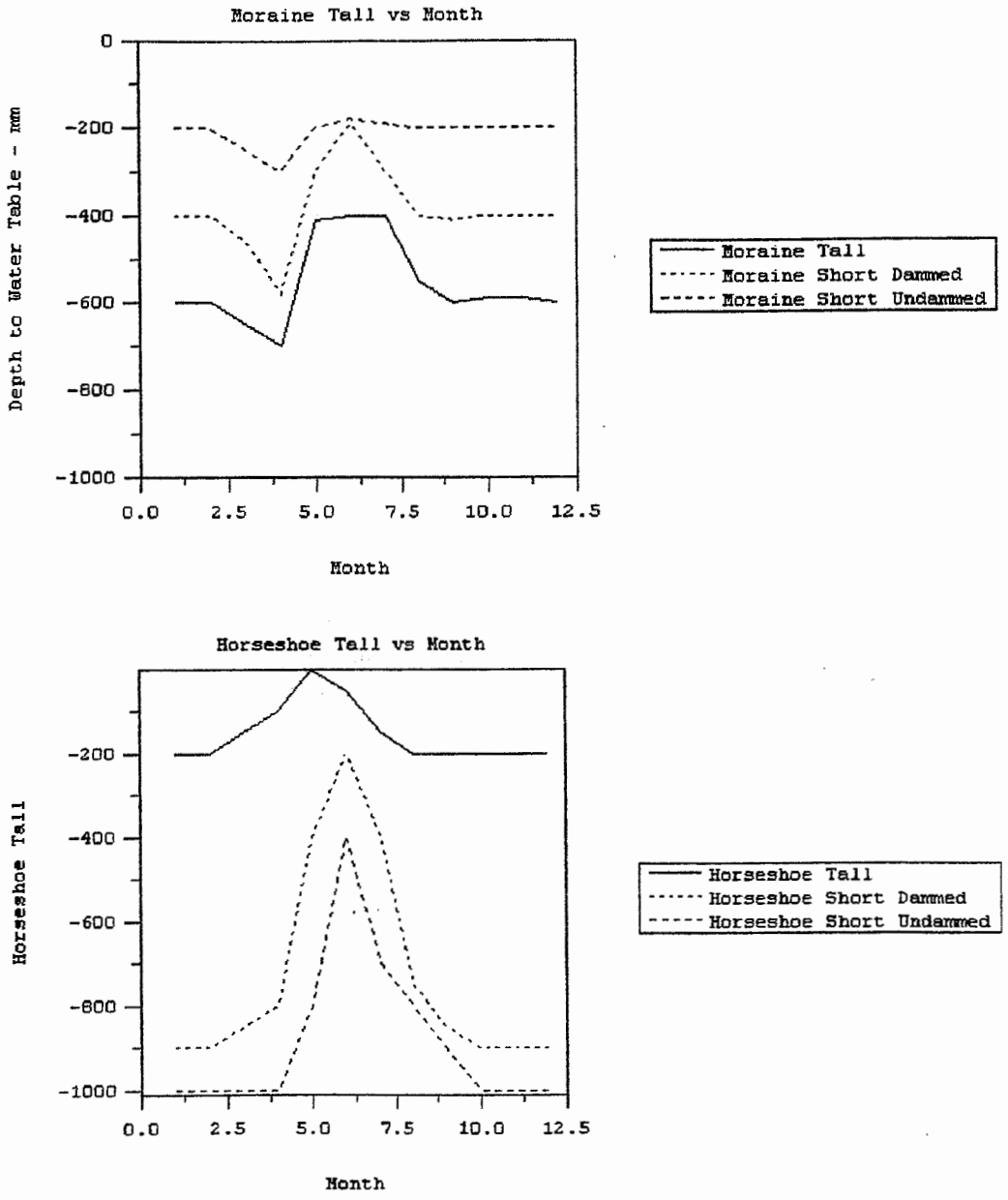


Figure 20. Water table depths as observed (April-October data from Zeigenfuss et al. 2002) and as used in model experiments examining effect of water table depths on willow growth.

Plant Biomass Production

The net primary production (NPP) submodel simulates plant biomass flows and dynamics. Plant biomass production is affected by light, water, temperature, nitrogen and herbivory. The NPP submodel is explicitly linked to the water budget submodel through transpiration and plant water use. Herbaceous biomass is allocated to leaves, stems and roots. Woody plants allocate to leaves, fine branch, coarse branch, fine root, and coarse root. Allocation between fine roots and leaves in both herbaceous and woody plants is influenced by nutrient and water availability, with slightly more allocation to roots when soil resources are limiting. The allocation to various tissues in woody plants depends on plant size. Allometric relationships of allocation versus size are embedded in the biomasses of leaves, fine and coarse stems, and fine and coarse roots, per plant for each of six plant age/size classes. Plant tissues die due to water or temperature stress or phenological stage, and they turn over at a nominal rate that reflects their maximal longevities. Simulated plants maintain a pool of labile carbon, largely consisting of carbohydrates. Early regrowth in the spring or following grazing is supported by this pool, until needs can be met by photosynthesis.

Potential net photosynthesis is calculated as

$$Psl = PAR/\sqrt{(1+(\alpha \times PAR/Psmx)^2)}$$

$$Ps = Psl \times Efwp(Awpet) \times Eftp(Tday) \times Efnp(Pnb)$$

where Psmx is maximal net photosynthesis rate, PAR is photosynthetically active radiation, α is the initial slope of the light response curve, and Psl is light-limited photosynthetic rate. The initial slope α is also equal to the light use efficiency, and the light response asymptotes at saturating light intensities. The 0-1 function Efnp describes how *Ps* decreases as plant nitrogen concentration (*Pnb*) decreases. The 0-1 function Efwp reduces *Ps* due to water stress. *Awpet* is the ratio of available water ($mm\ d^{-1}$) to potential evapotranspiration ($mm\ d^{-1}$). Eftp is a bell-shaped temperature effect, generated from optimum, minimum, and maximum temperatures for photosynthesis.

After potential photosynthesis is calculated, stomatal conductance is calculated based upon the equation of Ball et al. (1997), in which stomates open wider as photosynthesis (Ps) and humidity (H) increase, and as atmospheric CO_2 (C) decreases.

$$g_s = e_0 + e_1 \times (Ps \times H/C)$$

From stomatal conductance, atmospheric water vapor pressure deficit, windspeed, and radiation, the model uses the Penman-Monteith approach to calculate transpiration. From transpiration and net photosynthesis, the model calculates water use efficiency.

Root water uptake to supply transpiration demand is allocated among soil layers in proportion to the products of available water and root biomass in each layer. The water demands for competing plants are summed, and if total demand exceeds supply, water is allocated among species in

proportion to demands. Photosynthesis is then recalculated from water use using the water use efficiency calculated above. Thus, plants rooted in the same soil layer compete for water, but when water is limiting, it is allocated among species in proportion to their demands. The demand for water in a layer depends on transpiration rate, and the proportion of roots and water in that layer

Parameters affecting photosynthesis and stomatal conductance are shown in Table 2. Some parameters were based upon previous modeling of N. American temperate grasses (Coughenour and Chen 1997). Values are set with reference to the generic values for plant functional groups in Woodward and Smith (1994). Shrub ecophysiology was parameterized largely based upon information for sagebrush (Doeschler et al. 1990, DeLucia and Heckathorn 1989, DeLucia and Schlesinger 1991, Branson et al. 1976, Fetcher 1981). Conifer parameter values were based upon Fahey et al. (1985), Pearson et al. (1987), Day et al. (1989), Prescott et al. (1989), DeLucia and Schlesinger (1991), Levernz (1995), and Ryan et al (1996). Peinetti (2000) and Peinetti and Coughenour (2001) used ecophysiological data of Alstad et al. (1999), Peinetti (2000) and other sources to parameterize willow. Weisberg (2000) parameterized aspen based on Bartos and Johnson (1974), Bonan (1993), and Kubiske et al. (1997).

Photosynthate is allocated between roots and shoots to preserve a functional balance in herbaceous plants, and allometric relationships in woody plants. Phenology and water affect shoot:root partitioning, with an increased fraction being diverted to roots in later phenophases, and under higher water stress. In woody plants, allocation is more complex due to differences in allometry (ratios among tissue types) among size classes. Allocation varies to preserve the proper allometric relationships. Allometry data for willow were developed by Peinetti (2000), based on original data, and data of Zeigenfuss et al. (1999, 2002), and Cannell (1987). Allometry parameters for upland shrubs were based upon sagebrush data reported by Sturges and Trlica (1978), Branson et al. (1976), and Fetcher (1981). Aspen allometry was parameterized by Weisberg (2000). Coniferous tree allometries were parameterized from information in Brown (1978), Keane et al. (1989), Kerr and Smith (1955), Dale et al. (1986), Knight (1991), Kaufman et al. (1982), and Vogt (1991). Allometry parameters for one size class of woody functional groups are shown in Table 3.

Respiration is separated into growth and maintenance components. Maintenance respiration depends upon nitrogen concentration (Ryan 1991), and temperature. Due to high biomass, maintenance respiration in woody plants can outstrip carbon supply, so must be limited to 50% of available photosynthate.

Plant tissues senesce at rates affected by water stress, temperature, and phenology. Shoot tissues (leaves and stems of herbs and shrubs, leaves of trees) are transferred to "standing dead" upon senescence. Then the standing dead falls to "litter" on the soil surface. Dying roots are transferred directly to belowground "litter". Plant tissue senescence rates, and transfer rates from standing dead to litter are calibrated to match observed biomass dynamics, and ratios of live to dead shoot tissues. Root turnover rates are based on previous modeling experience (Coughenour and Chen 1997, Parton et al. 1997, 1993), which are in turn based on data from comparable species.

Table 2. Key plant ecophysiological parameters, and digestibility for ruminants. *denotes a series of x,y pairs defining function. For example, 0,0,0.1,1.0 means that when x is 0, y is 0, and when x is 0.1, y is 1.0, where x is the variable causing the effect (eg. RWC). When x is greater than the maximum x specified (.1 here), then y equals the maximum y specified (1.0 here). Similarly when x is less than the minimum x specified, y equals the minimum y specified. In the case of an 0-1 "effect" function, the resultant 0-1 effect is multiplied by the maximum rate.

Parameter	Dryland Grass	Dryland Forb	Mesic Grass	Mesic Forb	Upland Shrub	Willow	Aspen	Mont Conif.	Subalp. Conif.	Alpine Herb
Maximum photosynthesis rate μmol m^{-2} s^{-1}	16	16	18	16	16	15	25	12	12	16
Initial slope of photosynthetic light response curve μmol CO_2 $mmol^{-1}$ quanta	86	86	86	86	300	29	30	30	30	86
Max, min, opt temperatures for photosynthesis °C	35,2,20	35,2,20	35,2,15	35,2,15	4,0,18	39,2,15	36,-2,18	30,-5,12	30,-5,12	35,0,15
Effect of water (RWC) on photosynthesis*	0,0, 0.1,1	0,0, 0.1,1	0,0, 0.4,1	0,0, 0.4,1	0,0, 0.1,1	0.3,0.4, 0.5,1	0,0, 0.25,1	0,0, 0.3,1	0,0, 0.3,1	0,0, 0.1,1
Stomatal conductance parameter (e_1) mol m^{-2} s^{-1}	9	9	15	15	9	8	14	10	10	9
Specific Leaf Weight g m^{-2}	90	90	100	100	167	75	82	110	107	120
Effect of water (RWC) on fraction of Ps allocated to roots	0,1, 0.8,0.8	0,1, 0.8,0.8	0,1, 0.8,0.8	0,1, 0.8,0.8	0,0.5, 0.8,0.3	0,0.15, 0.8,1	0,0.15, 0.8,1	0,0.3, 0.8,1	0,0.3, 0.8,1	0,0.9, 0.8,0.6
CAG Leaf:Twig					1.0	1.3	0.876	0.80	0.70	
Max, min leaf N:B ratio	0.02, 0.0085	0.025, 0.0081	0.027, 0.011	0.028, 0.009	0.025, 0.012	0.0375, 0.022	0.026, 0.018	0.012, 0.008	0.012, 0.008	0.026, 0.018
Dead leaf N:B ratio	0.0081	0.0081	0.0085	0.009	0.007	0.008	0.008	0.0045	0.0045	0.0065
Current annual growth twig N:B ratio					0.007	0.007	0.0123	0.0036	0.0036	
Maximum and minimum leaf death rates due to water stress d^{-1}	0.033, 0.0075	0.033, 0.0075	0.033, 0.0075	0.033, 0.0075	0.012, 0.0015	0.003, 0	0.01, 0.001	0.00022, 0.00022	0.00022, 0.00022	0.33, 0.0075
Transfer rate from standing dead to litter d^{-1}	0.0016	0.006	0.0016	0.006	0.05	0.03	0.05	0.05	0.05	0.003

Table 2 continued.

Minimum, maximum green leaf digestibility	0.42, 0.71	0.27, 0.77	0.42, 0.71	0.45, 0.75	0.45, 0.70	0.35, 0.55	0.40, 0.45	0.35, 0.35	0.35, 0.35	0.42, 0.71
Dead leaf digestibility	0.42	0.45	0.42	0.45	0.45	0.50	0.50	0.35	0.35	0.42
CAG twig digestibility					0.50	0.49	0.45	0.30	0.30	

Table 3. Morphometric parameters for woody plants in 5th largest size/age classes (of 6).

Parameter	Upland Shrub	Willow	Aspen	Montane Conifer	Subalpine Conifer
Height -m	0.4	3.4	14.0	25.0	25.0
Crown diameter - m	0.67	2.95	3.35	5.5	5.5
Stem diameter - mm	not used	not used	262	514	413
Leaf - kg	0.105	1.0	4.38	24.8	24.6
Total stem and branch - kg	0.6	6.9	169	394	727
Fine branch - kg	0.16	4.13	1.6	39.4	72.7
Total roots - kg	0.168	5.0	36.0	148.0	276.0
Fine roots - kg	0.081	1.0	4.38	12.4	24.6
Fine root density - g m^{-2}	230	146	497	518	932

Plant Populations

Plant population submodels simulate plant establishment, size, and mortality. The woody plant population model represents six age/size classes of plants. Plants are promoted to subsequent age/size classes if they reach a certain age, and they are of a certain size. Woody plant establishment and mortality can both be set to zero to effectively turn off this section of the model, leaving plant densities fixed. For purposes here, only willow and aspen population dynamics were simulated. Population sizes of upland shrubs, pine, and other conifers were assumed to be constant. Establishment rate is affected by water and temperature, and woody cover. As cover increases, establishment rate declines to reflect effects of shading and competition for space and soil resources. Woody establishment is also affected by herbaceous biomass, to represent competition between seedlings and herbaceous plants. Because woody establishment only occurs on the herbaceous (non-woody) facet, when a closed forest is simulated, establishment will only occur in gaps, or openings resulting from tree death. Parameters affecting woody plant population dynamics are shown in Table 4.

In the case of herbaceous plants, the model represents an index of basal cover measured in units of potential shoot biomass. This index of basal cover increases if simulated root biomass becomes large relative to the value expected for the current basal cover. The basal cover index decreases when root biomass is at low values relative to the root mass expected for the current basal cover. Shoot production in a given year cannot exceed the amount expected for the current basal cover. In this way, the model simulates degradation, or a loss of potential production, due to overgrazing or climatic stress. Likewise, it simulates a gradual recovery of potential production under good growing conditions. Values for this function are given in Table 5 (vegetative growth rate vs. shoot:root ratio).

A micro-scale disturbance regime is imposed on herbaceous plants. Plants are killed at a specified rate (fraction of plant cover per year) to simulate disturbances due to other herbivores (e.g., small mammals, insects), or humans. Disturbance rates were set to 0.05 yr^{-1} for managed grasslands, 0.075-0.1 yr^{-1} for native communities, and 0.15 yr^{-1} for disturbed lands. An exogenous seed rain replenishes herbaceous plant populations (basal area). The composition of the seed rain is assumed to be invariant, and is usually assumed to have the same composition as initial conditions. The seed rain is expressed in the same units as basal cover, in grams of shoot biomass. These values of g m^{-2} shoot biomass are then multiplied by the exogenous seed-based reproduction rates in Table 5. An endogenous seed-based reproductive rate is also modeled in which the reproduction rate is multiplied by potential shoot biomass.

Vegetation Management

Some vegetation types outside the national park are managed through the addition of water, fertilizer, and mowing. These types include golf courses, lawns, and improved pastures. For these, a rate of water input is specified in mm $month^{-1}$, a rate of fertilizer N input is specified in gN m^{-2}

Table 4. Plant population model parameters for willow and aspen, for the 5th size/age class. Population dynamics of the other woody species are not simulated. * indicates x,y pairs defining a function (see Table 2 caption).

Parameter	Aspen	Willow
Establishment rate - mo^{-1}	0.06	0.005
Effect of water (RWC) on establishment*	0.99,0.,1.0,1.0	0.8,0.2,1.0,1.0
Suckering rate per dying stem (plants $plant^{-1}$)	0.35	0
Suckering rate per cut stem (plants $plant^{-1}$)	0.35	0.125
Effect of woody cover (fraction) on establishment *	0.4,1.0,0.6,0.0	0.2,1.0,0.3,0.3,0.9,0
Nominal plant mortality rate yr^{-1}	0.008	0.009
Fraction plants killed vs. fraction stems (willow) or CAG (aspen) browsed*	0,0,1.0,0.2	Not used
Fraction saplings killed vs. fraction stems (willow) or CAG (aspen) browsed*	0,0,0.082,1.0	0,0,0.85,1.0

Table 5 Population parameters for herbaceous plants. * denotes x,y pairs defining a function (see Table 2 caption)

Parameter	Dryland Grass	Dryland Forb	Mesic Grass	Mesic Forb	Alpine Herb
Endogenous seed-based reproduction yr^{-1}	0.01	0.015	0.02	0.015	0.1
Exogenous seed-based reproduction yr^{-1}	0.01	0.01	0.02	0.015	0.02
Vegetative growth rate vs. Shoot:Root ratio*	0.25,-0.15, 1.0,0.1 1.25,0	0.25,-0.15, 1.0,0.08 1.25,0	0.25,-0.1, 1.0,0.15 1.25,0	0.25,-0.05, 1.0,0.05 1.25,0	0.25,-0.05, 1.0,0.05 1.25,0
Effect of herbaceous root biomass on establishment*	300,1,1000,0	300,1,1000,0	700,1,22000,0	700,1,2200,0	300,1,1000,0
Fraction of plant killed vs. fraction grazed*	0,0,1,0.15	0,0,0.75,1.0	0,0,1.0,0.05	0,0,1.0,0.2	0,0,1.0,0.15

month^{-1}, and a cutting regime is specified as a biomass density to cut to. When grass is cut, phenology is reset to a juvenile stage, which in turn maintains a high leaf nitrogen concentration in the green regrowth, to the extent that it regrows. Golf course grass is assumed to be fertilized with 20 g N m^{-2} yr^{-1} and irrigated with 1400 mm water yr^{-1}. Other domestic lawns are assumed to be irrigated with 90 mm water yr^{-1}. Golf courses are assumed to be mowed to 150 g m^{-2} year around.

Litter Decomposition, N Cycling, and Soil Organic Matter Dynamics

A decomposition and N cycling submodel simulates the breakdown of dead plant materials and animal feces and urine, and the formation and turnover of soil organic matter (SOM). The decomposition submodel is based upon the CENTURY model (Parton et al. 1987, 1993). Dying plant tissues are divided into fast (metabolic) and slowly (structural) decomposing litter, as well as fine and coarse branches and roots. The fractionation between metabolic and structural litter depends upon the ratio of lignin to nitrogen in the dying tissues. As lignin increases and nitrogen decreases, the fraction partitioned to structural litter increases. The two litter fractions are decomposed at rates that depend upon soil moisture and temperature, with faster decomposition rates under warm, wet conditions (Parton et al. 1987). A fraction of the decomposed carbon is respired by microbes. Nitrogen is released during decomposition to mineral forms that can be taken up by the plants or incorporated into the active SOM pool. Three SOM pools having different turnover rates are simulated. Decomposing metabolic litter flows to active SOM and respiration, while decomposing structural litter flows to the active and resistant pools and respiration. Decomposing active SOM flows to the intermediate and slow turnover SOM pools. Decomposing intermediate SOM flows to active and slow SOM pools, and respiration. Decomposing slow pool SOM flows to the active pool, and respiration. Inorganic nitrogen (ammonium and nitrate) is released upon decomposition if substrate nitrogen concentration is higher than the N concentration of microbial biomass. Mineral N is taken up from the soil if substrate nitrogen concentration is lower than microbial N concentration. Parameters for the decomposition model are taken from Parton et al. (1987, 1993).

Nitrogen consumed by herbivores is recycled as either urine or feces. It is assumed that 50% of N flows to feces and 50 % to urine. The undigestible fraction of carbon intake flows to feces. Fecal C and N are partitioned to structural and metabolic litter. Urine N flows to inorganic N (ammonium).

Nitrogen enters the system through atmospheric wet and dry deposition and biotic fixation, and it leaves the system through denitrification and the volatilization of ammonia from urine. Denitrification losses are simulated as a 5% fraction of N gross mineralization, as in Parton et al. (1987, 1993). Nitrogen lost to urine volatization is assumed to be 20% of urine N. N deposition from precipitation and the atmosphere is based on data from the National Atmospheric Deposition Program data from their Beaver Meadows site (data obtained from NADP web site). There are 0.21 gN m^{-2} input irrespective of precipitation, and an added 0.0033 g N per mm precipitation. Biotic fixation is modeled as a function of annual precipitation, as in Parton et al. (1987, 1993).

An added amount of N input to riparian and water subsidized communities was necessary to support observed levels of plant growth. This N likely is transported into the system as N dissolved

in ground or stream water. The N could originate from precipitation, and leacheate from upstream soils. The additional N requirement is consistent with findings of Menezes (2000) who showed N inputs from stream water to willow based on ^{15}N stable isotope concentrations in plants, soil, and stream water. An amount of 0.5 g N m^{-2} yr^{-1} was necessary for willow and heavily subirrigated vegetation, 0.35 g N m^{-2} yr^{-1} was needed for aspen, and 0.25 g N m^{-2} yr^{-1} was needed for partly subirrigated sites.

Plant nitrogen uptake is represented using an equation that specifies a maximal uptake rate per gram of root tissue. The uptake rate is reduced at low soil N concentrations using a Michaelis-Menton function. Only mineral N is taken up, i.e., the N released during decomposition of litter and soil organic matter, and assumed to be ammonium and nitrate. Competition for soil N is calculated when the total plant demand exceeds supply. As with water, uptake is then allocated among competitors in proportion to demands.

Plant nitrogen is regulated within bounds by curtailing uptake as plant N concentration increases to the maximum value. Nitrogen in green leaves is calculated based on phenology. In most plants, young leaves have a higher N concentration than old leaves. N in dying plant tissues is transferred to litter based on a specified N concentration of dying tissues. Because the N concentration of dying tissues is usually lower than that of the live plant, N is effectively conserved through retranslocation when tissues die.

Parameters for plant N concentrations are given in Table 2. Values for live and dead leaf N concentrations for herbs and upland shrubs are taken from Hobbs (1979), Singer et al. (2001a, 2002), and Zeigenfuss et al. (1999, 2002). Values for willow N were parameterized by Peinetti (2000), from original data, Menezes (2000), and Thilenius (1990). Values are consistent with those of Zeigenfuss et al. (2002). Aspen tissue N concentrations were parameterized by Weisberg (2000) from multiple sources. Conifer N concentrations were based on Fahey et al. (1983), Pearson et al. (1987), Prescott (1989), Doescher et al. (1990), and Ryan (1996).

Herbivore Forage Intake

Herbivore forage intake is determined by diet selection, forage quantity and quality, and snow cover. Forage intake rate responds to forage biomass according to a functional response (Holling 1959, Caughley and Lawton 1975). As forage biomass increases, forage intake rate increases, with intake rate eventually reaching a maximal value. Here, the functional response is approximated as a linear function (Table 6). Forage intake rate is also affected by snow depth. Above a certain depth, intake rate declines linearly with increasing depth, until it reaches zero. The effect of snow depth is only applied to that fraction of the plant that is covered by snow. Thus, for that portion of the woody plants extruding above the snow, snow depth has no effect.

Animals choose among available plant types and tissues to achieve a preferred diet composition. Diet composition is determined by using preference weightings, similar to Ellis et al. (1976). In this approach, diet composition is affected by the relative availabilities of different forage

Table 6. Parameters affecting the forage intake and energy balance of the herbivores. * denotes x,y pairs defining a function (see Table 2 caption). In the case of an 0-1 "effect" function, the resultant 0-1 effect is multiplied by the maximum rate.

Parameter	Elk	Deer	Beaver
Maximum forage intake rate kg kg^{-1} d^{-1}	0.031	0.025	0.09 (herbs) 0.08 (woody)
Effect of forage biomass (g m^{-2}) on intake rate*	0,0, 60,1	0,0, 17,1	0,0, 20,1
Effect of snow depth (cm) on intake rate*	20,1, 80,0	15,1, 42,0	0,0, 5,0 (effect on herb intake only)
Reach height (m)	2.25	1.5	unlimited due to cutting
Effect of forage digestibility on intake*	0.3,0.75, 0.6,1	0.3,0.75, 0.6,1	not used
Body sizes - newborn, yearlings, mature female, mature male (kg)	114,162,240,330	30,45,65,90	1,5,24,24
Minimum and maximum energy use rates (MJ kg^{-1} d^{-1})	0.12, 0.16	0.1,0.21	0.247,0.412
Effect of condition on energy use rate*	0,0, 0.5,1	0.1,0, 0.5,1	0.1,0, 0.5,1
Gestation costs	as in Robbins (1983), Hobbs (1985)	as in Robbins (1983), Hobbs (1985)	not used
Travel costs	based on time and movement rate, as in Hobbs (1985), equation of Robbins (1984)	not used	not used
Hours spent traveling by month	0.9,0.9,1.1,1.1,1.1,3.1, 3.1,3.1,0.9	not used	not used
Hours spent eating by month	11,11,11.5,12,13,13.5,14, 13,13,12,11.5,11	not used	not used
Walking rates while traveling and feeding m min^{-1}	50,1.5	not used	not used
Lower critical temperature for thermoregulation °C	-10	not used	not used

types as well as by herbivore preferences. This ensures that diet flexibly responds to temporal and spatial changes in the mixture of available forage. Preference indices in the dietary selection model were calibrated so that the diets of elk were similar to those reported by Riorden (1948, cited in Stevens 1980), Baker and Hobbs (1982), Hobbs et al. (1981), Stevens (1980), and Singer et al. (2002). Deer diet selection was calibrated to attain diets similar to those observed by Stevens (1980).

When herbivores consume plant tissues plants may also die. Death of plants is distinct from death of tissues. Thus, while aboveground tissues may be eaten, the plant may still be alive due to uneaten above- and belowground tissues. Plant mortality is expressed as a function of the fraction of the shoot biomass that is eaten. Seedlings of woody plants are more susceptible to browsing than established individuals.

The distribution of browsing over woody size classes is determined from plant height and animal reach height. Plants with canopy bottoms above the reach heights of the herbivore are unavailable. The fraction of plant biomass buried by snow varies with plant type. Browsing is apportioned among size classes in proportion to available biomass.

Beaver impacts on woody plants are treated differently than ungulate impacts due to the fact that they cut stems at the base. Beaver herbivory on leaves, current annual growth twigs and fine branches is calculated in the same way that ungulate herbivory is calculated. However, a significant amount of biomass, especially coarse branch, is wasted, i.e., not eaten. The amount wasted is derived from the allometry of tissue types on each size class of plant that is eaten. For example, if a certain amount of leaf is eaten from a willow size class, then an allometric matching quantity of coarse branch is felled, and transferred to coarse wood litter. The plant, or fraction of plant, is not necessarily killed, but may resprout. Resprouts are added back to the youngest age/size class, and the allometric root biomass for the youngest size class is protected from death. The remainder of the root biomass is transferred to belowground litter.

Maximum intake rates for elk are based on Watkins et al. (1991). They found an 0.027 kg kg^{-1} d^{-1} intake rate for a 200 kg elk, and a 0.031 kg kg^{-1} d^{-1} intake rate for a 150 kg elk. These values must be adjusted upwards to compensate for the reducing effect of forage digestibility in the model. The functional response for elk was based on Wickstrom et al. (1984) and Hudson and Watkins (1986), but their values for the forage biomass at half-saturation proved to be too low to be workable in RMNP. Consequently, this value was calibrated, but to a value that is still biologically reasonable. The effects of snow depth on forage intake are poorly studied, but a synthesis of data suggest that intake declines above 20 cm, and become severely constrained by 75 cm (Cassier and Able 1990, Coughenour 1994). Maximum forage intake rate of deer was set on the high side of observed values, to offset the simulated reduction due to digestibility and the suboptimal forage biomass in field trials. Walmo et al. (1977) found 1.7-2.1 kg $kg^{-1}d^{-1}$. Hobbs (1989) used 1.7 kg $kg^{-1}d^{-1}$ based on data from Alldredge et al. (1974), who in turn found a range of 1.5-2.3 kg $kg^{-1}d^{-1}$. Based on 2.22 g min^{-1} and 16 hr feeding (Hobbs 1989, Wickstrom et al. 1984), a value of 3.2 kg $kg^{-1}d^{-1}$ is derived. The functional response for deer is variable in the literature, ranging from a half saturation at 2 g m^{-2}

(Wickstrom et al. 1984) to a value of 15 g m^{-2}, derived from a scaling relationship between body size and maximal forage intake (Kshatryia 1999). A median value was used. The maximum forage intake of Beaver was set based on data in Aleksiuk and Cowan (1969a,b), adjusted upwards slightly to account for less than optimal conditions for foraging in their experiment. The value describing the functional response was based on body size and maximal forage intake rate (Kshatryia 1999).

Herbivore Energy Balance

The herbivore energy balance submodel simulates body weight of the mean animal of each herd or subpopulation, based on differences between energy intake and energy expenditure. Energy intake depends on forage biomass intake and forage digestibility. Expenditures depend on body weight and travel patterns. The body weight of the mean animal is used to derive an animal condition index, which affects ungulate population dynamics. Metabolizable energy intake from forage consumption is the product of kg total forage intake per animal per day, the mean digestibility of the forage, the gross energy content of digestible plant matter, and its metabolizability.

The energy balance model is partly based upon the models of Coppock et al. (1986) and Hobbs (1989). Energy requirements consist of a "base cost" metabolic energy demand per unit body weight per day and added energetic costs of activity, growth, thermoregulation, gestation, and lactation. A minimum and maximum energy requirement is specified, with the minimum corresponding to a resting metabolic rate. The maximum includes energy for activities. The model lets energy use vary between the minimum and maximum in relationship to condition index. If the condition index is high, animals use more energy on activity. If condition index is low, animals conserve energy by reducing activity. If energy intake exceeds requirements, then the animals convert the excess energy to fat. If energy intake is less than requirements, the deficit is drawn from fat reserves.

Animal condition index is a number that varies between 0.0 and 1.1, and is calculated as the ratio of kg's below maximum body weight to the difference between maximum and minimum body weights (kg). At condition index 0.0, animals are at the minimum weight while at condition index of 1.0, animals are at maximum weight. Condition index can increase slightly above 1.0 to allow forage intake to continue above maximum body weight. However, above 100% of maximum body weight, forage intake rate is reduced due to satiation.

Metabolic energy costs for elk were based on prior analyses of Hobbs (1982) and Watkins et al. (1991). Hobbs' calculations result in approximately 0.19 MJ kg^{-1} d^{-1}, including all activity costs. Watkins' data suggest 0.12-0.16 MJ kg^{-1} d^{-1} for resting and standing animals. Since activity costs of traveling are calculated separately, I used a range of 0.12-0.16 MJ kg^{-1} d^{-1}. Thermoregulatory costs are based on lower critical temperature and thermal conductance values given by Parker and Robbins (1985). Gestation costs are based on the equation of Robbins (1984), and also used by Hobbs (1985), where the cost is a function of body size and stage of gestation. Travel costs per unit distance are based on the function of body weight of Parker and Robbins (1984). Distance traveled is computed from time budget and speed of movement while traveling and feeding at 50 m s^{-1} and 1.5 m s^{-1}

respectively. Hours per day spent traveling are from Craighead et al. (1973), while hours spent eating are from Green and Bear (1990). Energy budgets of deer are more simply modeled, as costs of traveling, and thermoregulation are not distinguished. A total energy cost is estimated based on numerous sources. The Hobbs (1989) model for white-tailed deer gives 74 kcal $kg^{0.75}$, which is 0.12 MJ kg^{-1} d^{-1} for a 60 kg deer in severe winter, and 0.098 MJ $kg^{-1}d^{-1}$ for just a lying cost. A range of values of 82-140 kcal $kg^{0.75}$ is reported by Mautz and Fair (1980). The upper limit corresponds to a maximum of 0.21 MJ kg^{-1} d^{-1} for a 65 kg deer.

Herbivore Population Dynamics

The herbivore population dynamics submodel is an age-sex class model with one age class for each year, for each sex. Recruitment rates and death rates are affected by animal condition indices. Recruitment rather than birth is simulated, because very early calf/fawn survival rate is not distinguished. As condition index increases, recruitment rates increase and death rates decline. The effect of condition index on recruitment rate is multiplicative. For example, a condition index of 0.2 might reduce recruitment rate to 35% of the maximum. The effect of condition on death rate supercedes the nominal death rate if it is larger. The effects of condition index represent population responses to ecological conditions governing forage availability (e.g., forage production, snow depth) and intra- and interspecific competition. As competing animals can reduce forage supply, forage intake rate, and thus body condition, they can consequently reduce population growth rate of the species in question. The equation for recruitment is

$$\text{Recruit} = \sum \text{Female}_i \times \text{Birthrt}_i * F(CI_{gest})$$

where Recruit is number of surviving newborns in the season, Female_i is the number of females in age class i, Birthrt_i is the maximum birth rate by age class (Table 7), and CI_{gest} is the condition index averaged over the period of gestation. The functions of CI_{gest} are shown in Figure 21. The equation for deaths is

$$\text{Deaths}_i = \text{Animals}_i * \max[\text{Deathrt}_{Nom}, \text{Deathrt}_{CI}]$$

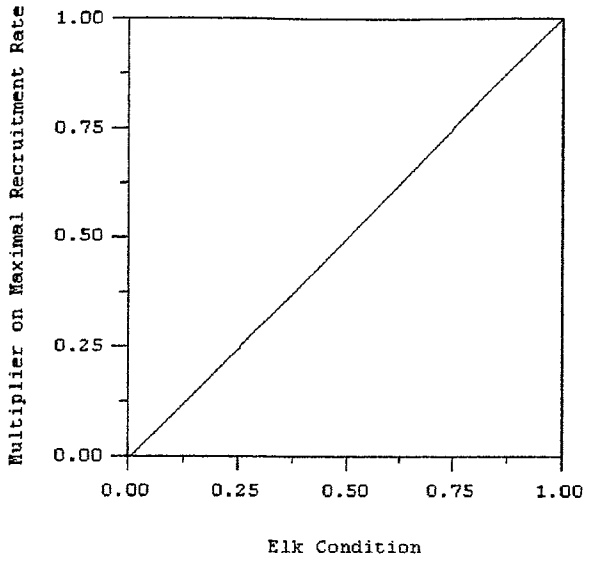
where Deaths_i is the number of animals dying in age class i, Animals_i is number of animals in age class i, Deathrt_{Nom} is the nominal death rate (Table 7), and Deathrt_{CI} is the death rate as a function of body condition (Figure 21).

Animals can be removed in a rule-based manner. A removal will occur at a specified "trigger" population size, to reduce the population to a specified "target" number. Removals can also be prescribed with an observed number of animals per year, or an observed fraction of animals per year. This latter option was used to simulate observed population dynamics. Elk reduction data for the park elk herd and mule deer population for 1939-1978 were obtained from Stevens (1980). Data for hunter harvest in Game Management Unit (GMU) 20 for 1983-1996 were obtained from Colorado Division of Wildlife. Unfortunately, it is unknown what fractions of the deer and elk harvested by sport hunters in GMU 20 are derived from the populations which winter in the park or

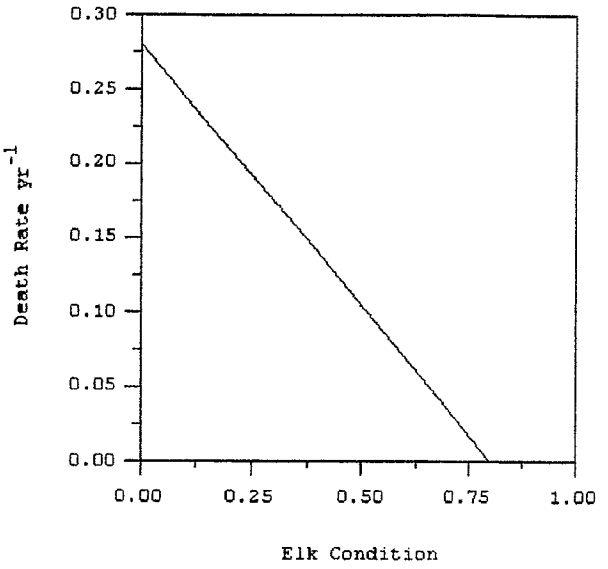
Table 7. Population parameters for elk and mule deer. Age class 1 refers to animals 0-1 years old, 2 refers to 1-2 years old, etc. Maximum survivorship is the fraction of animals that survives to that age class. Maximum birth rate is births per female per year.

Age	Elk			Mule Deer		
	Maximum survivorship - females	Maximum survivorship - males	Maximum birth rate	Maximum survivorship - females	Maximum survivorship -males	Maximum birth rate
1	0.929	0.929	0	0.88	0.88	0
2	0.929	0.929	0.08	0.97	0.97	0.75
3	0.929	0.929	0.74	0.97	0.97	0.75
4	0.929	0.929	0.88	0.97	0.97	0.75
5	0.929	0.929	0.88	0.97	0.97	0.75
6	0.929	0.929	0.88	0.93	0.93	0.75
7	0.929	0.755	0.88	0.88	0.88	0.75
8	0.929	0.787	0.89	0.83	0.83	0.75
9	0.929	0.735	0.89	0.70	0.70	0.75
10	0.929	0.700	0.80	0.45	0.45	0.75
11	0.929	0.670	0.75	0	0	0.75
12	0.929	0.600	0.75			
13	0.929	0.500	0.75			
14	0.929	0.435	0.75			
15	0.929		0.75			
16	0.882		0.75			
17	0.830		0.75			
18	0.747		0.75			
19	0.700		0.75			
20	0.700		0.75			
21	0		0.75			

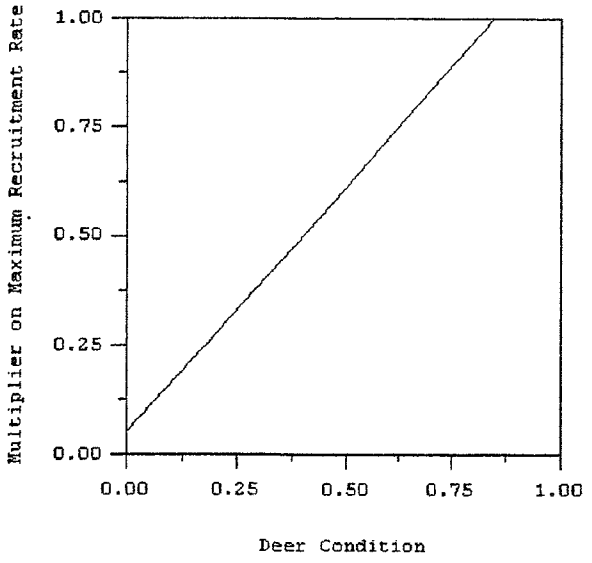
A)

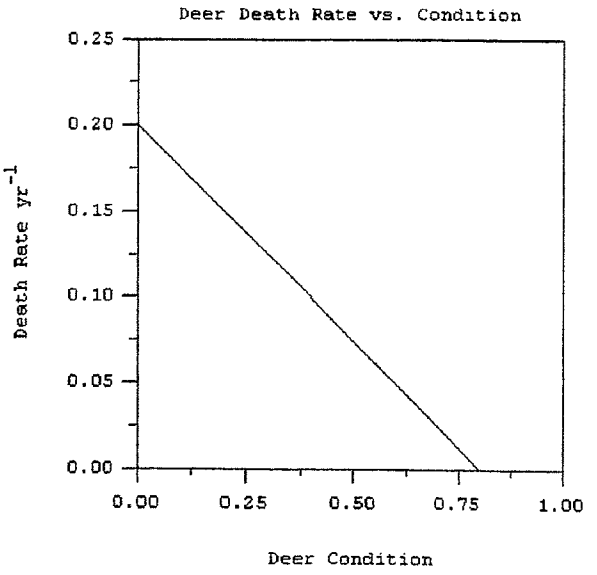


B)



C)





D)

Figure 21. A) Effect of condition index on elk recruitment rate, B) elk mortality rate vs. condition index, B) effect of condition index on deer recruitment rate, and D) deer mortality rate vs. condition index.

town elk ranges. There were many elk and deer wintering outside the park/town range, largely in the National Forest, throughout this period, and this is where the hunting occurred. GMU 20 is very large, extending from the continental divide, to the eastern boundaries of the towns of Loveland and Fort Collins, and from the northern boundary of the park to the southern boundary of the town of Longmont. The large number of deer and elk that were harvested could not have entirely come from the herds which winter inside the park or in the town of Estes Park. For example, there were many years where the reported deer harvest exceeded the number of deer estimated to be on the park winter range. There were very few elk wintering in town in the 1970s, yet Stevens (1980) reports sport harvests from GMU 20 of an average of 203 per year from 1969/70 through 1978/79. Furthermore, it appeared that "hunting, although significant along the park boundary, probably affects the overall herd, but would not appear to have much effect on the numbers wintering within the park" (Stevens 1980). Model results to be presented below support this statement. It, therefore, seems most likely that hunter harvests prior to the time when elk began to winter in the town in significant numbers were primarily from herd segments which neither wintered in the park, nor in the town, but elsewhere in Roosevelt National Forest. For this reason, I did not apply the harvest data reported by Stevens for 1939-1978 to the park herd segment. I only applied the number taken out by direct management reductions (e.g., 340 removed from within the park in 1949-1950). It was assumed that no animals wintered in town prior to 1968 (see below), so the harvest data prior to that time were simply not used. Given the fact that the town herd was probably very small through the 1970s, the uncertainty of how many of the sport harvested animals would have come from that small herd, and the strong likelihood that this fraction probably varied during that time, I made the following simplifying assumptions. Between 1988-1999, when count data for the town herd are available, the annual sport hunt from GMU 20 was on average 20% of the size of the town herd. I assumed this value of 20% could be used to calculate a recalled sport harvest for 1969-1987, which is the size of the sport harvest adjusted for the growth of the town herd over that time. Thus, I assumed that the recalled harvest was 20% of the number of animals simulated in the town herd. For the years 1988-1998, I used the actual rate, i.e., the actual harvest divided by the size of the town herd. As explained above, rates rather than actual numbers were used in the model. The model used the rates to calculate the size of the harvests from GMU 20. Finally, only a fraction of the GMU harvest was likely to have come from the town herd, and it was assumed that none of it came from the park herd. The fraction that comes from the town herd could only be derived by model fitting. Lubow et al. (2001) used this procedure to estimate that 35% of the harvest was from the town herd. I found this estimate to be too high, given the other values of the elk model parameters that fit the park herd dynamics. Through model fitting, I found that only 16% of the GMU 20 harvest could be supported by the town herd. To put this in context, the average annual harvest 1988-1998 was 269. Thus, the difference between 35% and 16% is 51 elk per year compared to a mean herd size of 1,572.

Emigration rate can be specified in terms of a certain fraction of the population per month. Emigrators from a source population can be directed into another simulated population, or they can be removed from the herd and not put into any other herd, thereby representing their dispersal out of the simulated study area. For the purposes of this study, elk from the park herd were assumed to disperse to the town herd, while animals from the town herd were only assumed to disperse out of the simulated study area. There was assumed to be no flow of animals from the town herd back to

the park herd. The emigration was assumed to begin in 1968, at the time of cessation of reductions within the park. Monthly emigration rates of 0.0055 and 0.01 for yearling females and males were found by fitting the model to the park and town herd population data. Other age/sex classes were assumed to not be involved in emigration.

Survival and births rates are shown in Table 7. Survival rates are used to calculate the nominal death rates ($Deathrt_{Nom}$). Survivorships in the younger age classes for elk are based on Lubow et al. (2001), while survivorships in the older age classes are taken from Houston (1982). Maximum birth rate (i.e., pregnancy rate) for elk is based on information obtained by the CDOW (1966). The effects of condition on recruitment were calibrated so that the model predicted observed values of calf:cow ratios, as reported by Lubow et al. (2001) and Stevens (1980) over a wide range of elk densities. The condition-dependent death rate function ($Deathrt_{CI}$) was calibrated to fit observed population data for the park elk herd. Deer population parameters (Table 7) were largely based on Bartholow (1988). Effect of condition on recruitment was calibrated to achieve observed fawn:doe ratios (Stevens 1980). Effect of condition on death is set to a biologically reasonable value, since a good data set for deer population dynamics was lacking.

Herbivore Spatial Distribution

The herbivore spatial distribution submodel dynamically simulates animal distributions over the simulated landscape or region. The habitat suitability index (HSI) of a grid-cell is affected by 0-1 effects of preference-weighted forage biomass, forage intake rate, green and dead herbaceous biomass, snow depth, slope, tree cover, and a prescribed "force".

$$HSI = F(Pforage)\times F(\text{energy intake rate})\times F(\text{green herb})\times F(\text{dead herb})\times F(\text{snow})\times \min[F(\text{slope}),F(\text{cover})]\times F(\text{force})\times \text{Noise}$$

The preference-weighted forage biomass (Pforage) is the sum of dietary preference indices times forage biomass over all dietary items in the grid-cell. Multiplicative effects are used so that each effect always has an impact on HSI, irrespective of the values of other effects. Pforage represents an effect of dietary selection. The intake rate effect implicitly includes the digestibility of the forage. The effect of green herb biomass represents selection for green leaf, while the effect of dead herb biomass represents a negative preference for dead leaf and a interference effect of dead leaf on selectivity for green leaf. The minimum of the slope and cover effects is taken, hypothesizing that either one or the other will govern selection for the grid-cell, eg. if the slope is too steep it doesn't matter what the cover is, and if cover is unsuitable it doesn't matter what the slope is. "Noise" is a uniform random variate (0.8-1.0) that prevents animals from attaining an ideal free (ie. perfect) distribution.

"Force" maps are read into the model that define the a population's range at different times of the year. A range is defined as the total area available to the population. The spatial distribution model calculates how the population is distributed within its range. The value of F(force) will be 1 inside the range, and 0 outside the range. In the case of elk and deer, summer and winter range maps are read in, with the winter range map being used during November through April. The summer range

map was used in June through September. A transition range map, which includes all of the summer and winter ranges, was used in May and November, giving the animals freedom to move in response to snow cover during those months. Range maps used in the model are shown in Figure 22. Singer et al. (2002) delimited three subherd winter ranges based upon Larkins' (1997) radiolocation data. I combined their range maps for the Moraine Park and Horseshoe Park subherds to represent the range for my park subherd. I similarly delimited the combined summer range myself by circumscribing the majority of Larkins radiolocation data (Larkins 1997). I used a map of the area covered by in-town ground counts (T. Johnson, R. Monello, pers. comm.) to represent the town herd winter range. For lack of other data, deer ranges were assumed to be the same as elk ranges. Beaver habitats were defined by the distribution of willow and aspen on the vegetation map within the area where beaver have been historically observed (Packard 1947b, Stevens and Christiansen 1980, Hickman 1964, Zeigenfuss et.al. 2002). Only the habitats on the elk winter range were included in these modeling analyses, although beaver do occur at low elevations on the western slope. The total area for beaver on the 500 km resolution maps was 425 ha. Thus, if 450 beaver are simulated, this is a density of 1.06 beaver per ha, or 106 per km^2. If colony size is 6 animals per colony, this is 5.67 ha per colony.

Once the HSIs are computed for every grid-cell in the animal's range, they are summed, and normalized (so that they sum to 0.0). Then the animals in the population are distributed across their range in proportion to the distribution of the normalized habitat suitability indices among grid-cells. The redistribution occurs on a weekly basis.

Parameters which determine animal spatial distributions are shown in Table 8. The effect of energy intake rate was scaled to observed ranges of energy requirements for the animals. The effect of slope on elk was estimated from the distribution of radio locations of Larkins (1997). The effect of slope for deer was set so they use steeper slopes than elk. Beaver are assumed to only use flat terrain. The effect of snow depth for elk was set based on previous modeling experience and literature review (Coughenour 1994, Coughenour and Singer 1996). The effect of snow depth for deer was scaled to that of elk, based on difference in body size, particularly brisket height. The effect of green herbaceous biomass was set to span a range of values typical of upland herbaceous communities in RMNP. Although the foraging functional response saturates at lower values, the function here is intended to affect animal density rather than individual animal responses. The maximum density for elk was set based upon aerial survey data (Lubow et al. 2002). The minimum density for beaver was set to prevent unreasonably low concentrations at low simulated population sizes. Assuming there are 6 beaver per colony (Packard 1947b), a value of 40 beaver km^{-2} would give 15 ha per colony.

Wolf Population Dynamics and Predation

The wolf submodel simulates wolf predation on ungulates and resultant wolf population dynamics. It is derived from a model that was used to assess wolf reintroduction into Yellowstone National Park (Boyce and Gaillard 1991, Boyce 1993).

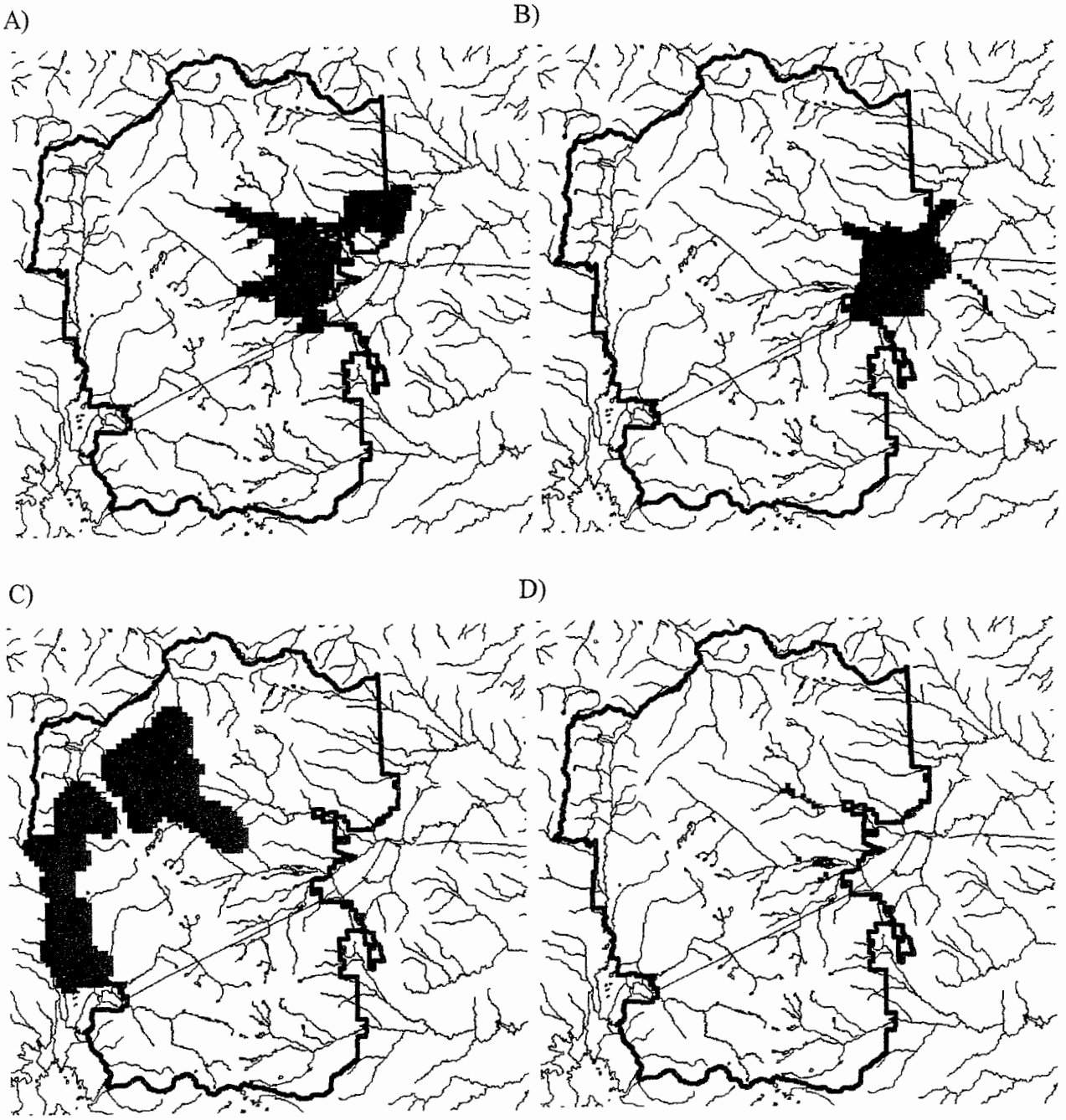


Figure 22. Animal ranges at 500 m grid-cell size used in model. A) Winter range of the park elk herd. B) Winter range of town elk herd. C) Summer range of both herds. D) Beaver habitat.

Table 8 Parameters affecting the habitat suitability index (HSI) and spatial distributions of herbivores. * denotes x,y pairs defining a function. Effect functions are unitless multipliers, and may be >1, since the HSI's are normalized amongst grid-cells (HSI's are rescaled so the sum of all HSI's equals 1).

Parameter	Elk	Deer	Beaver
Effect of metabolic energy intake rate (MJ kg^{-1} d^{-1})*	5, 0.01, 200,1	0,0, 0.25,5	0,0, 0.25,5
Effect of slope (degrees)*	15,1, 30,0.7, 45,0	15,1, 45,0.5, 60,0	5,1, 15,0
Effect of snow depth (cm)*	10,1, 50,0.01	0,1, 20,.01	Not used
Effect of green herbaceous layer biomass*	5,0.2, 100,1	5,0.01, 100,1	5,0.01, 100,1
Effect of dead herbaceous biomass*	0,0.001, 100,1	Not used	Not used
Maximum Density (animals km^{-2})	90	50	Not used
Minimum Density (animals km^{-2})	1	1	40

Population Dynamics

Wolf population dynamics are modeled with the logistic equation for population growth, in which the value of the population finite rate of increase (R) is dependent on the number of prey killed per wolf per year and the maximum number or carrying capacity of wolves in the system. R is defined in

$$Wolf_{t+1}=R\times Wolf_t$$

where $Wolf_t$ is wolf numbers at time t. The conversion of prey killed into rate of population increase is scaled so that the maximum possible increase rate is achieved at the maximum predation rate,

$$R = R_{max} \sum Prkill_i/Fmax_i$$

where R_{max} is maximum finite rate of increase, Prkill is actual predation rate on each species, and Fmax is maximum predation rate on a species. Thus, R declines linearly as predation rate declines. Values for R_{max} are found in Table 9. The value for R_{max} was selected based on the maximum value observed in Yellowstone. In 1996, there were 40 wolves while in 1997, the population had increased to 86, giving a finite rate of increase of 2.1. Boyce used a value of 1.8, although he noted Ballard et al. (1987) observed a value of 2.4 in Alaska.

When the number of wolves reaches a maximum value, R is capped at a value of 1.0 (i.e., no further increase is allowed). The maximum number of wolves is specified based on the size of the range being simulated. Territory size is assumed to decrease with increasing prey density, using the data of Walters et al. (1983). Although these calculations could be based on pack size, and maximum density expressed in terms of packs per km^2, this adds little to the final result unless the mechanisms governing pack size are simulated. Since pack size is not a modeled variable, I simply express wolf density in terms of numbers of animals per km^2.

Walters et al. (1983) summarize empirical data by plotting territory size against prey biomass density. I converted their data to form an equivalent plot of wolf density versus prey biomass density (Figure 23). Pack size has varied from 3-16 animals in recent reintroductions in North America (USFWS 1999). In Montana, the mean pack size in 1999 was 6.7, while in Yellowstone, it was 7.5. However, these included young packs and non-breeding packs with 2-5 animals. On the Yellowstone elk winter range, the 5 established packs averaged 11.4 animals, while in Montana, with a probable lower prey density, the mean breeding pack size was 8.6. Accordingly, I assumed a typical pack size of 10 to convert territory size (area per pack) in Walters et al. (1983) to area per wolf. The inverse of the latter gives maximum number of wolves per area. (i.e. carrying capacity). In addition to the data given in Walters et al. (1983), I estimated maximal density of 0.05-0.075 wolves km^{-2}. Peterson (1976) reported 0.084 wolves km^{-2} was observed in Isle Royal, probably the highest ever observed. Mech (1966) observed 0.038-0.056 km^{-2} on Isle Royal. In comparison, densities in northern Minnesota have varied from 0.023-0.039 km^{-2}, while in Alaska densities have ranged 0.006-0.002 km^{-2}, and in Canada 0.003-0.007 km^{-2} (Ballard et al. 1987). The resulting plot (Figure 23) can be

Table 9. Parameters governing wolf population dynamics and predation. * Indicates x,y pairs defining a function (see Table 2 caption.).

Parameter	Value
WOLVES	
Size of wolves range (km^2)	388
Maximum wolf density (wolves km^{-2}) vs. prey biomass (kg km^{-2})*	0.0,0.0024, 500, 0.0425, 1700, 0.08
Maximum rate of increase (R) yr^{-1}	2.1
ELK PREDATION	
Prey body weight (kg)	220
Fraction of predator mortalities that are compensatory	0.3
Size of prey range (km^2)	177 (winter), 197 (summer)
Max. predation rate by wolves (elk $wolf^{-1}$ yr^{-1})	25
Elk density (wolves km^{-2}) at inflection point of functional response	3.5
Vulnerability indices of calves, prime female, prime male, old female, old male	7,1,1,5,5
Predator-Prey spatial overlap year-long	0.75
DEER PREDATION	
Prey body weight (kg)	55
Fraction of predator mortalities that are compensatory	0.3
Size of prey range (km^2)	177 (winter), 197 (summer)
Max. predation rate by wolves (elk $wolf^{-1}$ yr^{-1})	110
Elk density (wolves km^{-2}) at inflection point of functional response	8.03
Vulnerability indices of fawns, prime female, prime male, old female, old male	7,1,2,3,5
Predator-prey spatial overlap year-long	0.75

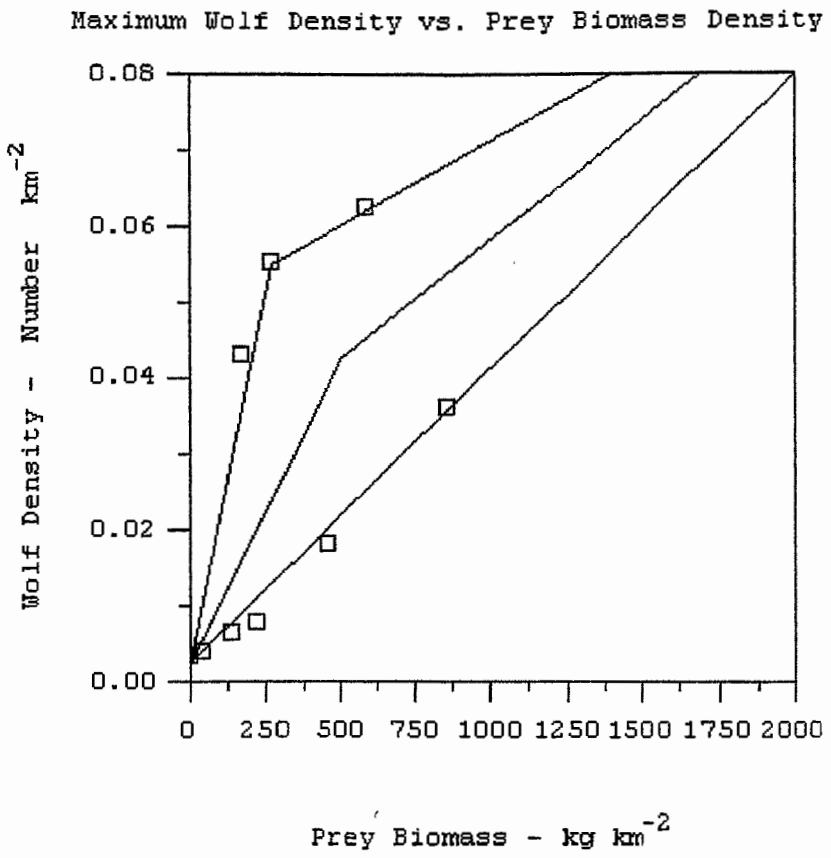


Figure 23. Maximum wolf density versus prey biomass density, based on the data of Walters et al. 1983 (points), and maximum density observed at Isle Royal (Peterson 1976), and an assumption of 10 wolves per pack. Maximum, minimum and median value functions are shown.

interpreted as describing a range of values bounded by the upper and lower extreme data points, with a median-value function lying in between. I used the median-value function in most of the model runs presented here.

The wolf densities in Figure 23 can be converted to pack territory sizes as follows. At the maximum density of 0.08 km^{-2}, and a pack size of 10, the pack territory would be 125 km^2. At a density of 0.05 km^{-2}, territory size would be 200 km^2. At a mid-range density of 0.02 km^{-2}, territory size would be 500 km^2, and at a low density of 0.01 km^{-2}, territory size would be 1,000 km^2. In comparison, pack home ranges in NW Montana averaged 480 km^2, with a minimum of 63 km^2 and maximum of 1,190 km^2. In Yellowstone, home ranges varied from 88-2,419 with a mean of 890 km^2. On the northern winter range, mean home range was 465 km^2 (USFS 1999).

It is important to put prey biomass densities in the context of other observed values, since prey biomass density affects predator number as in Figure 23. If there are 2,000 elk and 300 deer on the total wolf/elk range (388 km^2), the prey biomass density is 1,134 kg km^{-2} elk plus 42 kg km^2 of deer, using body weights of 220 kg and 55 kg for each. The total of 1,176 kg km^{-2} is near the saturating value of 1,300 kg km^{-2} used in Figure 23. With half as many elk, the biomass density is 610 kg km^{-2}. In comparison, in 1998-1999 about 11,700 elk were counted on the Yellowstone northern range, which could feasibly correspond to 14,000 animals after correcting for sightability. The total size of the wolf home ranges is 2,326 km^2, giving a prey biomass density of 1,324 kg km^{-2}.

Predation

The number of prey animals killed depends on the relative densities of prey and wolves. A multispecies disk equation, modified to incorporate a Type III functional response is used (Holling 1959, Abrams and Allison 1982). This version of the equation assumes prey overlap on the same range. The equation is

$$Prkill_i = (Attack_i \times Prden_i \times Tprden)/(1+Attack_i \times Handtm_i \times Tprden^2)$$

where Prkill is the number of prey of type i killed per predator per year, Prden is prey density (number per km^2 in the prey's range, size of prey range given in Table 9), and Tprden is the sum of Prden over all prey species. The size of the prey range is used here rather than the size of the predator range, because the predation process is presumably affected by the prey density in the area where the predation is occurring. Attack is the attack rate, computed as

$$Attack_i = 1/(W_{0i}^2 \times Handtm_i)$$

where W_0 is the prey density (number per km2) at the inflection point of the functional response. This equation is derived from knowing that

$$W_0 = \sqrt{[1/(Attack \times Handtm)]}\,.$$

Handtm is handling time, computed as

$$Handtm_i = 1/Fmax_i$$

where Fmax is the maximum predation rate on prey type i.

It can be shown algebraically from the set of equations above that

$$Prkill_i = (Fmax \times Prden_i \times Tprden) / (W_0^2 + Tprden^2)$$

which is another form of the functional response equation.

Total predation (number of prey per year) is calculated as the product of per-predator kill rate and total number of predators in the range of the prey.

$$Tkill_i = Prkill_i \times Wolf$$

The total number of predators in the range of the prey is affected by predator and prey relative migration patterns. For example, if prey move out of the range of the predators on a seasonal basis, then in effect, there are that many fewer predators preying on the prey. Conversely, predators may migrate along with prey. Alternatively, a portion of the predators may have territories in one seasonal prey range, while another portion of predators may have their territories in another seasonal prey range. For example, in Yellowstone, certain wolf packs have established territories on elk winter range while others have territories on elk summer range. This complexity is not represented explicitly in the model. Instead, the user specifies an estimate of the fraction of prey that are in range of all of the predators for each month. These fractions must be derived by creating a conceptual scenario of the seasonal overlaps between predator and prey ranges. The scenario which I chose was that two wolf packs would be likely to occur over the total range. I estimated two packs based on typical pack sizes, the typical range of wolf densities (or conversely of pack territory sizes), and the size of the combined elk summer plus winter ranges. I surmised that one pack would be based on the west slope and the other on the east slope of the continental divide. The pack territory on the east slope would cover the winter range, and portions of the summer range. The pack territory on the west slope would cover the remainder of the summer range. In this scenario, half of the predators would overlap with elk in the six winter months (November-April). All of the predators would overlap with elk in the six transition and summer months (May-October). Thus, the fraction of predator-prey overlap on a year-long basis is $[(6\times0.5)+(6\times1.0)]/12 = 0.75$.

The multi-species form of the equation represents shifting of predation from one species to another as their relative densities change. Predation is distributed among sex and age classes of prey using a prey vulnerability index. This is used to make very young animals, and older animals more vulnerable than prime aged animals. Predation can either be additive, compensatory, or some mixture of both. Additive mortality due to predation is assumed to be additional to the normal prey mortality rate due to age and nutrition. Compensatory mortality is subtracted from the normal prey mortality,

with the idea being that wolves are killing animals that are most likely to be dying due to other causes.

Predation is distributed among age and sex classes within a species using a vulnerability index. It is commonly observed that predators focus on weaker or otherwise more vulnerable animals. For example, in Yellowstone, 56% of predator mortalities on elk were calves, 22% were prime-aged (1-9yrs) and 22% were old (>9yrs) (Kerry Murphy, pers. comm.). This represents a disproportionate mortality of calves. Vulnerability indices are weighting factors, to indicate relative vulnerabilities among age/sex classes. The product of vulnerability (V) times the number of animals (N) is normalized to the total to give the fraction of predation on each age/sex class k.

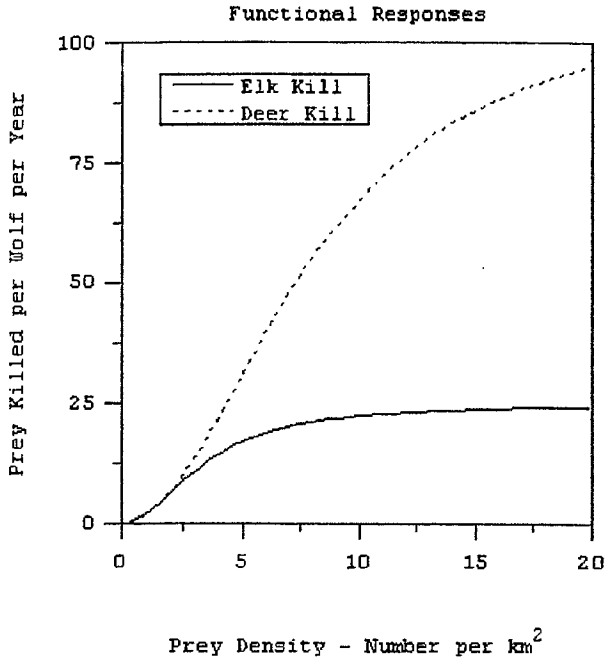
$$PrAgeSex_k = (V_k \times N_k) / (\sum V_k \times N_k)$$

The maximum predation rate for elk is set at the value used by Boyce (25 elk wolf^{-1} yr^{-1}, Table 9). Recent kill rates in Yellowstone have been about 1 kill per 2.5 days per pack in early winter and 1 kill per 1.5 days in late winter (K. Murphy pers. comm.). Assuming there are on average 10 wolves per pack, this converts to 18-24 elk wolf^{-1} year^{-1}. Boyce calculated from the data of Carbyn (1983) that wolves kill 0.21 kg prey per kg wolf per day. If wolves are on average 40 kg and elk are 220 kg, this would be equivalent to 14 elk wolf^{-1} yr^{-1}. Boyce used a higher value than typically observed to account for surplus killing when elk are highly abundant, i.e., when elk density is high enough for wolves to actually achieve the maximum predation rate. Another reason to use a value on the high side of the observed range in Yellowstone is that predation rates observed in Yellowstone thus far are unlikely to be maximal. For deer, I used Boyce's value of 110 deer wolf^{-1} year^{-1}, based on the assumption that deer are 1.3 times as preferred as elk after Cowan (1947, cited in Boyce 1993), and the difference in body sizes between deer and elk.

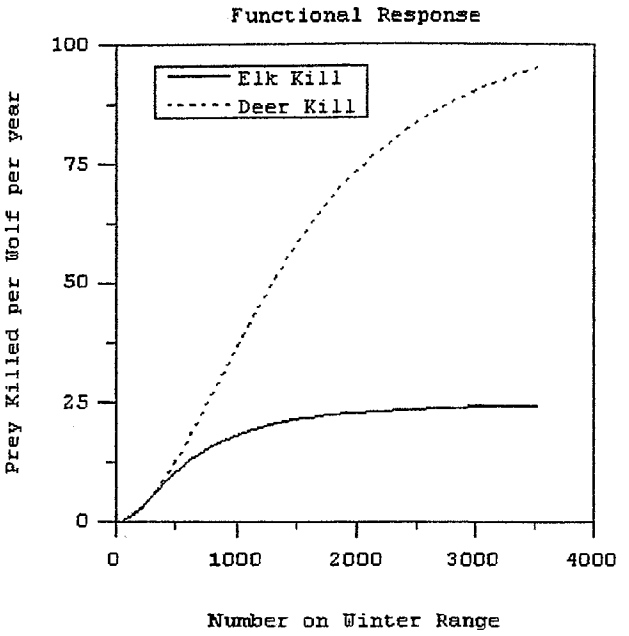
The characteristic shape of the functional response is shown in Figure 24a. Although this is a Type III response, the S-shape is minimal. When densities are converted to numbers based on winter prey range size (Figure 23b), it can be seen that there is a continuous increase in predation rate between 0 and 1,000 elk, and that above 1,500 elk, the predation rate is saturated. Saturation for deer does not occur until a much larger population size of over 3,000. The sensitivity of the equation to the parameter W_0 is demonstrated in Figure 24c.

Compensatory mortality is potentially an important modifier of predator impact on prey populations, but is still little understood. Compensatory mortality is defined as the fraction of prey killed by predators that would have died anyway due to disease, malnutrition, or other causes. This fraction of predation would therefore have no impact on prey population dynamics. It would be expected that the fraction of compensatory mortality would increase with the degree of selectivity of predators for weak or old prey animals. Additive mortality is the mortality that predators exert in addition to the other causes of prey mortality, so it is this fraction which would cause predators to affect prey populations. Compensatory and additive mortalities are distinguished by simply specifying the proportion of prey killed that is compensatory. The remainder is additive. The fraction of predation that is compensatory is not removed from the prey population, but does count towards increasing the predators population growth rate.

A)



B)



C)

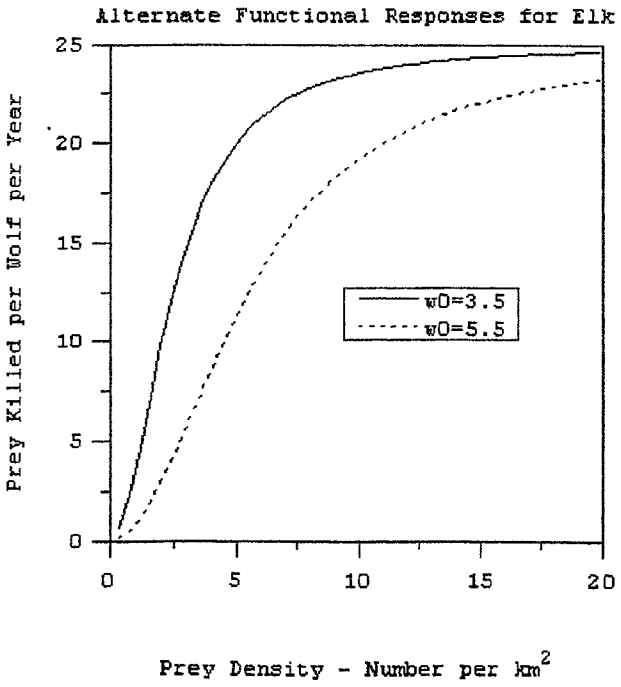


Figure 24. Functional responses for elk and deer versus A) density and B) number of animals on the winter range (277 km^2). C) Effect of the parameter w_0 on the form of the functional response.

MODEL VERIFICATION - PLANT BIOMASS

Herbaceous Biomass Production

The plant growth model was verified by comparing model outputs to observed biomass data from Hobbs (1979), Fiske et al. (1998), Singer et al. (2001a,2002), and Zeigenfuss et al. (1999, 2002). Comparisons were made for several major vegetation types including: dry grasslands, mesic riparian herbaceous, upland shrubs, willow, low elevation woodlands dominated by ponderosa pine (montane woodland), high elevation woodland and forest dominated by lodgepole pine, Engelman spruce and subalpine fir, and alpine tundra. Simulations were generally run for 5 years beginning in 1994, using real weather data. The simulations were then carried forward for an added 45 years using stochastic weather (see Model Description/Weather section above for the method of generating stochastic weather). Means for the first five years correspond to conditions in the recent field studies of Singer et al. (2002) and Zeigenfuss et al. (2002), and means for the final 30 years represent a sample from a larger range of weather years. These simulations did not represent the entire study area, but only a sample of eight locations (grid-cells) having the same vegetation type, but spanning the range of topographic and weather conditions for that vegetation type. The mean of those eight locations is what is reported. Grazing or browsing conditions are given in terms of elk densities. Elk densities were prescribed, and held constant. Elk densities were simply chosen to be representative of conditions on the winter range over the last decade. For example, Singer et al. (2002) reported a mean density of 9.5 elk km^{-2} in the park winter ranges, 13.5 elk km^{-2} in Moraine Park, and 2.7 elk km^{-2} in Horseshoe Park. However, they also show maximum density contours of 15 elk km^{-2} in Horseshoe Park and 90 elk km^{-2} in Moraine Park. It was assumed that elk were present at the specified densities on the winter range from mid-September to mid-May (eight months).

Simulated herbaceous biomass in low elevation dry grasslands (Table 10) in the first 5 years was largely insensitive to grazing, consisting of about 55 g m^{-2} of grass and 30 g m^{-2} of forbs. In the last 30 years, biomass increased in the ungrazed run, and decreased in the grazed runs, resulting in a >2-fold difference in biomass between heavily grazed and ungrazed conditions. Simulated biomass amounts with elk densities of 15 km^{-2} were comparable to biomass amounts observed by Hobbs(1979), Singer et al. (2002), and Zeigenfuss et al. (2002).

No studies have been conducted of long-term herbaceous aboveground biomass responses to grazing in the grasslands of RMNP. Stohlgren et al. (1999) sampled foliar cover inside and outside of long-term (30-year) grazing exclosures. They found 50% higher grass cover, and 58% higher forb cover inside the exclosures. However, the difference could have been at least partly due to an accumulation of standing dead, or offtake during the current growing season, rather than a production difference. Schoenecker et al. (2002) sampled a total of 30 root cores at 2 long-term grazing exclosures and found no differences in root densities inside compared to outside the exclosures.

Low elevation shrublands are by comparison, more productive than the dry grasslands Table 11). These are mostly upland sites at slightly higher elevations, with an average 25% cover of bitterbrush (*Purshia tridenta*). These sites are intermixed with, or comprise the understories of the

Table 10. Simulated and observed herbaceous biomass in low elevation dry grasslands. Observed data are from Singer et al. (2002) and Hobbs (1978). Simulated data are from model runs for 5 years beginning with 1994-98 initial conditions and using actual weather data, or from the last 30 years of a 50 year simulation using stochastically generated weather data.

Vegetation Type	Grazing	Simulated/ Observed	Years	Loca-tions	Grass Biomass g m^{-2}	Forb Biomass g m^{-2}	Total Biomass g m^{-2}
Grassland	Ungrazed	Simulated	30	8	60±14	58±18	118±35
	Grazed-15 elk km^{-2}			8	47±5	33±4	80±6
	Grazed-34 elk km^{-2}			8	33±4	20±2	54±6
	Ungrazed		5	8	56±11	31±4	87±8
	Grazed-15 elk km^{-2}			8	55±13	30±3	85±9
	Grazed-34 elk km^{-2}			8	55±13	29±3	83±11
Grassland	Grazed	Observed - Hobbs	1976	4	46±3	43±3	72±3
			1977	4	43±3	24±2	67±3
	Grazed	Observed - Singer town samples	2	2	56 (32-81)	28 (22-34)	84 (54-115)
	Annually moved cages		1	2	50	26	76

Table 11. Simulated and observed herbaceous biomass in low elevation shrublands. Observed data from Zeigenfuss et al. (2002) and Hobbs (1978). Simulated data are from model runs for 5 years beginning with 1994-98 initial conditions and using actual weather data, or from the last 30 years of a 50 year simulation using stochastically generated weather data.

Vegetation Type	Grazing	Simulated/ Observed	Years	Locations	Grass Biomass g m^{-2}	Forb Biomass g m^{-2}	Total Biomass g m^{-2}
Upland Shrublands 25% Cover	Ungrazed	Simulated	30	8	86±16	86±12	173±26
	Grazed - 15 elk km^{-2}				70+12	56±11	126±24
	Grazed - 34 elk km^{-2}				46±7	27±3	74±10
	Ungrazed		5	8	71±7	60±7	131±14
	Grazed - 15 elk km^{-2}				65±7	53±5	119±13
	Grazed - 34 elk km^{-2}				66±6	50±4	117±9
Upland Shrubland 12%Cover Burned	Ungrazed	Simulated	30	8	95±13	96±15	192±27
	Grazed - 15 elk km^{-2}				77±10	59±7	137±16
	Grazed - 34 elk km^{-2}				54±6	32±4	86±9
	Ungrazed		5	8	75±5	64±4	140±7
	Grazed - 15 elk km^{-2}				73±5	59±3	132±7
	Grazed - 34 elk km^{-2}				68±6	50±4	118±8
Upland Shrub Bitterbrush 25% Cover	Ungrazed for 3 years	Observed - Zeigenfuss Bitterbrush sites	3	4	77±50	69±54	147
	Annually moved cages			4	70±31	56±53	127
	Grazed			4	62+23	44+24	107
Sagebrush	Grazed	Observed -Hobbs	1976 1977	4 4	45±4 21±1	17±2 6±1	62±6 27±2

montane woodlands dominated by Ponderosa pine. As in the dry grasslands, grazing had little effect in the first five years, but after sustained use, production declined with increased grazing pressure. The model simulated herbaceous biomass densities that were comparable to those observed by Zeigenfuss et al. (1999, 2002). Prior to a burning treatment, shrub cover averaged 25%. Following burning, cover declined to 12% (Zeigenfuss et al. 1999, 2002). This was simulated in the model by altering shrub cover accordingly. The model simulated more herbaceous production when the shrub canopy was reduced, demonstrating that the model represents competition between shrubs and herbs for limiting resources such as water, nitrogen, and light. The data reported by Hobbs (1979) for low elevation shrublands are markedly lower than values observed by Zeigenfuss et al. (2002) or simulated by the model. Hobbs' (1979) sites were dominated by mountain sagebrush (*Artemesia veysianum*), indicating drier conditions.

The model predicted that low elevation Ponderosa pine woodlands would support less herbaceous biomass as woody canopy cover was increased from 22%, to 40%, and to 60% (Table 12), indicative of competition between trees and herbs. Grazing had reduced biomass after 20 years. Simulated values with 15 elk km^{-2} and 22-61% tree cover were comparable to those observed by Hobbs (1979) and Zeigenfuss et al. (2002). In contrast, aspen woodlands at similar elevations supported more herbaceous biomass than Ponderosa pine woodlands, as a result of differences in soil water holding capacity, and the presence of a water table for part of the year. There was good agreement between simulated and observed data from aspen woodlands.

Simulated herbaceous biomass production was much higher in low elevation willow communities (Table 13) than in dry grasslands, due to elevated water tables and higher soil fertility resulting from many years of soil organic matter accumulation. Short willow communities and tall willow communities produced similar amounts of biomass at low to moderate levels of willow cover. In both short and tall willow, if willow were allowed to grow freely to a maximum of 77% cover, herbaceous biomass was reduced. This, again, was a consequence of competition, but in this case, for nitrogen and light rather than water. Grazing had little effect on herbaceous biomass in these communities.

Simulated levels of herbaceous production in willow communities were comparable to those observed by Zeigenfuss et al. (2002, Table 13). As in the model, there were no significant differences between herbaceous biomass densities in short and tall willow. In contrast to 5-year model predictions, the data of Zeigenfuss et al. (2002) suggested lower herbaceous biomass under grazing than under no grazing. However, variances were high. In three of the four study years, they found no difference in herbaceous biomass between grazed and ungrazed. Only in the final year, after five years of treatment, was a difference observed, but only between biomass in ungrazed swards and biomass inside permanent exclosures. The difference between biomass inside moveable cages outside the permanent exclosures, and biomass inside the permanent exclosure was less, suggesting that standing biomass was reduced by grazing offtake during the growing season, but that biomass production was not diminished by grazing. It appeared that there was a trend of increasing biomass production inside permanent exclosures over the five-year period. However, much of the increase could have been due to an accumulation of standing dead rather than an increase in annual

Table 12. Simulated and observed herbaceous biomass in low elevation woodlands and forests with grazing during winter only. Observed data from Singer et al. (2002), Zeigenfuss et al. (unpublished data), and Hobbs (1978). Simulated data are from the last 30 years of a 50 year simulation using stochastically generated weather data.

Vegetation Type	Cover	Grazing	Simulated/ Observed	Years	Loca -tions	Grass Biomass g m^{-2}	Forb Biomass g m^{-2}	Total Biomass g m^{-2}
Ponderosa Pine	22	Ungrazed	Simulated	30	8	42±8	32±6	75±13
	40					35±8	26±6	61±13
	61					28±3	20±3	49±5
	22	Grazed - 15 elk km^{-2}			8	29±5	12±1	42±5
	61					21±3	9+1	30±3
Aspen	65	Ungrazed			8	59±13	46±12	106±24
	54	Grazed - 10 elk km^{-2}			8	55±7	36±6	91±13
	54	Grazed - 20 elk km^{-2}				40±5	22±2	63±6
Ponderosa Pine		Grazed	Observed - Ziegenfuss landscape samples	1	8	35±21	22±14	57
Aspen					11	52±40	54±30	106
Ponderosa Pine		Grazed	Observed - Singer town samples	1	2	41-56	18-32	59-86
		Ungrazed			2	23	37	60
Ponderosa Pine		Grazed	Observed - Hobbs	2 (1976, 1977)	4	31.7±2.3	11.9±1.1	50.3±3.8
					4	20.4±1.7	9.2±1.3	35.1±2.6
Aspen					4	79	26	112
					4	46±4	26±3	106±6

Table 13. Simulated herbaceous biomass in low elevation willow. Simulated data are from model runs for 5 years beginning with 1994-98 initial conditions and using actual weather data, or from the last 30 years of a 50 year simulation using stochastically generated weather data. Willow cover was either allowed to reach its normal value (free) or was limited to a value typical of browsed conditions (fixed).

Vegetation Type	Willow Cover	Grazing	Years	Loca-tions	Grass Biomass g m^{-2}	Forb Biomass g m^{-2}	Total Biomass g m^{-2}
Short Willow	16(fixed)	Ungrazed	30	8	246±41	91±23	339±26
	16(fixed)		5		250±13	42±27	292±14
	77(free)	Ungrazed	30		146±22	82±23	229±20
	26(free)		5		257±19	46±5	302±22
	77(free)	Grazed - 15 elk km^{-2}	30		168±35	74±23	242±25
	26(free)		5		255±17	43±3	298±18
	19(free)	Grazed - 60 elk km^{-2}	30		292±27	21±17	312±22
	17(free)		5		250±13	39±1	289±14
Tall Willow	26(fixed)	Ungrazed	30	8	282±36	52±46	334±19
	26(fixed)		5		287±13	55±4	343±16
	77(free)	Ungrazed	30		147±19	58±39	206±46
	56(free)		5		280±9	55±6	336+11
	77(free)	Grazed - 15 elk km^{-2}	30		177±24	69±40	247±24
	52(free)		5		282±12	56±5	338±13
	52(free)	Grazed - 60 elk km^{-2}	30		222±52	16±7	239±45
	44(free)		5		288+12	53±5	341+13

production. In the last year, there was 173 g m^{-2} dead biomass inside the permanent exclosures, while there was only 37 g m^{-2} outside, and 84 g m^{-2} inside moveable cages located outside the permanent exclosures. If so, then the modeled rate of transfer from standing dead to litter could be low.

In contrast to increasing production, over a 30-year period, a lack of herbivory reduced herbaceous production in simulated willow communities (Table 13), which was likely a response to increased willow cover. As willow cover increases, it competes with herbaceous plants for light and nutrients.

Data from other studies of herbaceous biomass in wet meadows and willow show markedly lower biomass values (Table 14) than those of the willow communities reported above. The discrepancy could arise from differences in weather. However, the data collected by Zeigenfuss et al. (1999, 2002) from meadows in the town elk range were taken during the same period as the willow community data. Other differences could arise from grazing, from soil, and from differences in water subsidies. The results illustrate the complexity of explaining variance in herbaceous biomass production in these environments. If much of the variance is due to differences in level of a water subsidy to local sites, then the model will have difficulty, because this part of the model is not highly developed, and because the data inputs for fine-scale variations in water table depths and topographic relief either do not exist, or would be smoothed over by modeling with 500 m grid-cells in any event.

The effect of precipitation redistribution is illustrated by comparisons of high-elevation grassland grid-cells with full precipitation input, as compared to cells with snow blow-off, or water run-off (Table 15). A 70% reduction in precipitation input resulted in a 33% reduction in herbaceous biomass. Simulated values were comparable to dry and moist or wet meadows studied by Fisk et al. (1998). They also found large differences in biomass production among these sites were ultimately caused by precipitation redistribution, from swales to ridgetops, for example.

Few data exist for herbaceous biomass in high elevation woodlands and forests. A single estimate, from five locations in lodgepole pine was made by L. Zeigenfuss and F. Singer (unpublished data) in their "landscape" sampling in 1996. A very small biomass density was observed (Table 16), consistent with the combined stresses of reduced light, thin rocky soils, and low water holding capacity. The model produced similar values at a tree canopy cover of 83-85% (Table 17). Herbaceous production in these woodlands is highly sensitive to tree cover, with a fourfold difference in simulated production between stands with 65% and 85% cover. Grazing at a low intensity during summer had little effect on biomass production when tree cover was 65%.

Willow and Upland Shrub Production

Peinetti (2000) parameterized the SAVANNA model for willow and conducted a range of verification tests against the field data set he collected (Peinetti and Coughenour 2001). Here, I make comparisons to a different data set (Zeigenfuss et.al. 2002), with a larger number of plants but less morphometric and physiological detail. In this experiment, willow stands were exclosed (protected from elk) for a period of five years, and samples were taken inside and outside each exclosure.

Table 14. Observed herbaceous biomass in low elevation mesic grasslands and shrublands. Observed data from Zeigenfuss et al. (2002), Hobbs (1978), and Singer et al. (2002).

Vegetation Type	Grazing	Data Source	Years	Locations	Grass Biomass g m^{-2}	Forb Biomass g m^{-2}	Total Biomass g m^{-2}
Short and Tall Willow	Ungrazed - Permanent Exclosures	Zeigenfuss	4	12	280±179	48±33	328
	Ungrazed - Seasonally Moved Cages			12	311±140	65+55	376
	Grazed			12	219±102	36+30	255
Willow	Grazed	Hobbs	2	4	195±10 155±27	3±1 6±2	199 161
Wet Grass Meadow				4	183±9 97±3	15±2 17±3	198 114
Mesic Meadow				4	137+8 108±8	3±0.4 6±1	140 168
Wet Shrub Meadow				4	137±12 107±8	13±2 19±3	150 126
Wet Meadow	Grazed	Singer-town samples	1	2	139-250	19-30	159-269
	Ungrazed - Seasonally Moved Cages		2	2	133	33	166

Table 15. Simulated and observed herbaceous biomass in high elevation grasslands (tundra). Observed data from Fisk et al. (1998). Simulated data are from the last 30 years of a 50 year simulation using stochastically generated weather data.

Vegetation Type	Grazing	Simulated/Observed	Years	Locations	Total Biomass g m^{-2}
Dry Tundra (Net Precipitation Input = 30%)	Ungrazed	Simulated	30	8	168±13
	Grazed - 30 elk km^{-2}				139±9
Moist Tundra (Net Precipitation Input = 100%)	Ungrazed				249±16
	Grazed - 30 elk km^{-2}				202±50
Dry Meadow	Unknown	Observed - Fisk	3	1	137±45 (peak live)
Moist Meadow	Unknown			1	202±36(September) 328±87 (peak live)
Wet Meadow	Unknown			1	289±59 (peak live

Table 16. Simulated and observed herbaceous biomass in high elevation woodlands and forests with grazing during summer only. Observed data from Zeigenfuss (Unpublished data). Simulated data are from the last 30 years of a 50 year simulation using stochastically generated weather data.

Vegetation Type	Cover	Grazing	Simulated/Observed	Years	Loca-tions	Total Biomass g m^{-2}
Lodgepole Pine	63	Ungrazed	Simulated	30	8	68±15
	83					15±6
	100					3±1
	63	Grazed - 10 elk km^{-2}				60±19
	83					15±5
Spruce-fir	65	Ungrazed			8	62±20
	85					16±6
	100					3±1
	65	Grazed - 10 elk km^{-2}				58±15
	85				8	15±6
Lodgepole Pine		Grazed	Observed - Zeigenfuss landscape samples	1	5	16±22

Table 17. Simulated and observed cover and current annual growth (CAG) twigs and leaf biomass, and the ratio of CAG to canopy cover in willow stands corresponding to the 5 year exclosure study of Singer et. al. (2002) and Zeigenfuss et al. (2002). Values are means over the entire study. Also shown are data gathered in a 1 year landscape scale sample over a broader area, and cover data based on surveys of plant size and density by Peinnetti (2000)..

Vegetation Type	Browsing	Simulated/ Observed	Locations	Cover %	CAG kg/ha	CAG/Cover kg/ha
Short- Low Elevation	Unbrowsed	Simulated	8	39	393±81	1034±113
	Browsed - 15 elk km^{-2}		8	27	294±26	1067±110
	Browsed- 60 elk km^{-2}		8	14	170±27	1212±108
Tall - Low Elevation	Unbrowsed		8	37	587±117	1580±53
	Browsed - 15 elk km^{-2}		8	34	531±76	1580±54
	Browsed - 60 elk km^{-2}		8	22	357±49	1561±151
Short - Low Elevation	Unbrowsed	Observed - Singer, Zeigenfuss, Piennetti	8	27±29	368±42	1160±388
	Browsed		8	16+15	161±229	904±410
Tall - Low Elevation	Unbrowsed		4	56±32	903±767	1502±592
	Browsed		4	26±22	501±991	1400±941

Over a five-year period, willow cover increased twofold in unbrowsed tall willow and threefold in unbrowsed short willow (Figure 25), demonstrating the high growth capacity of this species, even after years of being suppressed to a short growth form. The model estimates of rate of cover increase over this time period were very close to those observed in the experiment. Browsed willow also increased in cover over the course of the experiment. Both short and tall willow cover increased nearly twofold under browsing in the experiment, while similar results were achieved by simulating a browsing pressure of 15 elk km^{-2}.

Current annual growth (CAG) amounts simulated by the model were also comparable to those observed in the exclosure experiments (Table 17). Since total CAG increases with canopy cover, comparisons must be made between observed and simulated CAG at similar cover values. Alternatively, it is useful to compare values of CAG per unit cover (kg CAG/ha canopy cover). If the simulated value of CAG/cover is comparable to observed values, then if the model simulates cover correctly, it is ensured that total CAG will also be simulated correctly. Indeed, the model simulated values that were comparable to those observed in the exclosure experiment. When the model was run for an additional 30 years, cover reached the maximum allowed value of 77% if not browsed (Table 18). CAG/cover also increased to levels higher than those observed in the exclosure experiment. However, if cover values were fixed at those observed in browsing treatments, CAG and CAG/cover values remained comparable to those observed. Over the long-term, browsing by 15 elk km^{-2} was insufficient to hold cover values at levels observed in the field. A browsing pressure of 60 elk km^{-2} was necessary to hold cover values to those observed in the field. Similar responses were simulated in willow that occur on the summer range, at high elevation.

CAG and cover values were collected from bitterbrush (*P. tridentata*) in upland shrublands (Singer et al. 2001a,2002, Zeigenfuss et.al. 2002). A burning experiment was conducted, which reduced canopy cover from a mean of 26% to a mean of 12%. In the model verification runs, cover values were held at either 12% or 26% (Table 19). Simulated CAG and CAG/cover were comparable to those observed in the field. Browsing had little effect on shrubs held at 26% cover except during the first five years when browsing appeared to stimulate growth. The apparent browsing response is likely confounded by effects of elk grazing on competing herbaceous plants, and by the fact that elk have a relatively low preference for upland shrubs compared to herbaceous plants. Thus, an increase in elk density could cause an increase in herbaceous offtake, which then releases shrubs from competition with herbaceous plants. When shrub cover was held at 12%, to simulate burning, elk suppressed CAG and CAG/cover over the long-term, but not the short-term.

Human-impacted herbaceous vegetation types were sampled in the town of Estes Park by Singer et al. (2002). Mowed golf course grassland had 145 g m^{-2} (Table 20). In comparison, model estimates for ungrazed-mowed and elk grazed-mowed bracketed this value, as mowing, irrigation and fertilization treatments were imposed in the model. The effects of irrigation and fertilization are demonstrated by the high value in the simulated unmowed golf course. They also sampled improved "cattle grazed" pastures that could have been irrigated, subirrigated, and nutrient subsidized either through fertilization or supplemental animal feeding. Their "slightly sub-irrigated" site was also probably grazed by domestic stock. Simulated values for the ungrazed for 5 years, and grazed for 30

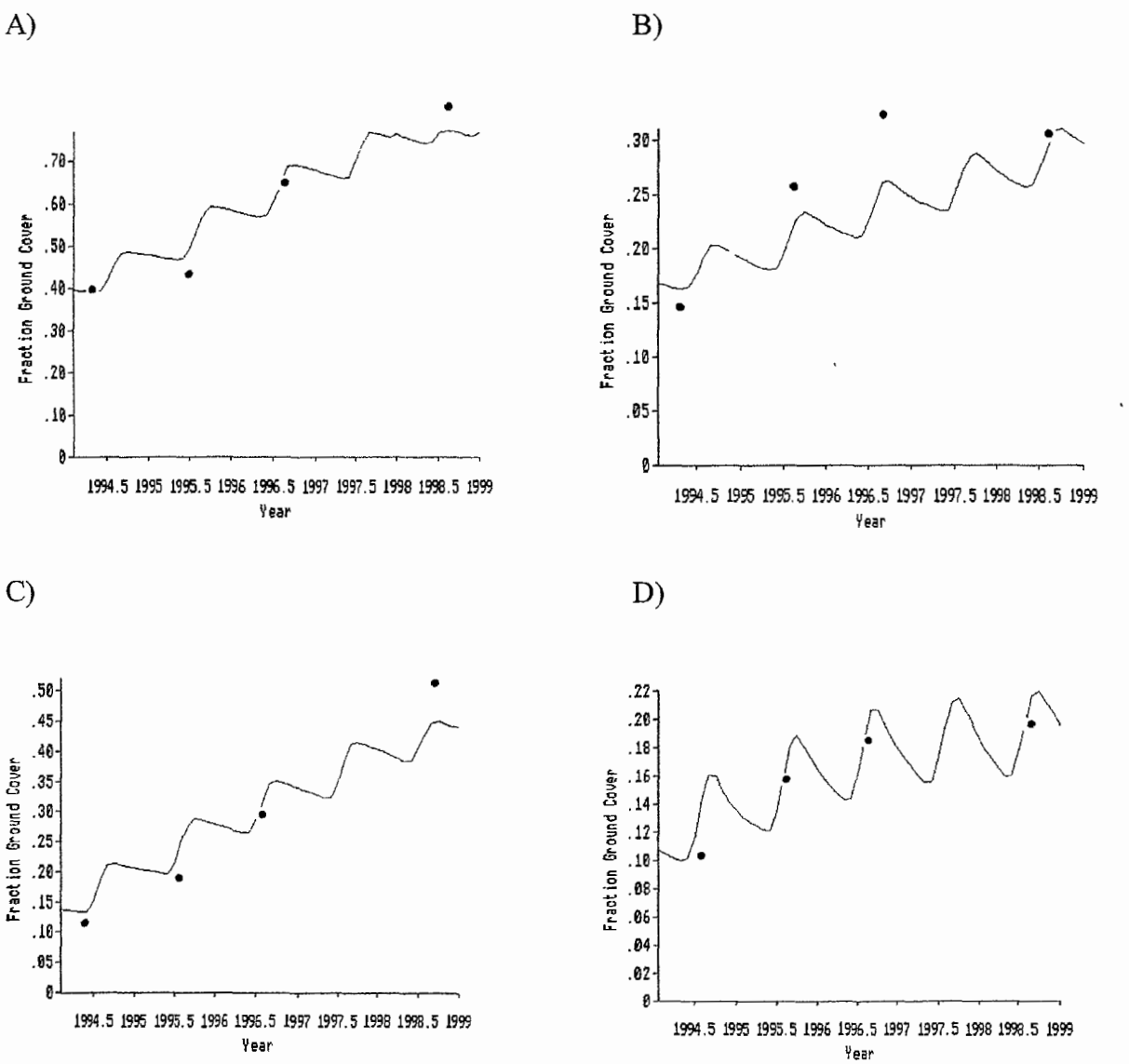


Figure 25. Comparison of simulated (lines) and observed (points) data for willow cover over the course of the experiment conducted in 1994-98. A) Tall willow, unbrowsed. B) Tall willow, browsed with 15 elk km $^{-2}$. C) Short willow, unbrowsed. D) Short willow, browsed with 15 elk km^{-2}.

Table 18. Simulated cover and current annual growth (CAG) twigs and leaf biomass, and ratio of CAG to canopy cover in willow stands in the last 30 years of a fifty year simulation. The cover values were either allowed to reach their maximal values (free), or were constrained to a set maximum (fixed) similar to that which might be observed under browsing.

Vegetation Type	Browsing	Cover %	CAG kg/ha	CAG/Cover kg/ha
High Elevation	Unbrowsed	77 (free)	1672±100	2174±132
		52 (fixed)	941±173	1809±33
	Browsed	77 (free)	1632±82	2123±107
Short - Low Elevation	Unbrowsed	77(free)	1534±126	1997±168
		17(fixed)	1890±101	1119±59
	Browsed - 15 elk km^{-2}	74 (free)	1571±167	2134±131
	Browsed - 60 elk km^{-2}	11 (free)	106±33	966±90
Tall - Low Elevation	Unbrowsed	77(free)	1575±89	2048±117
		27(fixed)	419±34	1551±127
	Browsed - 15 elk km^{-2}	77 (free)	1727±65	2246±85
	Browsed - 60 elk km^{-2}	16 (free)	236±100	1442±262

Table 19. Simulated and observed cover and current annual growth (CAG) twigs and leaf biomass in upland shrublands. Observed data from Ziegenfuss et al. (2002). Simulated data are from model runs for 5 years beginning with 1994-98 initial conditions and using actual weather data, or from the last 30 years of a 50 year simulation using stochastically generated weather data

Vegetation Type	Burning	Browsing	Simulated/ Observed	Years	Locations	CAG kg/ha	CAG/Cover kg/ha
Shrubland - 26% Cover (fixed)	Unburned	Unbrowsed	Simulated	30	8	583±100	2170±420
		Browsed - 15 elk km^{-2}				564±110	2120±390
		Browsed - 60 elk km^{-2}				533±114	2070±420
		Unbrowsed		5		553±110	2050+420
		Browsed - 15 elk km^{-2}				682±124	2530±460
		Browsed - 60 elk km^{-2}				806±110	2990+410
Shrubland - 12% Cover (fixed)	Burned	Unbrowsed	Simulated	30	8	275±62	2140±480
		Browsed - 15 elk km^{-2}				200±75	1690+530
		Browsed - 60 elk km^{-2}				139+85	1350±590
		Unbrowsed		5		256±39	1980±310
		Browsed - 15 elk km^{-2}				287±75	2240±580
		Browsed - 60 elk km^{-2}				283+55	2220±420
Bitterbrush - 26% Cover	Unburned	Browsed, Unbrowsed (no difference)	Observed - Zeigenfuss	1	4	558±229	2268
Bitterbrush- 12% Cover	Burned					304±127	2471

Table 20. Simulated and observed herbaceous biomass in certain vegetation types in the elk "town range" in and near Estes Park. Observed data from Ziegenfuss et al. (2002). Simulated data are from model runs for 5 years beginning with 1994-98 initial conditions and using actual weather data, or from the last 30 years of a 50 year simulation using stochastically generated weather data

Vegetation Type	Grazing-Mowing	Simulated/ Observed	Years	Loca-tions	Grass Biomass g m^{-2}	Forb Biomass g m^{-2}	Total Biomass g m^{-2}
Golf Course	Ungrazed-Unmowed	Simulated	30	1	350-473		350-473
	Ungrazed-Mowed				110-145		110-145
	Grazed-Mowed				90-145		90-145
	Grazed-Mowed	Observed	1	1	145±32		145+32
Rural Slightly Subirrigated/ Irrigated	Ungrazed	Simulated	30	2	226±18	43±11	269±29
			5		173±3	9±1	182±4
	Grazed - 20 elk km^{-2}		30		137±24	12±1	149±25
			5		169±7	8±2	177±7
	Cattle Grazed	Observed	1	1	171	8	179
Urban Lightly Irrigated	Ungrazed	Simulated	30	3	223±23	44±12	268±28
			5		173±6	9±1	182±6
	Grazed - 20 elk km^{-2}		30		145±9	13+1	159+9
			5		169+3	8±2	177±3
Urban Moderate-Heavy Irrigated	Ungrazed	Simulated	30	3	296±23	3±2	299+23
			5		255±30	37±11	293±40
	Grazed - 20 elk km^{-2}		30		285±20	4±2	289±20
			5			37+11	293±39

Table 20 (continued). Simulated and observed herbaceous biomass in certain vegetation types in the elk "town range" in and near Estes Park.

Vegetation Type	Grazing-Mowing	Simulated/ Observed	Years	Loca-tions	Grass Biomass g m^{-2}	Forb Biomass g m^{-2}	Total Biomass g m^{-2}
Rural Moderate-Heavy Subirrigated	Ungrazed	Simulated	30	2	268±18	3±1	71±18
			5		305±32	29±9	335+37
	Grazed - 20 elk km^{-2}		30		240±15	5±1	245±15
			5		305±41	29±9	334±36
	Grazed	Observed	1	1	233	40	273
Rural or Urban Disturbed (some buildings/roads)	Ungrazed	Simulated	30	3	11+1	11+1	22±2
	Grazed - 20 elk km^{-2}				6+1	5±1	11±1

years bracketed the observed values. Two other types were recognized on the model input vegetation map (Figure 12), but were not sampled explicitly. The model shows responses to increased irrigation that are proportional to the difference in NDVI used to classify these types (Figure 12).

Summary

In summary, the model predictions of herbaceous and shrub CAG biomasses, the primary forage items for ungulates, were consistent with available data, however, available data were limited in some cases. Correct levels of production were estimated in both dry and wet environments. A moderate to heavy level of grazing reduced upland herbaceous biomass over the long-term. Herbaceous biomass in willow communities was not affected by observed levels of grazing, but a lack of willow browsing should lead to a decrease in herbaceous biomass. Simulated herbaceous biomass per m^2 of ground and shrub biomass per m^2 of canopy was consistent with available data, and the areal extents of the different vegetation types were represented based on aerial survey-based vegetation maps. Data for shrub canopy cover in shrub vegetation types were limited, but some were available from a few willow and bitterbrush communities. Thus, the total forage available to elk and deer should be reasonably accurate.

MODEL VERIFICATION - THE CONTROL RUN FOR 1949-1998

Description

A simulation was conducted to represent observed ecosystem dynamics for the period 1949-1998. This is referred to as the control run because it represents a set of standard conditions to which results from other model experiments can be compared. Control run output provides additional information for verifying the model's behavior - by comparisons of simulation results to observations. The control run is a calibration run for animal submodels, because key model parameters for diet selection, forage intake, energy use, and population dynamics were calibrated so that model outputs most closely matched observed values.

The control run was driven by observed weather data for the period. The first 10 years of the control run, 1949-1958, were used to allow the model to work through transient dynamics resulting from the selection of initial conditions. Initial conditions might have been different from actual conditions, due to lack of data. Results are presented for the subsequent period 1959-1998. Data from many of the weather stations in the region first became available in 1949, and weather data collection methods also became sufficiently standardized then to form a reliable and complete weather data set for input into the model. This is the primary reason for choosing 1949 as a starting date for the control run.

The simulated elk population was reduced using observed rates of elk reduction by hunter harvest and management removals, as explained above. Rates (i.e., fraction of the population removed per year) were used rather than absolute amounts (e.g., number of elk removed per year), because the use of absolute numbers amplified small differences between population model estimates and observed numbers of animals.

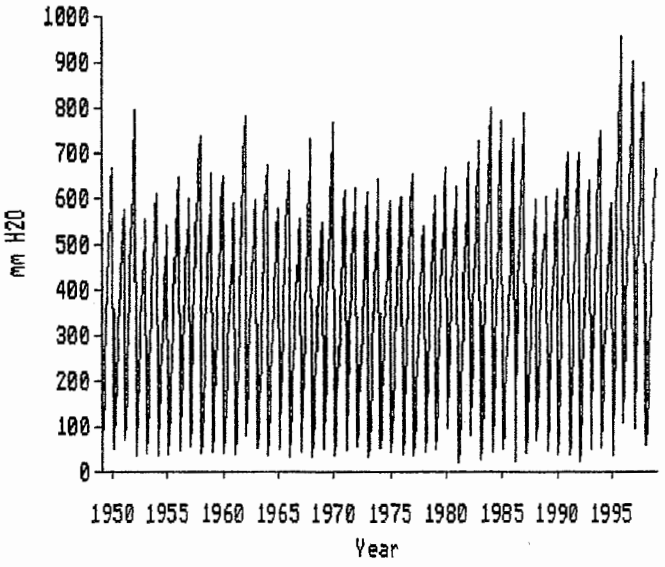
The deer population was maintained within a range of 400-600 animals throughout the simulation by removals as necessary. The only data available were those reported by Stevens (1980). There were apparently only six counts during the period 1949-1979. However, Stevens gives estimates of 675-740 in 1949/50-1951/52, declining to a mean of 343 from 1952/53-1978/79. The beaver population was assumed to decline from 650 in 1949 to 250 in 1964, to 150 in 1976, and 66 in 1998, to fit an interpolated time trend based on the observations of Packard (1947b), Hickman (1964), Stevens and Christiansen (1980), and Gense (1999).

Precipitation and snow

Mean annual precipitation over the domain varied within reasonable limits (Figure 26), showing that weather data inputs were being correctly processed. Mean snow water equivalent over the domain is shown in Figure 26b. There was a trend for increasing snow water, and snowpacks in the years 1995 and 1996 were high. At the same time, snowpack in 1989-1991 was quite low.

Spatial patterns of precipitation were realistic, with precipitation increasing with elevation

A)



B)

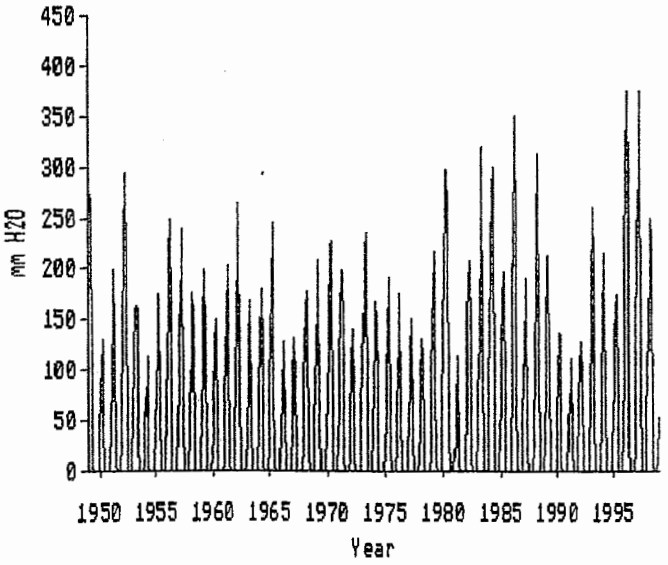


Figure 26. A) Mean annual precipitation over the domain in the period 1949-1998. B) Mean snow water equivalent as simulated.

(Figure 27). This aspect of the model was mainly data-driven, in that simulated data are guaranteed to pass through data values for each weather station as well as fit the observed effect of elevation. However, the spatial output demonstrates that the spatial interpolation algorithm was working properly. Mean annual precipitation ranged from 429-514 mm at lowest elevations to over 1,029-1,114 mm at highest elevations.

The snow submodel was verified by comparisons between observed and predicted data at seven SNOTEL stations 1979-1998 (Figures 28, 29). The locations of the SNOTEL stations are presented in Figure 11. Elevations of the SNOTEL stations ranged from 2,855-3,314 m (8,720-10,700 feet), so represented a wide range of snow accumulation and melt regimes.

The snow model performed satisfactorily at most of the sites. Agreements between observed and modeled data were very good at Bear Lake and Willow Park, the two sites closest to the elk winter range (Figure 28). The closest low elevation site to the winter range was Copeland Lake, where agreements were also satisfactory. Importantly, differences between high snowpack years and low snowpack years were realistically represented by the model. The fit at Lake Irene, a high elevation site not far from Willow Park, was less satisfactory, with the model underestimating the extremely high snowpacks in several years. Despite the fact that Willow Park and Lake Irene are at the same elevation, Lake Irene accumulates more snow, suggesting differences due to wind redistribution, possibly at a fine spatial scale. Estimates for three sites on the west side of the continental divide were generally satisfactory (Figure 29); however, snowpack was underestimated in some years at Joe Wright Reservoir.

The model represented snow depth distributions over the elk range which were consistent with the SNOTEL data (Figure 30). Mean snow depths in December-April ranged from 8 cm to over 400 cm on some sites at high elevations. On the winter range, mean snow depths ranged from about 10 cm to in excess of 150 cm. Generally the upper limit of the winter range had snow depths between 100-150 cm. Snow depths on the town elk winter range were markedly lower than on the park winter ranges. The boundary between town and park ranges fell along mean snow depths of 25-50 cm for the most part. The lowest parts of the Horseshoe Range had depths as low as 15 cm. Simulated dynamics of snow accumulation and melt were reasonable, with snow accumulating earlier and lasting longer at higher elevations.

Hydrology

Simulated streamflows for the Moraine Park and Horseshoe Park watersheds are shown in Figure 31. Flows increased in May in response to snowmelt. Peak flows generally occurred in June, and there were marked declines in streamflow in July. Flows in the Moraine Park watershed were larger than in Horseshoe, as expected given the difference in sizes of the watersheds (Figure 6). The model predicted above average streamflows in 1995-1997, and normal flows in 1998, which is consistent with observations (Zeigenfuss et.al. 2002). Streamflow data for the Big Thompson watershed displayed similar differences between wet and dry years. Observed streamflow was very high in 1995 and 1997, in agreement with the model. However, 1996 streamflow was not much above

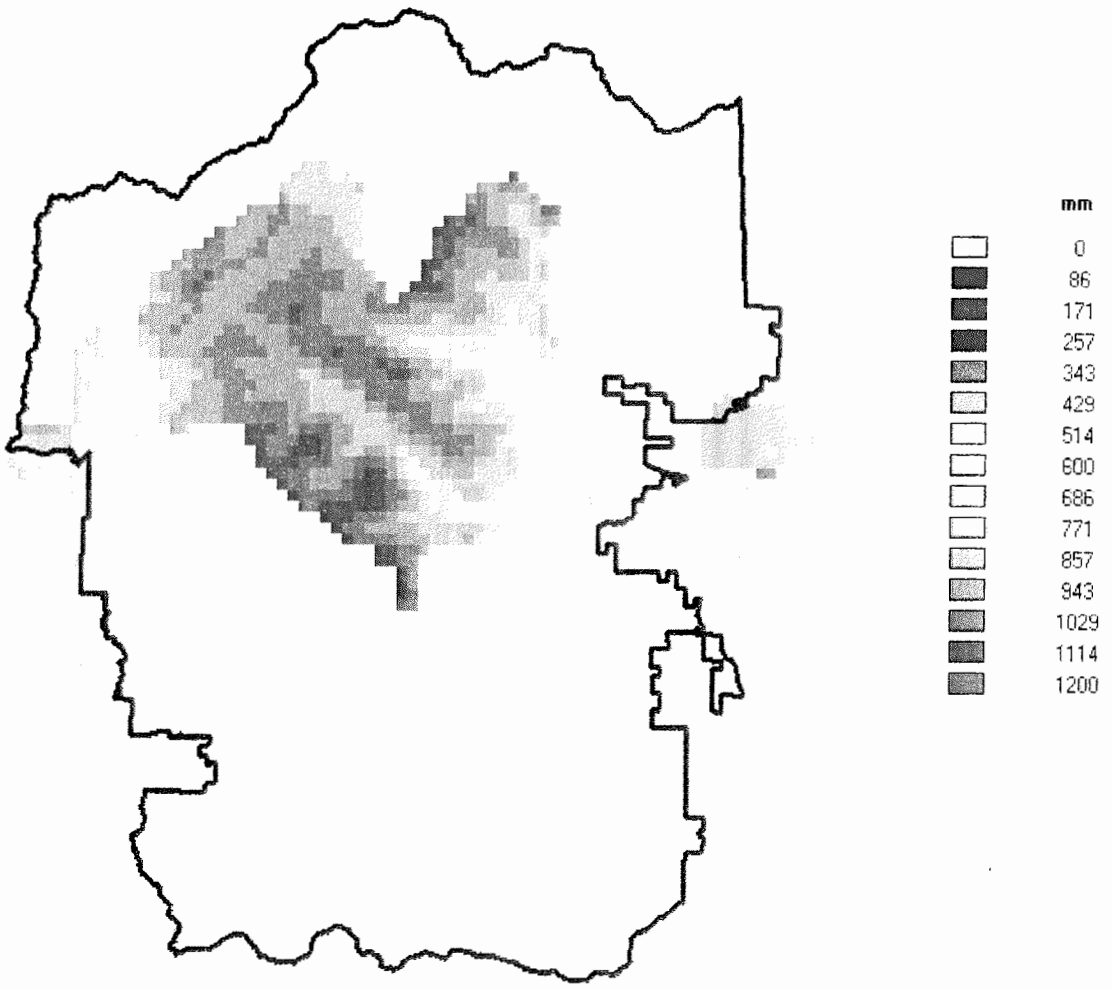
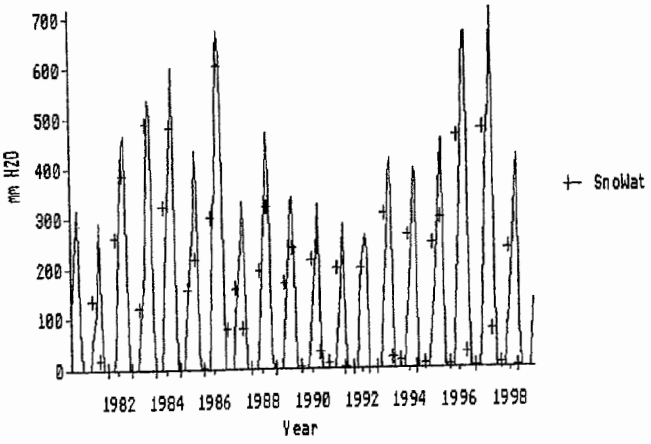
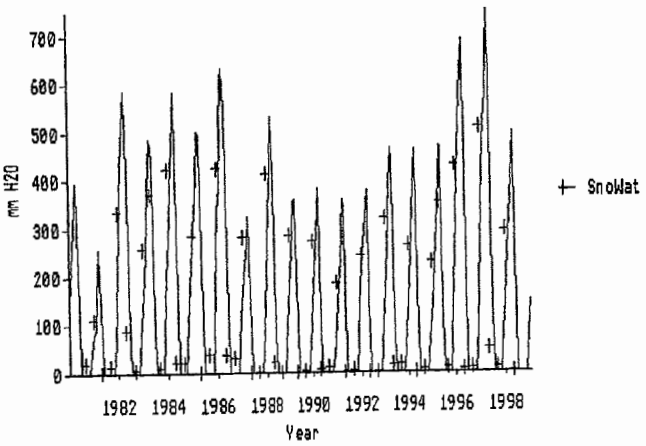


Figure 27. Mean annual precipitation (mm) 1970-1998 on the entire elk range.

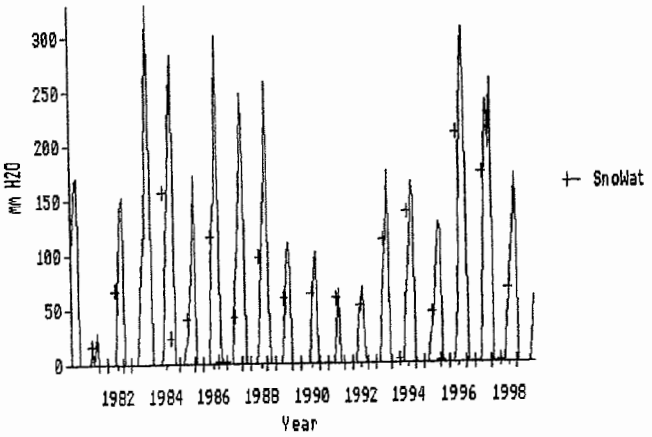
A)



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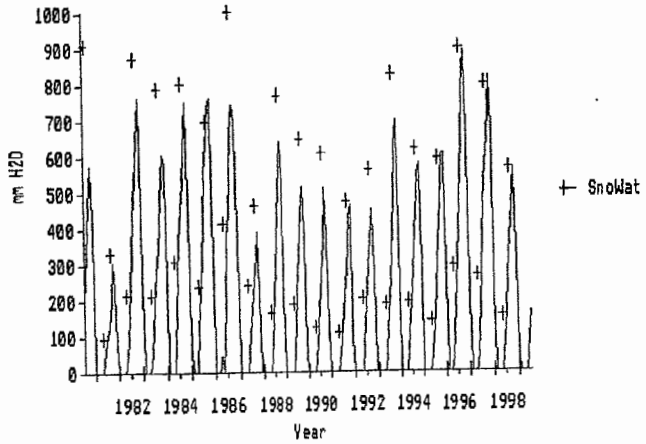
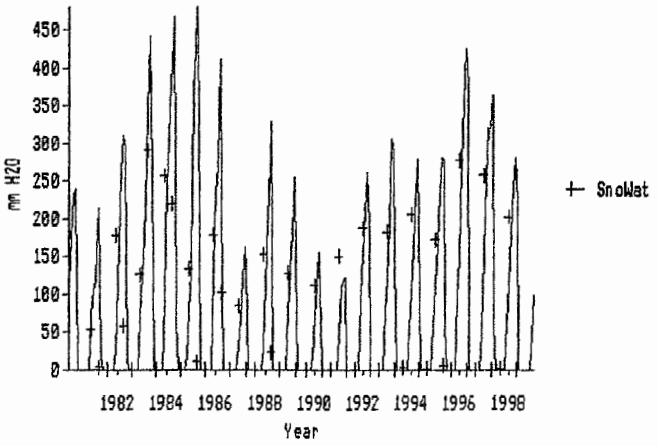
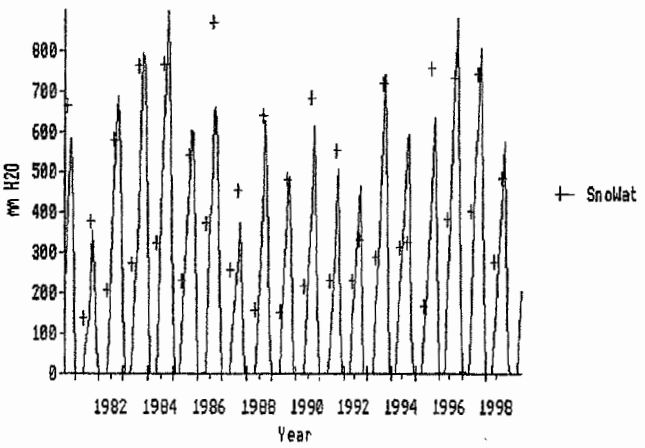


Figure 28. Comparison of observed and predicted snow water contents from A) Bear Lake, B) Willow Park, C) Copeland Lake, D) Lake Irene.

A)



B)



C)

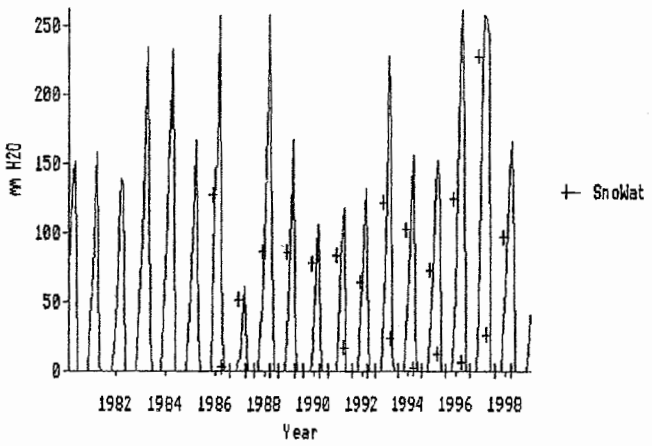


Figure. 29. Comparison of observed and predicted snow water contents for A) Phantom Valley, B) Joe Wright Reservoir, C) Stillwater Creek.

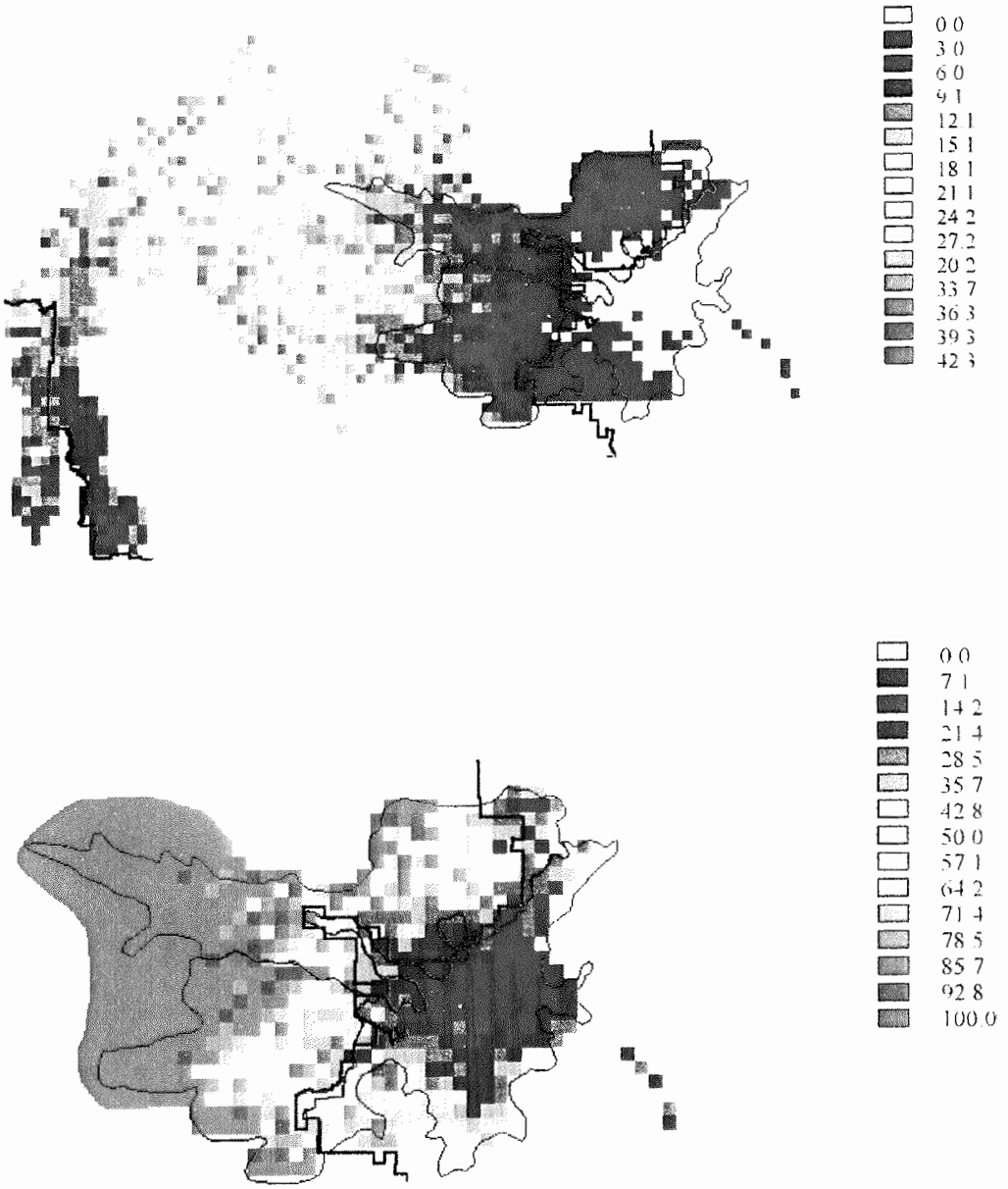


Figure 30. A) Mean snow depth (cm) on the entire elk range December-April. 1970-1998. B) Snow depth map with output rescaled for increased resolution on the elk winter range.

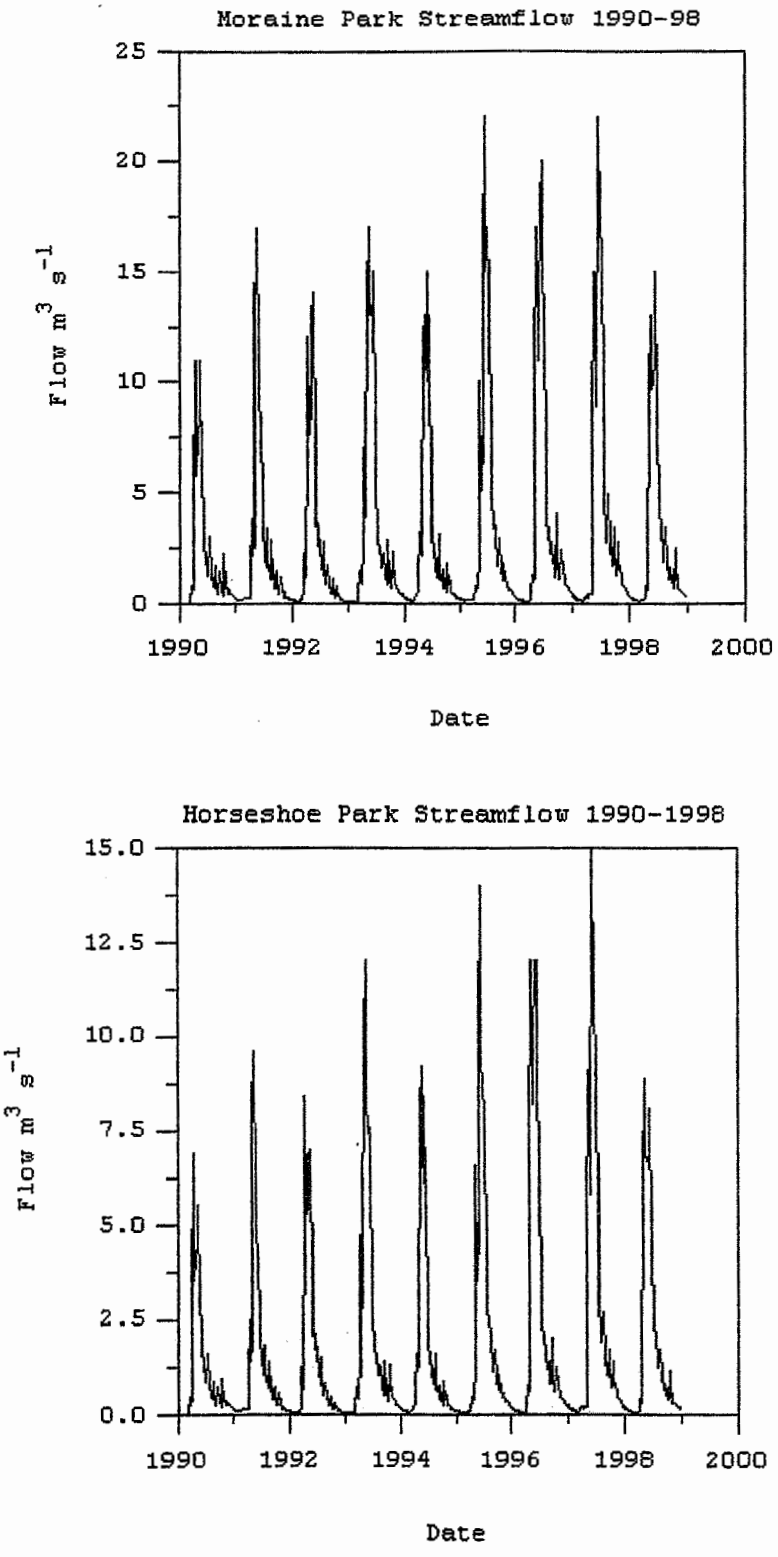


Figure 31. Interannual patterns of simulated streamflow 1990-1998.

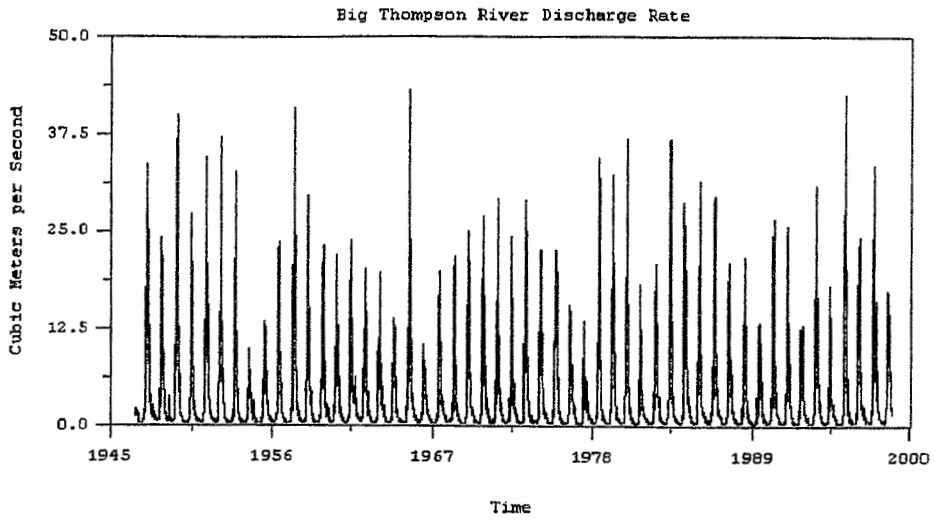
average (Figure 32).

Water table depths in riparian willow stands (Singer et al. 1999, Zeigenfuss et.al. 2002) (Figure 20) were used to parameterize model relationships between water table depth and streamflow in the watershed. These relationships were then used in the model to estimate water table depths for different willow sites within each watershed. As expected, water table depths became shallower with increasing streamflow (Figure 33). Correlations ranged from an r^2 of 0.33 to an r^2 of 0.79, and all were significant at $p<0.001$.

Elk populations and spatial distributions

The elk population model was calibrated to observed, sightability-corrected count data 1959-1998 (Figure 34). The model was calibrated to pass through the higher of the reasonable data points, on the assumption that lower values were undercounts. The model simulated the correct rate of population increase, and most importantly, represented the leveling-off of the park population during 1980-1998. This indicates that the model was representing density dependent competition for food, and thus food-limited carrying capacity, correctly. The model did not predict the wide fluctuations in population size that were present in the count data, and so did not pass through lower-valued data points. There are at least two explanations for this. One is that elk moved in and out of the counting area from year to year. This is supported by the analysis of Lubow et al. (2001), who found better fits of a simple population model to data when account was made of movements between the park and town subpopulations. There was clearly an over count in 1983. It is possible, but unlikely that there was an influx of 300 or more elk in that year that was not represented by the model. The other explanation is that some of the count data are underestimates, even after being statistically corrected for sightability. The corrections are based on mark-recapture statistical methods, and while they improve accuracy, the corrections are not guaranteed to be 100% accurate either. The model is constrained to realistic rates of population increase, which suggests that the observed fluctuations appear to be unreasonable, biologically. The rate of increase of the town population was correctly simulated (Figure 34b), indicating that the parameterization of elk outmigration from the park to the town population was consistent with data.

There was a clear decline in the ratio of calves to cows over the period 1949-1998 (Figure 35). This is consistent with data, and with the hypothesis that the elk population was exhibiting a density-dependent limitation on recruitment. Data from 1965-1978 showed calf ratios of 19-53, with a mean of 36.(Stevens 1980, Lubow et al. 2002), which is consistent with model output. An exceptionally low ratio was observed in 1973, when 19 calves:cow were observed. The model predicted this ratio exactly. In contrast, in 1972, 44 calves:cow were observed. The model predicted 46. In 1974 a ratio of 39 was observed, while the model predicted 40. This is strong support for the model's ability to separate the effects of density dependent limitations due to competition from density-independent effects due to snow cover and forage biomass. Interestingly, the model did not predict a markedly high snowpack in 1973 (Figure 26b), suggesting that fine timescale dynamics not evident in Figure 26 were responsible for the low calf ratio. There were no calf ratio data for the period 1979-1983. Ratios in 1984-1991 varied from 15-56, with a mean of 33 (Lubow et al. 2000).



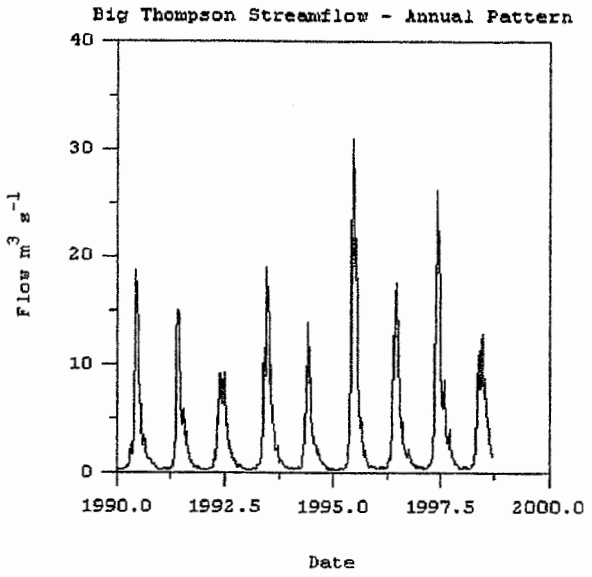


Figure 32. Observed streamflow data for the Big Thompson River, from the gauge above the dam at Lake Estes. A) Long-term daily. B) Weekly means 1990-1998.

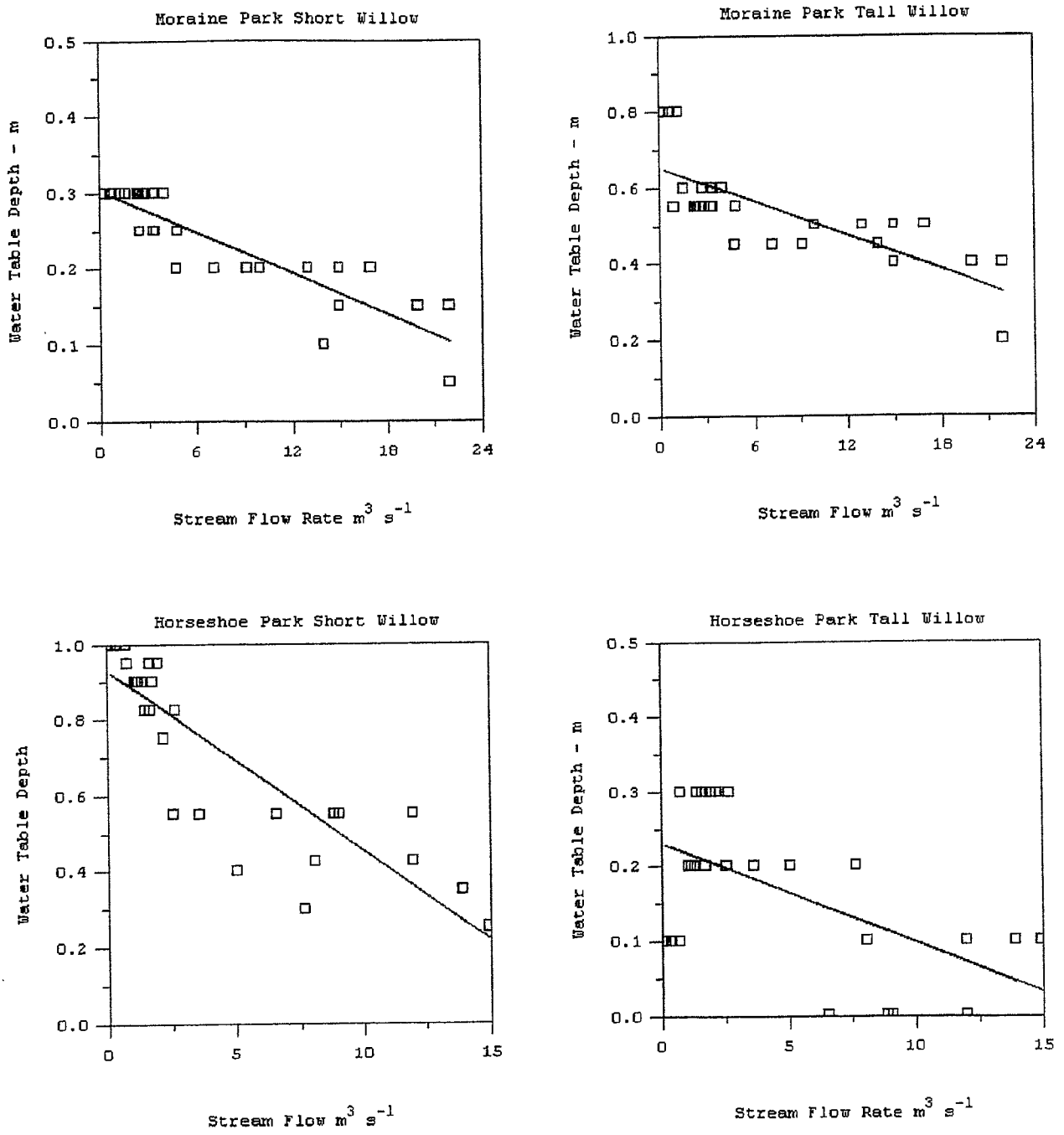
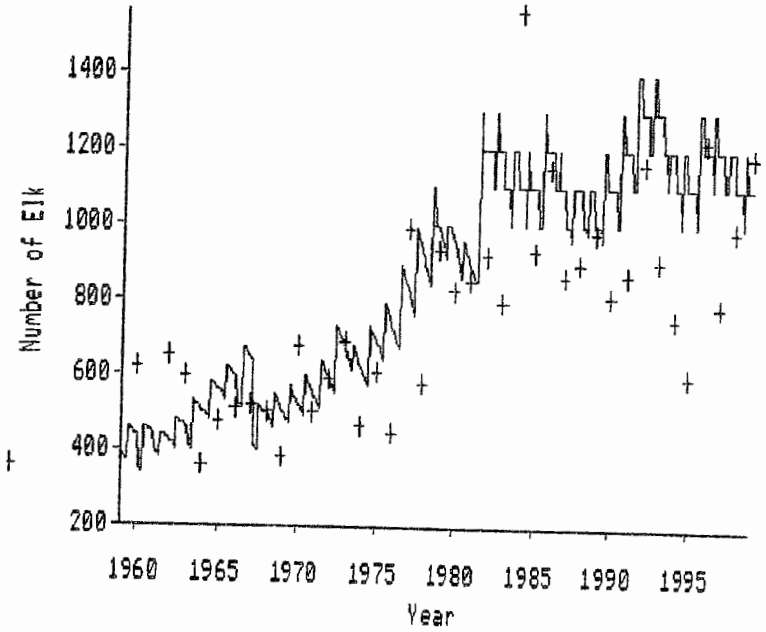


Figure 33. Relationships between simulated streamflow in Moraine and Horseshoe Parks and water table depths observed in short and tall willow by Zeigenfuss et al. (2002) The regression equations were used in the model to link water table depth to simulated streamflow.

A)



B)

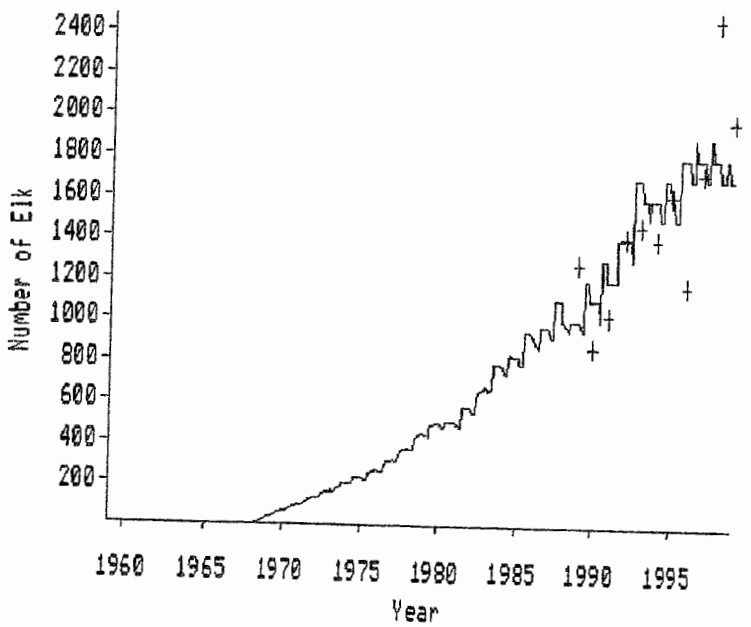
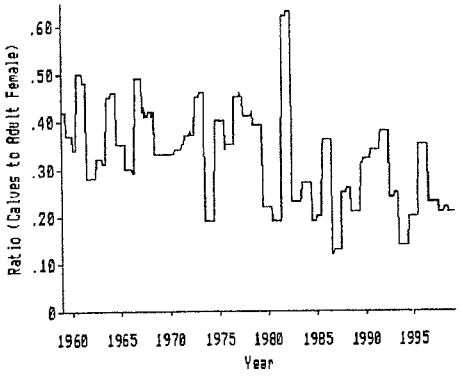
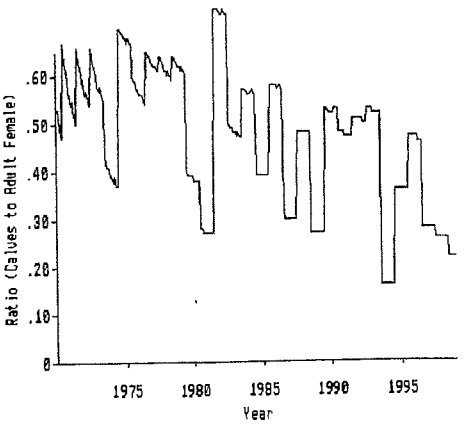


Figure 34. Simulated (lines) and observed (points) population dynamics for A) the park elk herd and B) the town elk herd.

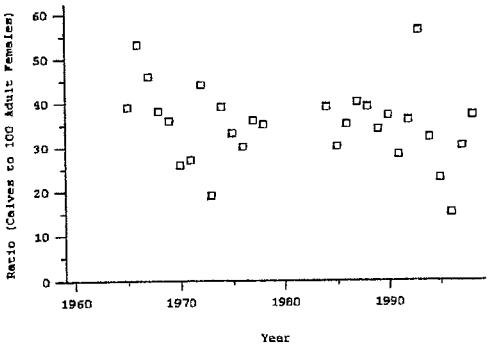
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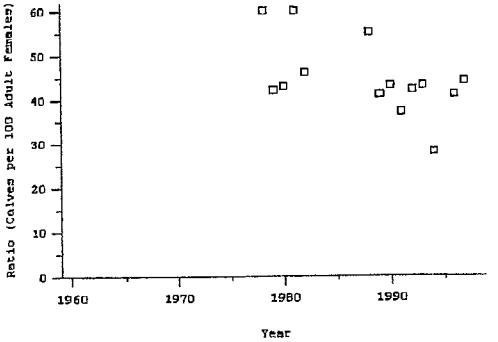
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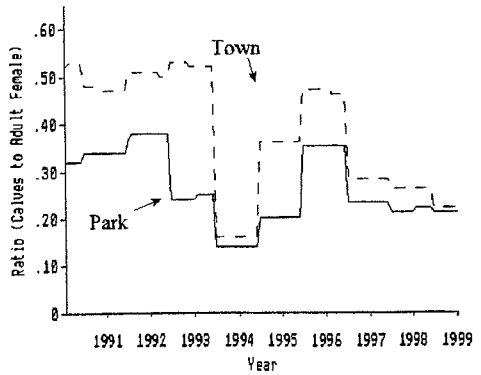
C)



D)



E)



F)

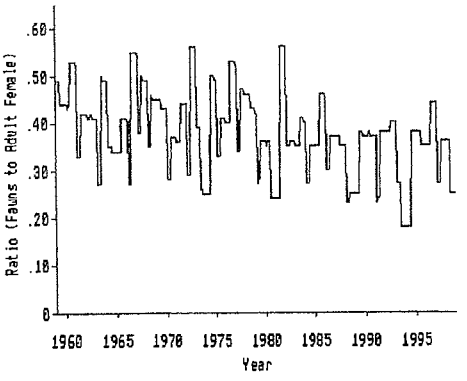


Figure 35. A) Calf:cow ratios for the park elk herd. B) Calf:cow ratios for the town elk herd. C) Observed calf ratios for park herd. D) Observed calf ratios for town herd. E) Detail comparing park and town calf:cow ratios 1990-1998. F) Fawn:doe ratios for the deer herd.

Model predictions were generally consistent with this range, and with the decline in calf ratio compared to the earlier period. Comparisons of year-by-year ratios were not as consistent. Ratios for the town population were also generally consistent with observed data (Figure 35). The notable decrease in calf ratio over the observation period was also simulated by the model. Ratios predicted by the model were in the range that was observed. The consistency of these predictions with observed data lends support for a correct parameterization of the effect of body condition on recruitment rate.

Simulated spatial distributions of elk were in agreement with observed data (Figure 36a). High densities of up to 90 elk km^{-2} were simulated in the Moraine Park area. High densities were also simulated in certain areas of Horseshoe Park, but overall density was less than in Moraine Park. These densities are consistent with the contour maps generated from aerial survey data (Singer et al. 2002), which show density contours of 12-16 km^{-2} in Horseshoe and >90 km^{-2} in Moraine Parks. The aerial survey data do not include sightings from the town population range (due to restrictions on flying over town), so contours slope to zero around the edge of the park population range. The model simulated moderate to high densities throughout the town range. Caution should be exercised in comparing contour data to grid-cell model outputs, because contour data may smooth over fine-scale variations, depending on the resolution of the underlying interpolation. A further limitation of aerial survey data is that they are snapshots in time, while the model results are integrated over the entire January-April period.

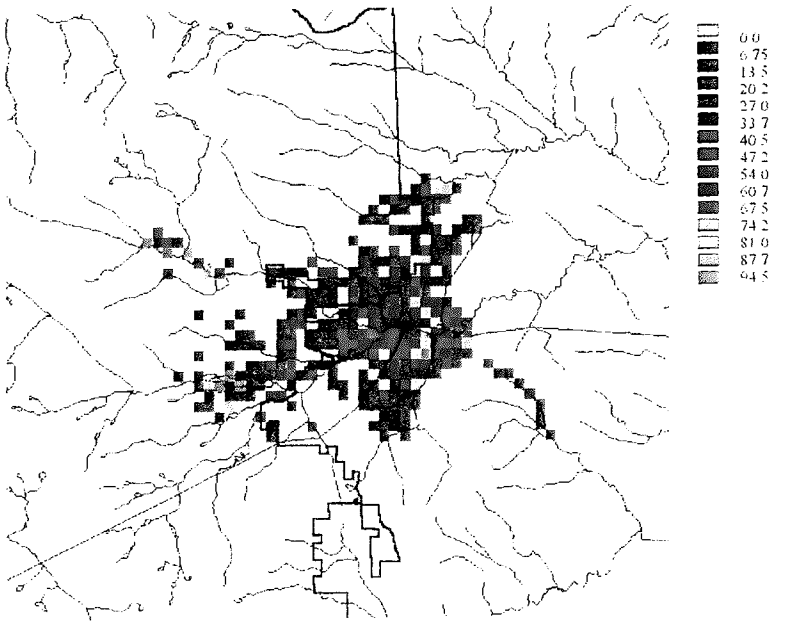
The model simulated ecologically reasonable distributions in summer (Figure 36b). Highest densities were simulated in riparian areas at high elevation. Moderate densities were simulated on alpine and subalpine meadows and tundra. Lower densities were simulated on the lower elevation areas of the western slope, with the exception of a few grid-cells in low elevation willow along the western park boundary. No density data existed for elk on their summer range.

A comparison of simulated elk density distributions in winter and summer to the density of elk radio locations (Larkins 1997) was favorable (Figure 37). An exception was that the model simulated elk use on the northeast portion of the winter range inside the park boundary, while the radio location data did not show any elk there. The aerial survey data showed high concentrations of elk just outside the park boundary in that area (Singer et al. 2002).

Plant production and offtake

Before presenting these outputs it is necessary to explain that although the model simulated the entire park and town herd winter and summer ranges, the temporal outputs presented below are averages over the park herd winter range only, the area of prime concern. Outputs are expressed in units of grams biomass per square meter of area where the plant group in question is located on the winter range. For example, riparian mesic grass only occurs on a small percentage of the total area. Biomass on that area may be 150 g m^{-2}, but if it were averaged over the entire range, the biomass would drop to a much smaller value due to zero biomass on non-riparian areas. Similarly, woody cover values are reported for the grid-cells having that vegetation type, not for the entire winter range. The vegetation classification was not changing during the runs, so the number of grid-cells

A)



B)

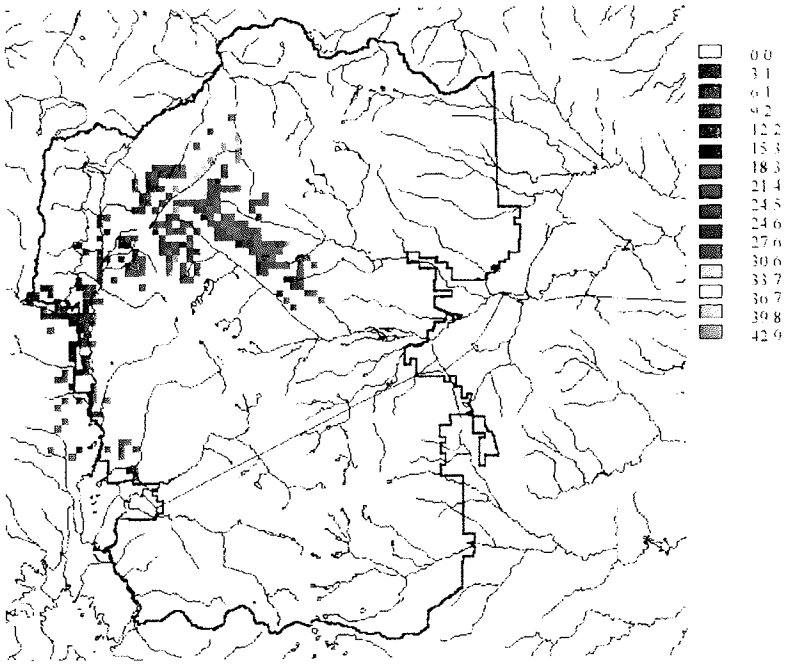


Figure 36. A) Simulated mean elk density distribution (elk km^{-2}) on the winter range during January-April 1994-1998. B) Simulated mean elk density distribution on the summer range during June-August 1989-1998.

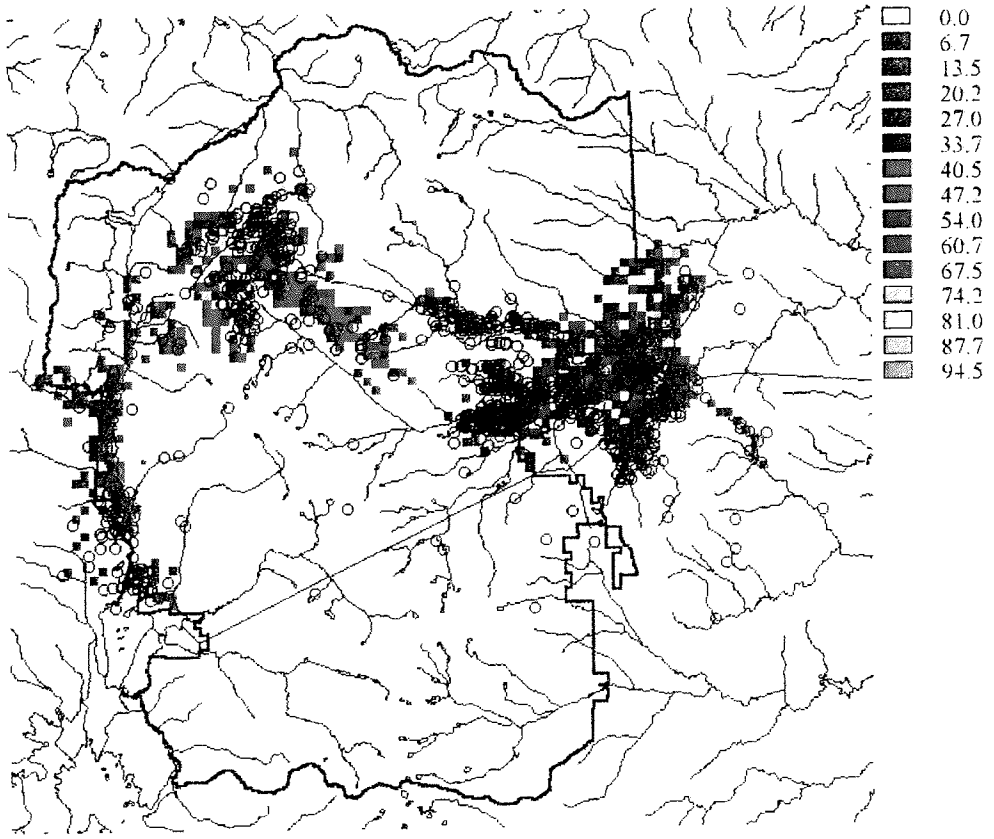


Figure 37. Comparison of simulated elk density distributions (elk km^{-2}) in summer and winter with density of elk radio locations as observed by Larkins (1997).

having each vegetation type was fixed throughout.

Dryland grass and forb biomass increased slightly over the simulated period (Figure 38a,b). This is not necessarily a depiction of reality, since there were no data to accurately initialize the model in 1949. The increase may simply be a gradual adjustment, or equilibration to conditions. Mesic grass decreased slightly, while mesic forb increased relative to initial conditions. What these outputs do show, is that there would be have been no wholesale degradation or loss of productivity due to elk grazing, averaged over the entire winter range. Offtake levels as a percent of biomass were low when averaged over the entire park winter range. With current elk densities, total offtake was only about 20% of grass biomass, forb offtake was less than 5%, mesic grass offtake was <10%, and mesic forb offtake was <10% of biomass. Because these are domain averages, offtake was likely to be much higher in winter elk concentration areas.

The model predicted a reasonable spatial distribution of herbaceous biomass over the winter and summer ranges (Figure 39). Peak biomass generally ranged 40-150 g m^{-2} on the winter range, on grassland, shrubland, and Ponderosa pine woodlands. Low production was simulated in the subalpine forests (20-40 g m^{-2}). Higher biomass levels were simulated on the alpine tundra, and subalpine meadows. Aboveground net primary production was not much higher than peak standing crop.

The spatial distribution of herbaceous offtake by elk was a reflection of elk distribution, and herbaceous forage biomass (Figure 40). Much of the winter range experienced low offtake, either due to low elk density or low production. Offtake varied spatially over a sevenfold range. Most of the summer range was not grazed. The highest offtake was on the alpine tundra and subalpine meadows. The percentage offtake varied over a smaller range (Figure 41). Offtake during 1989-1998 was 7-20% over most of the winter range. However, there were certain areas where offtake was 40-70%. A few areas experienced offtake rates of >70%. On the summer range, offtake was estimated at 40-60% on most of the alpine and subalpine grasslands. Forest biomass was generally <15%.

Live root biomass fluctuated between lows at the end of winter, to highs at the end of summer (Figure 42a,b). The long-term root biomass trend followed that of aboveground biomass. Root:shoot ratios were approximately 2:1 for the herbaceous plants. The spatial distribution of live root biomass was similar to the spatial distribution of aboveground biomass (Figure 43a). Root biomass was generally in the 60-130 g m^{-2} range on the winter range. On the tundra it reached 400-500 g m^{-2}.

Plant litter on the soil surface did not closely reflect the distribution of aboveground herbaceous biomass (Figure 43b). For example there was more litter biomass on forest floors than in the alpine tundra, despite the reverse pattern for herbaceous biomass. This was due to the input of slowly decomposing needle and branch litter. On the winter range, the spatial pattern of litter biomass showed less fine-grained variation than herbaceous biomass, indicating that some areas with high herbaceous biomass had lower than expected litter, possibly due to high offtake and decomposition.

Basal cover of dryland grasses and forbs remained relatively constant over the course of the

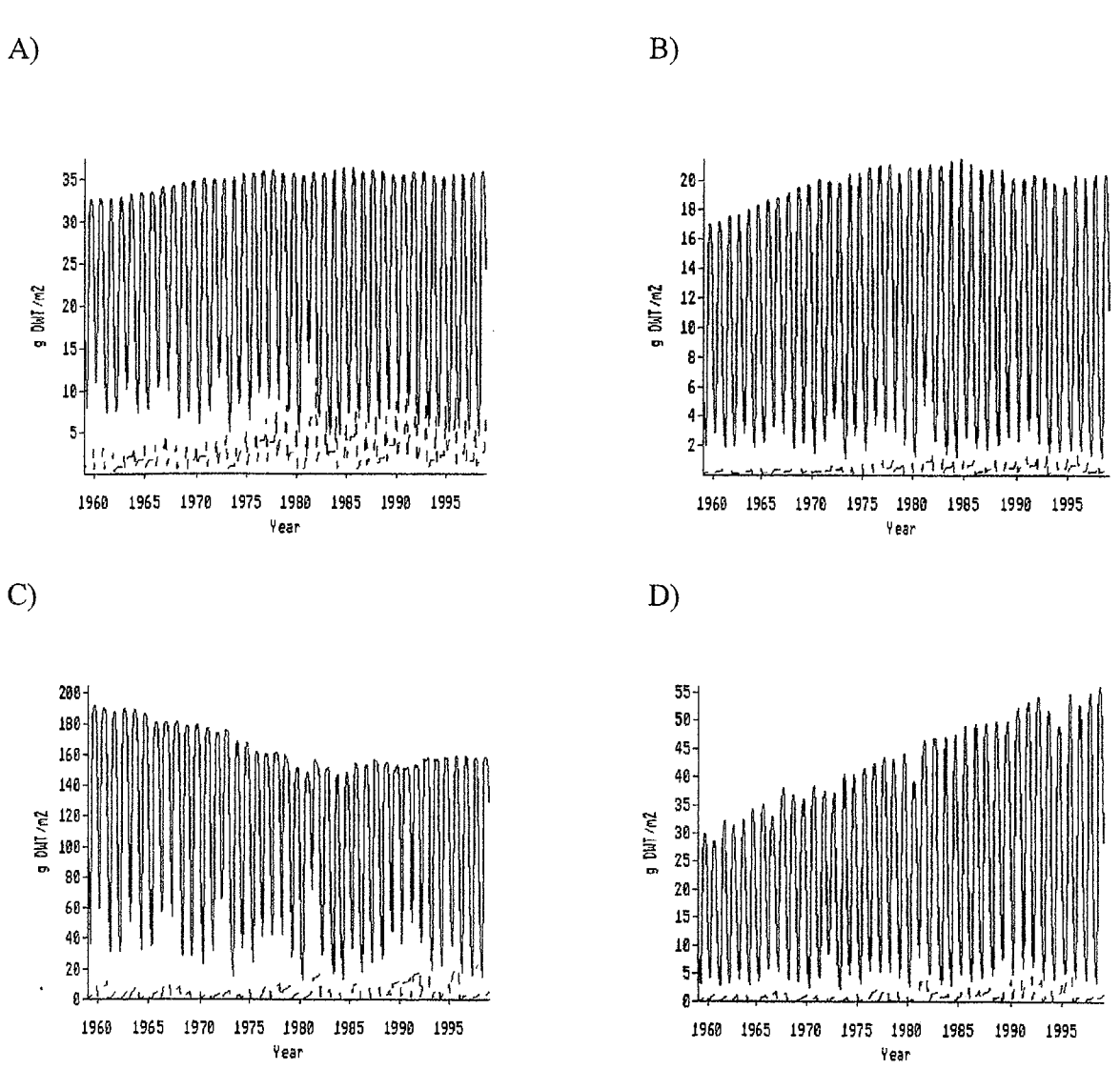


Figure 38. Simulated aboveground biomass and offtake in the control run for A) dryland grasses, B) dryland forb, C) mesic grasses, D) mesic forbs. Biomass is mean grams per square meter in vegetation types where the plant group is found. Dryland grasses are found in dry grasslands, shrublands, and Ponderosa pine woodlands. Mesic species are found in riparian willow communities and subirrigated wet meadows.

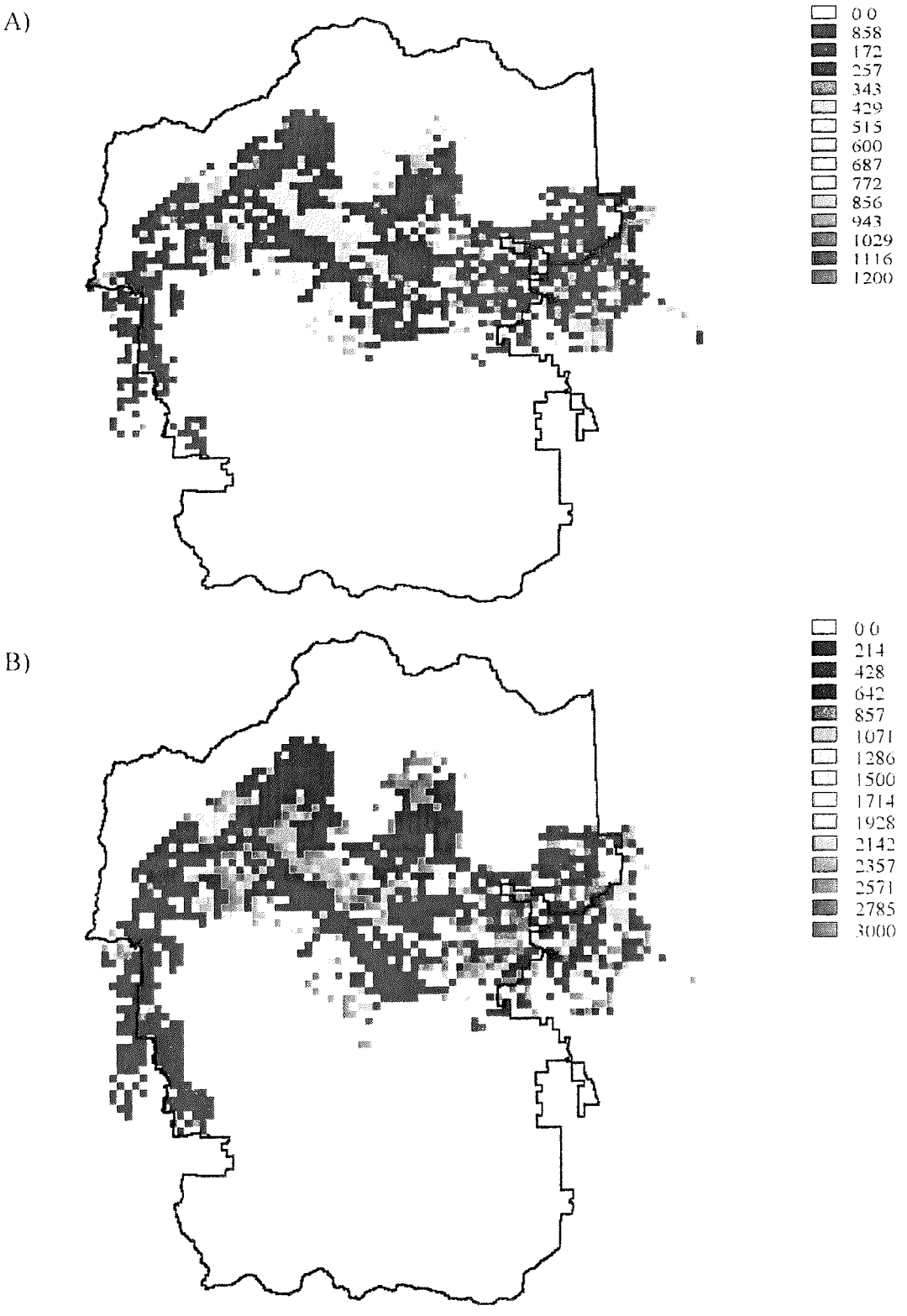


Figure 39. A) Peak aboveground standing crop of herbaceous plants on the elk range (kg/ha) mean 1989-1998. B) Aboveground net primary production of herbaceous plants (kg ha^{-1}).

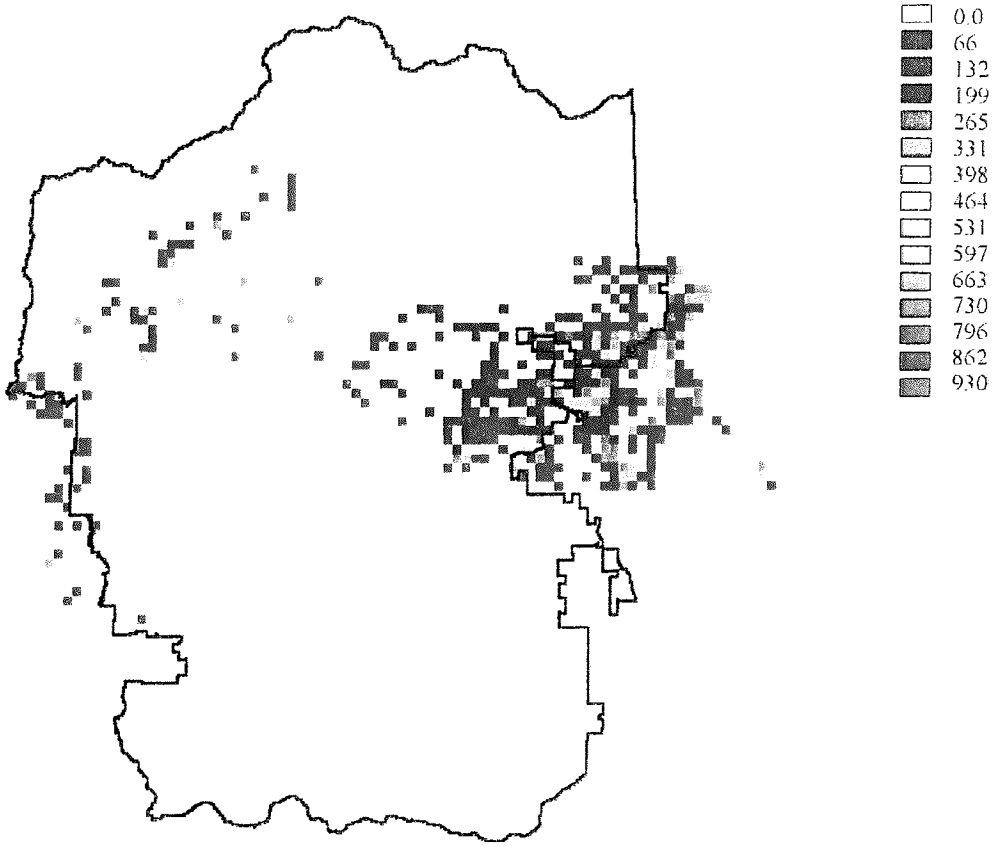


Figure 40. Annual offtake of herbacous biomass (kg ha^{-1}) by elk 1989-1998.

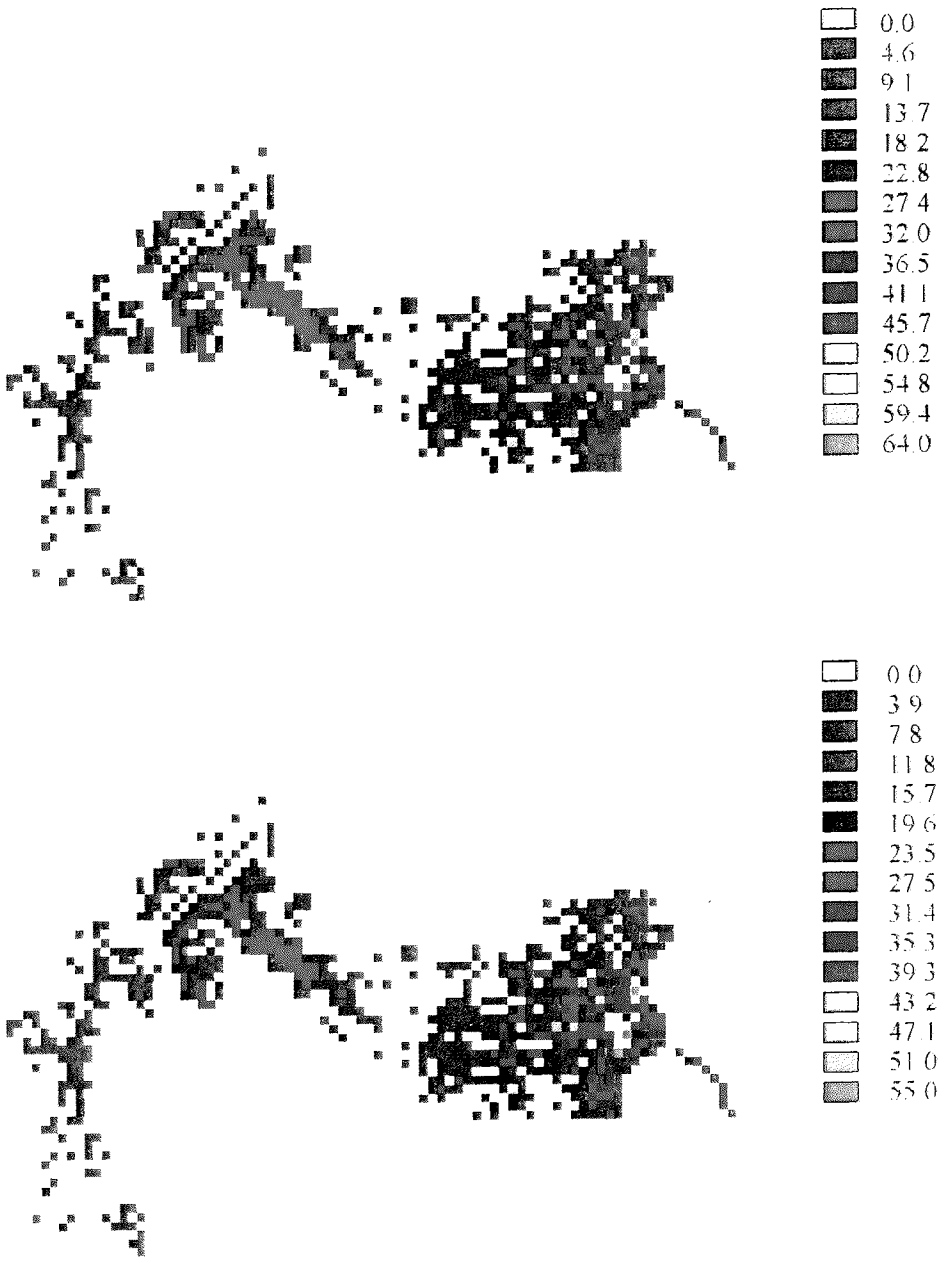


Figure 41. A) Offtake of herbacous plants by elk as a percentage of peak standing crop. B) Offtake of herbaceous plants by elk as a percentage of aboveground net primary production.

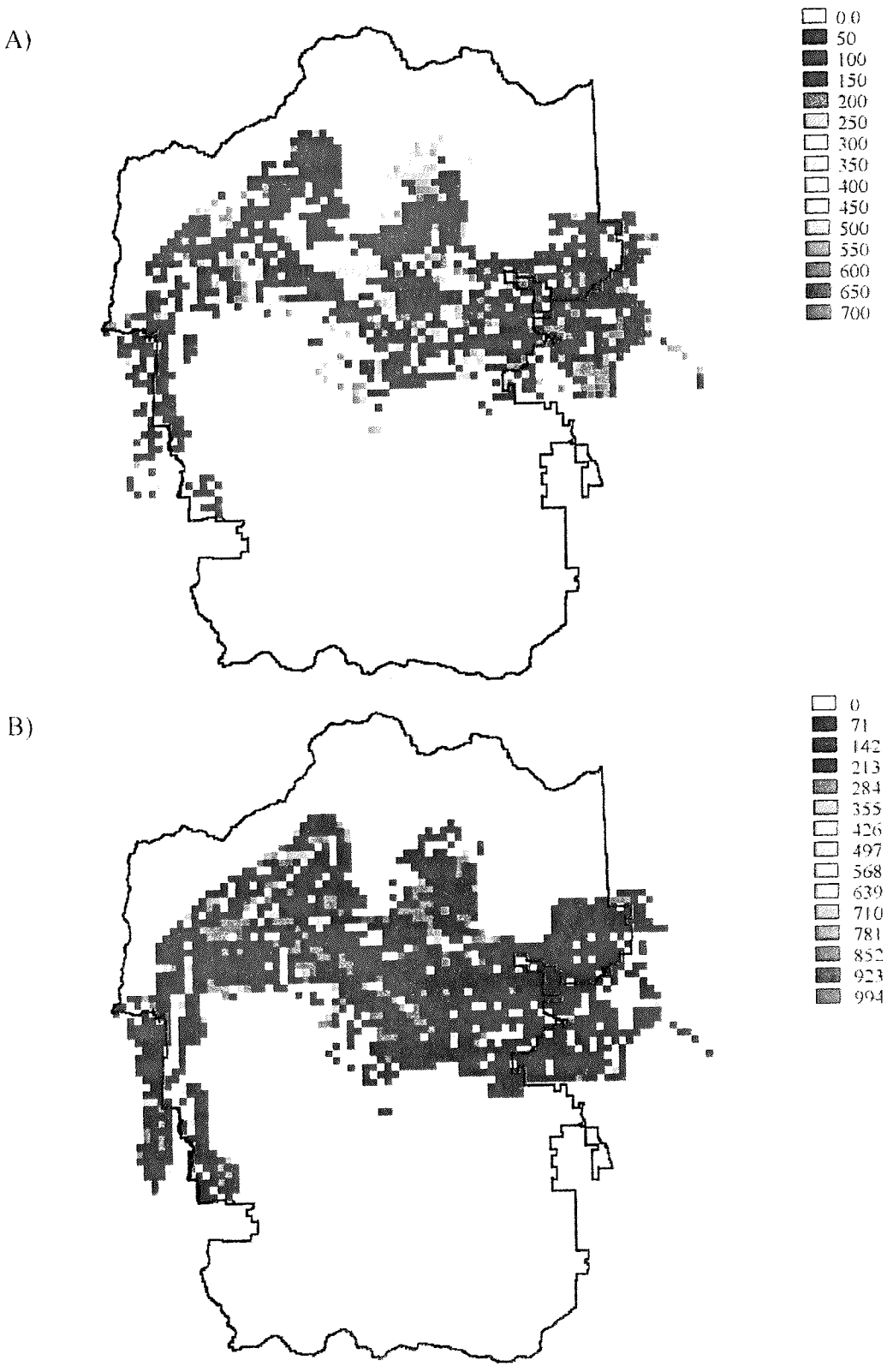


Figure 43. A) Mean root biomass (g m^{-2}) in summer, 1989-1998. B) Mean surface litter carbon (g m^{-2}) in summer 1989-1998.

simulation (Figure 44a). Mesic grass basal cover decreased, while mesic forb cover increased (Figure 44b). Upland shrub cover remained essentially constant at about 5%, partly as a result of the fact that shrub population dynamics were not simulated, but also because herbivory had little impact. Willow cover increased slightly, while aspen cover decreased slightly (Figure 44c) Montane conifer (pine) and subalpine cover (conifer) increased slightly, reflecting tree growth, rather than an increase in plant numbers, since population dynamics were not simulated.

Upland shrub CAG and leaf biomass varied seasonally, reaching about 12-14 g m^{-2} each year (Figure 45a). Offtake of upland shrubs was very low (<10%). Willow CAG and leaf biomass reached 100 g m^{-2}, and offtake was 60-70% (Figure 45b). The spatial distribution of willow offtake by elk was heterogenous (Figure 46). Offtake was highest in Moraine Park, reaching over 47%. Highest offtake rates in Horseshoe Park were in the 40-44% range. Offtake was in the 37-44% range in half of the grid-cells. Offtake was in the 25-37% range in 40% of the cells. Offtake was over 44% in 17% of the cells.

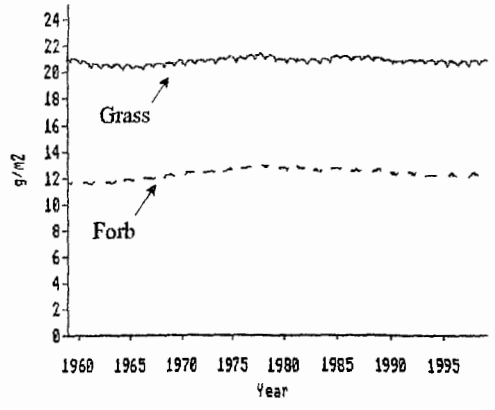
Aspen leaf and CAG biomass was about 175 g m^{-2}. Offtake was high at first, but declined to <10% after 1975. The early high level of offtake probably reflected a) higher beaver densities and beaver cutting down trees that had accumulated biomass from earlier growth, and b) browsing of younger plants within the reach of elk. Once beaver declined and had cut down available trees, and once elk had suppressed younger plants, the offtake rates were reduced. The fact that aspen biomass increased while cover declined was due to an increase in tree sizes throughout the simulation. Ponderosa pine biomass increased gradually reflecting an increase in plant size. Offtake of pine was essentially zero (Figure 45d).

Leaf nitrogen concentrations varied within the ranges prescribed in Table 2 (Figures 47,48). N concentrations were highest in the early growing season, reflecting a preponderance of young leaf tissues. The prescribed seasonal variation in leaf N concentration represented cell wall thickening and lignification, and increased C input relative to N, which together dilute leaf N.

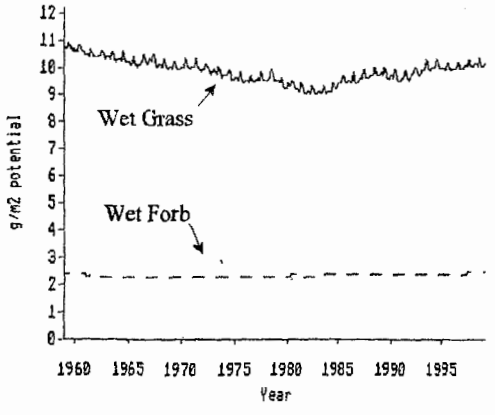
Herbivore diets, forage intake rates, and condition indices

Winter (Nov.-May) elk diets consisted of 35-40% dryland grass and 5% dryland forb (Figure 49a). This period includes one month of free access to all of the winter plus summer range (May) during which ranges are used in response to snow and forage distributions. Mesic grasses comprised 3-10% of elk diets, while mesic forbs only comprised 1-2%. Upland shrub comprised 8-15% of winter elk diets. The proportion of willow in winter diets ranged from 20-35%. Aspen comprised <0.5% of winter elk diets. In comparison, Stevens (1980) noted winter diets were 56% dryland grass, 20% mesic grass, 5% forb, 16% willow, 3% shrub, and a trace of aspen. Hobbs (1979) found 45% dry grass, 16% mesic grass, 6% forb, 11% willow, 13% shrub, 7% aspen. Singer et al. (2001b) found 40% dry grass, 18% mesic grass, a trace of forbs, 10% willow, 0% shrub, 12% pine, and traces of aspen. Riorden (1948, cited by Stevens 1980) found 79% grass, 8% forb, 8% willow, and 5% aspen. The model therefore appeared to estimate reasonable proportions of dry grass, forb, shrub, aspen. The model may overestimate willow dietary proportion, and underestimate the proportion of mesic

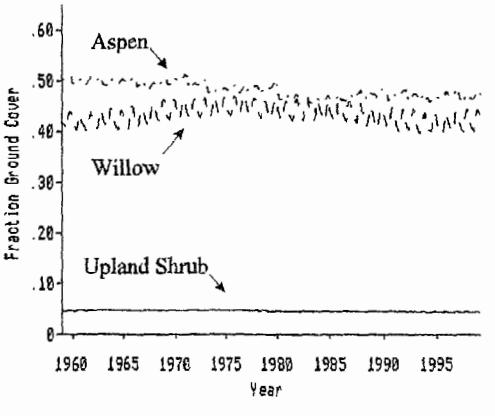
A)



B)



C)



D)

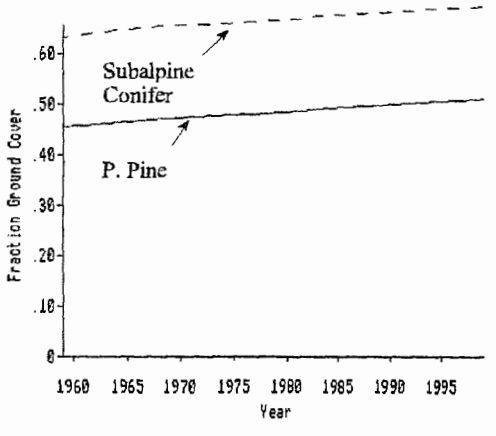


Figure 44. Basal cover of A) dryland grasses and forbs, B) mesic grasses and forbs. Canopy cover of C) willow, upland shrub, and aspen, and D) Ponderosa pine and subalpine conifers.

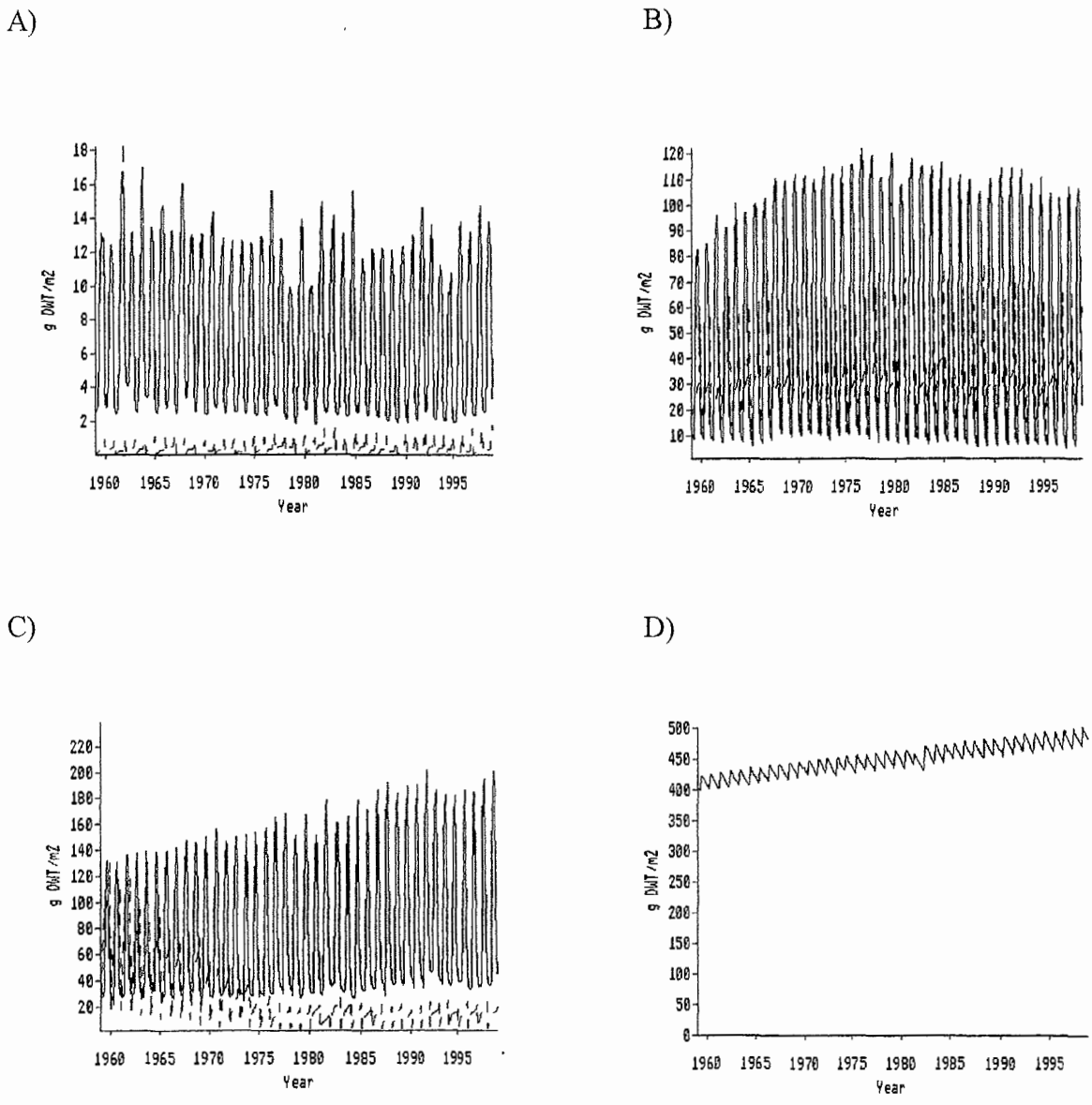
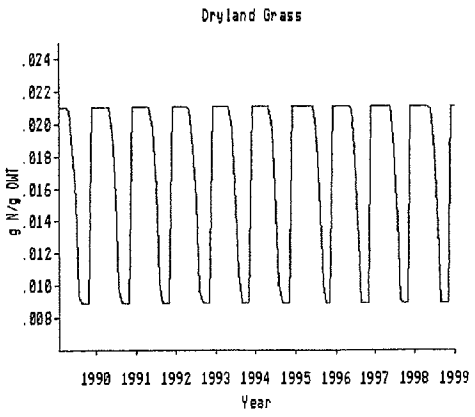


Figure 45. Simulated aboveground biomass and offtake in the control run for A) upland shrubs, B) riparian willow, C) aspen, D) Ponderosa pine. Biomass of woody species includes leaves and current annual growth twigs only.

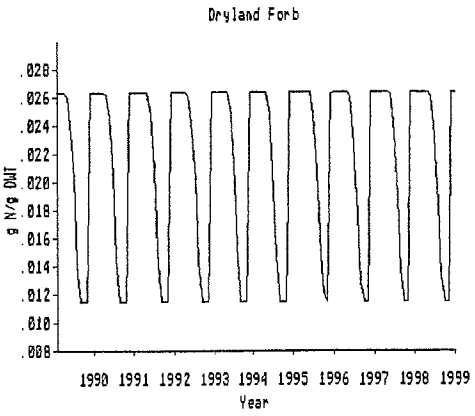


Figure 46. Offtake of willow by elk on the winter range, as a percentage of annual shoot production.

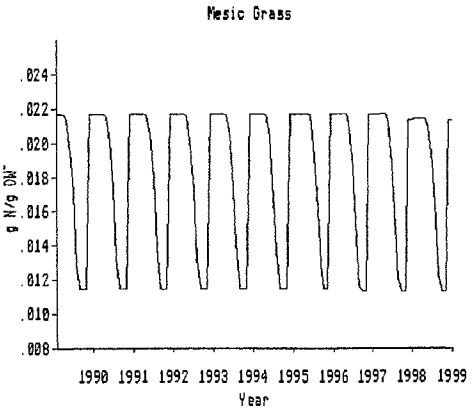
A)



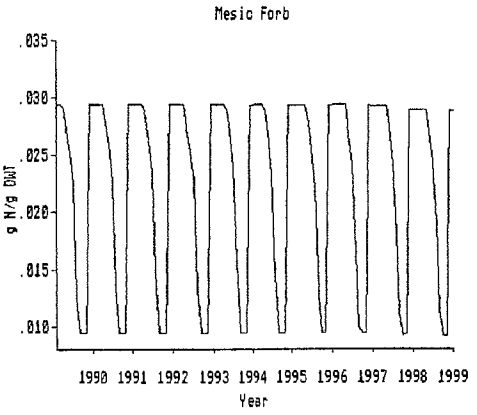
B)



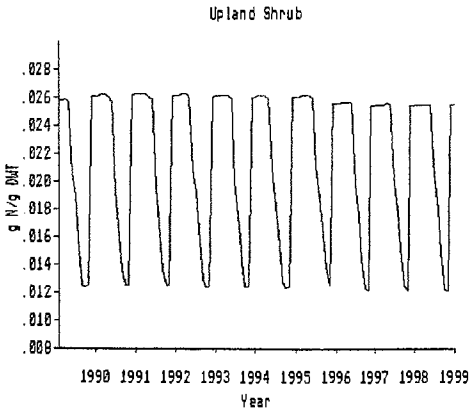
C)



D)



E)



F)

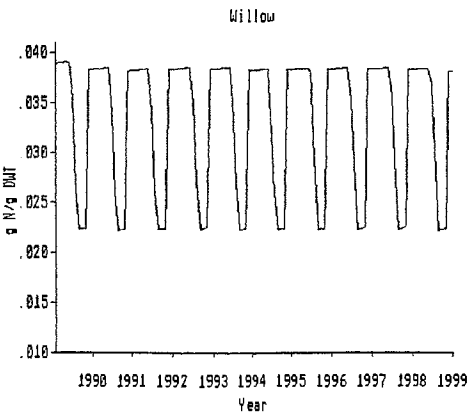
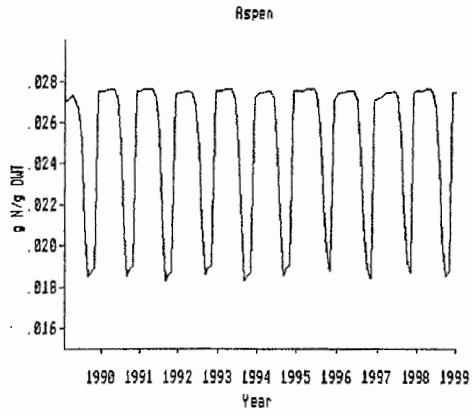
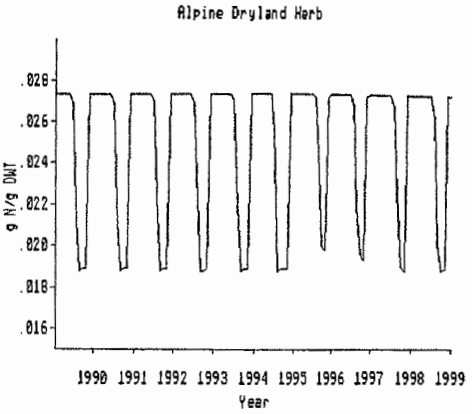


Figure 47. Nitrogen concentrations in green leaves of plants on the winter range expressed as grams N per gram of dry weight (DWT) biomass.

A)



B)



C)

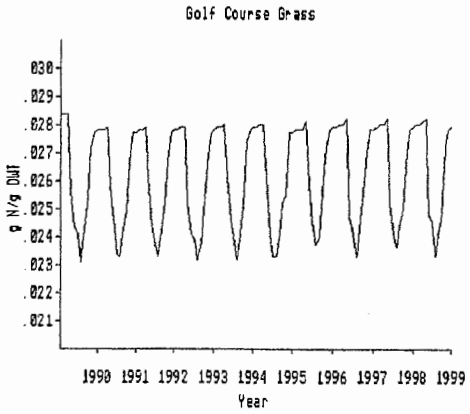
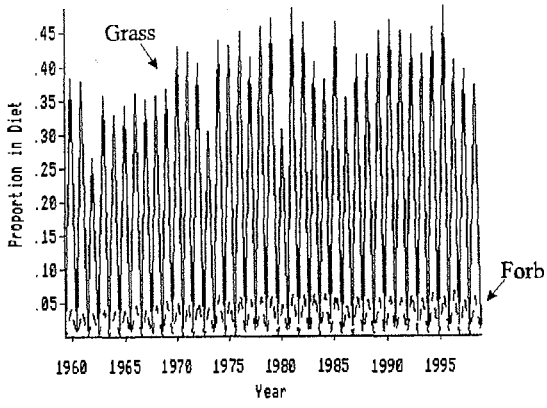
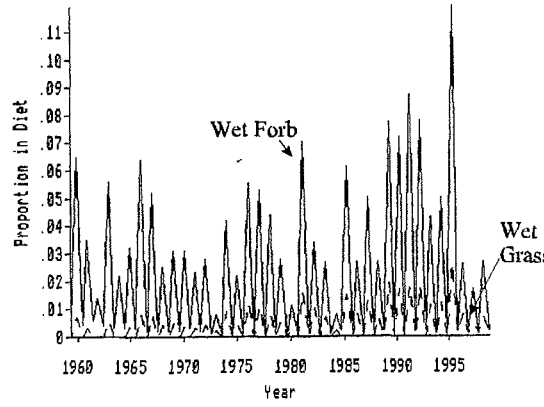


Figure 48. Nitrogen concentrations of plants on the summer and winter range, expressed as grams N per gram of dry weight (DWT) biomass.

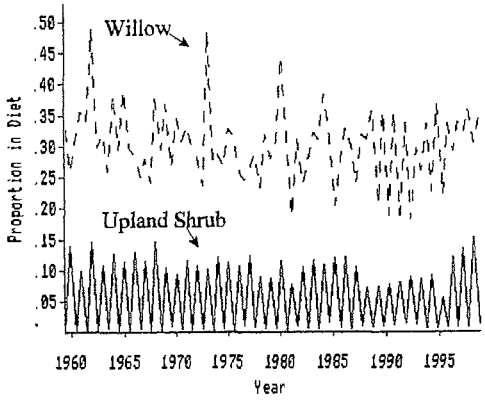
A)



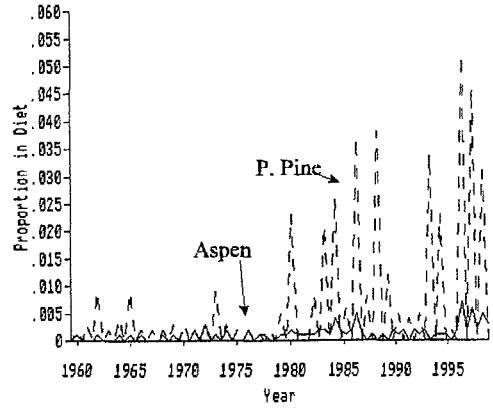
B)



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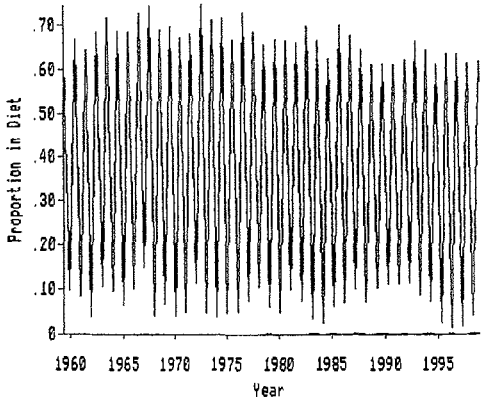


Figure 49. Components of park elk herd diets. A) Dry grasses and forbs, B) mesic grasses and forbs, C) upland shrubs and riparian willow, D) aspen and Ponderosa pine, E) alpine/subalpine herbs. Seasonal variations are due to elk migration among vegetation habitats. . In winter elk are in the vegetation types with dryland grasses and pine and in summer they are in alpine tundra and subalpine forests and meadows. Peaks in herb and upland shrub, aspen, and pine proportions are values for winter. Troughs are values for summer. Peaks for grasses and forbs, mesic grasses and forbs, and shrubs are in winter. Alpine herbaceous are in summer. Willow peaks are in summer, but peaks in one year may be less than valleys in another year.

grass. Diet composition data are dependent on when and where fecal samples are collected. If sampling occurs only on the core winter range, the results would be biased due to lack of representation of animals feeding in other vegetation mixtures. Given these uncertainties, the model estimates were reasonably accurate.

Summer (June-October) elk diets contained 60-70% alpine herb (grasses and forbs combined), and 30-45% willow. This period includes one month of free access to all of the summer plus winter range (October). In comparison, Stevens (1980) noted 79% herbs and 21% willow. Baker and Hobbs (1982) found 80% herbs and 16% willow. Singer et al. (2001b) found 46% herbs and 57% willow. The model produced results that are mid-range between those of Singer's and the other studies.

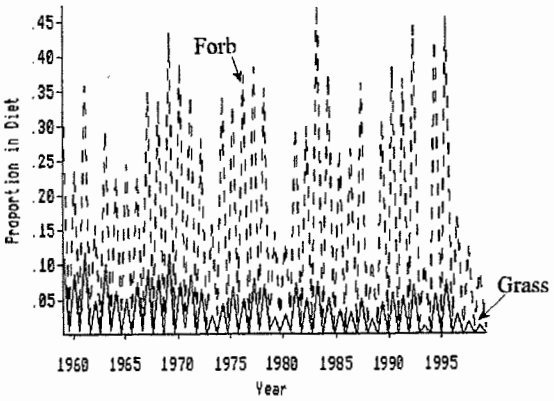
Winter deer diets (Figure 50) were 20-45% forbs, 3-10% mesic forbs, 35-50% shrubs, and 1-2% mesic grass, and 5-7% dry grass. Summer diets were 60-70% herbs and 30-40% shrubs. Willow were essentially absent from summer diets and comprised only 2-10% of winter diets. In comparison, Stevens (1980) observed 51% forb, 33% shrub, 2% grass, and 13% willow in summer diets.

Winter beaver diets (Figure 51) contained 10-20% mesic grass, 60-80% willow, 5-20% aspen, 1-2% mesic forb, and <2% shrub. Summer diets contained 40-45% mesic grass, 5-10% mesic forb, 35-45% willow, 10-15% aspen, and <2.5% shrub.

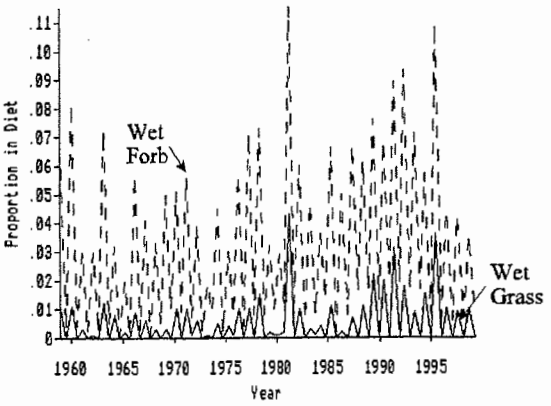
Intake rates for park elk reached summer maxima of 2.8 kg kg^{-1} d^{-1}, declining to winter minima of 0.5-1.5 kg kg^{-1} d^{-1}. (Figure 52). There was trend of declining minimal offtakes over the period 1959-98. Intake rates for the town population reached similar summer maxima, but winter minima were higher in the early years of the simulation. There was a marked declining trend in winter minima over the period, related to the increase in population density, and increasing competition for food. Deer intake rates in summer were 2-2.3 kg kg^{-1} d^{-1}. Winter intake rates declined to as low as 0.6% in some winters, but winter minima were highly variable. Beaver intake rates exceeded 7 kg kg^{-1} d^{-1} in summer and declined to 4-4.5 kg kg^{-1} d^{-1} in winter.

Condition indices of elk and deer reached maximum values each summer (Figure 53). End of winter minima declined over the period, in response to increasing elk density and competition for limited forage. The decreasing winter minima in deer were due to competition with the increasing elk population, since the deer population was kept constant by reductions in this simulation. There was considerable variability among winters, reflecting differences in winter severity, and foraging conditions. Condition indices of the town elk population showed a similar pattern, but when densities were extremely low, winter minima where much higher than observed in the park population. As the town population increased, winter minima decreased. Beaver condition indices varied within reasonable bounds, indicating a realistic balance between forage intake and energy use.

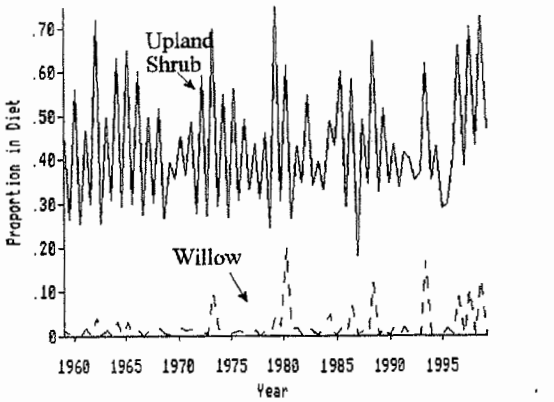
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B)



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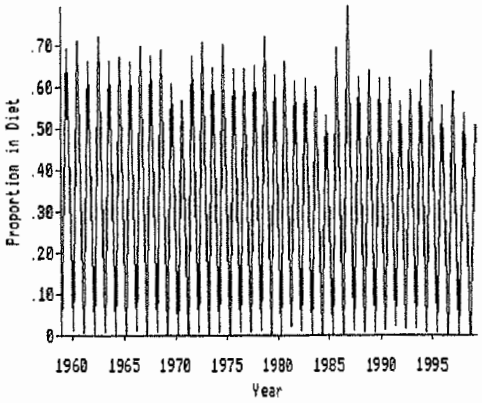
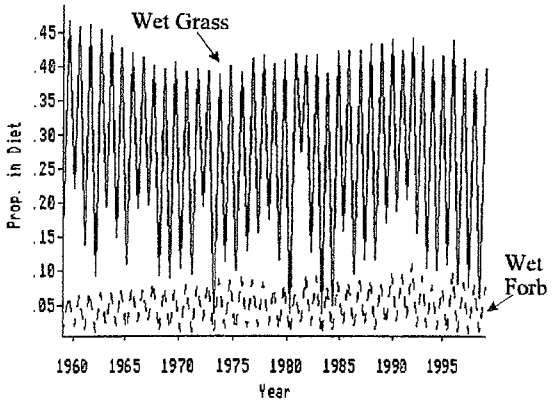
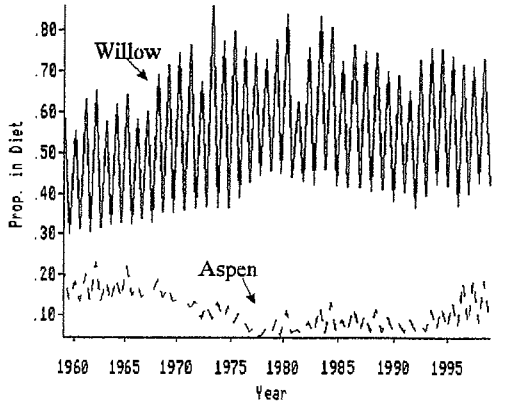


Figure 50. Composition of deer diets. A) dryland herbs, B) mesic herbs, C) upland shrubs and willow, D) alpine and subalpine herbs. Peaks for grasses and forbs, mesic grasses and forbs, and shrubs are in winter. Alpine herbaceous are in summer. Willow peaks are in summer, but peaks in one year may be less than valleys in another year.

A)



B)



C)

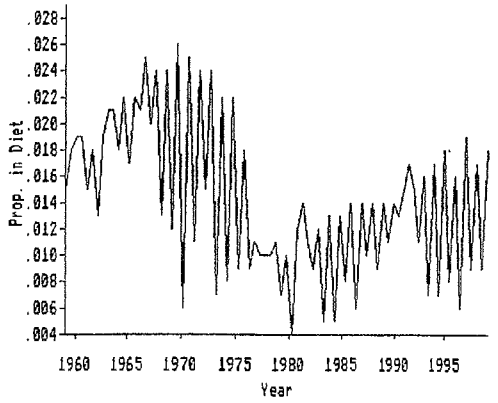
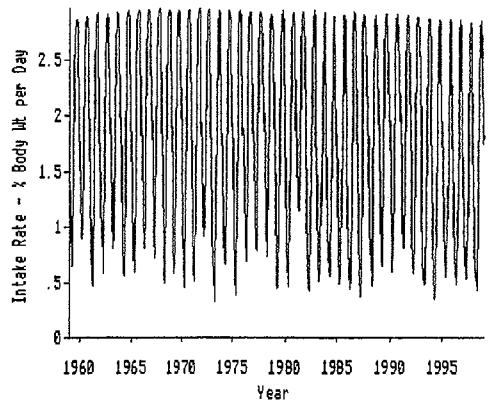
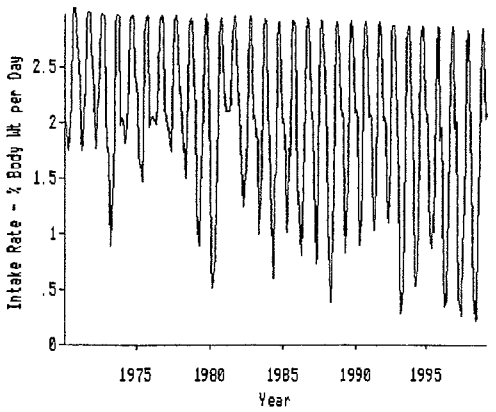


Figure 51. Composition of beaver diets. A) Mesic herbs, B) willow and aspen, and C) upland shrubs. Peaks in herbaceous occur during summer, while peaks in woody intake occur during winter.

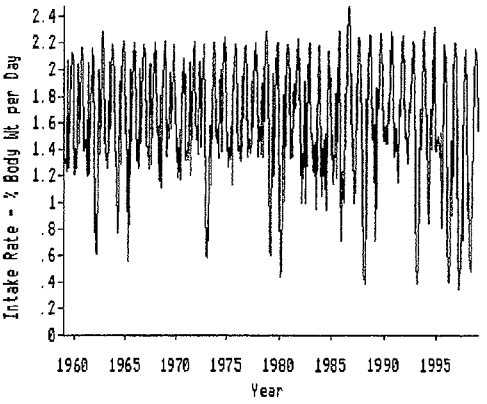
A)



B)



C)



D)

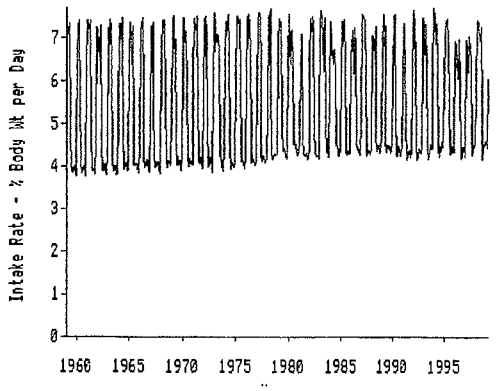
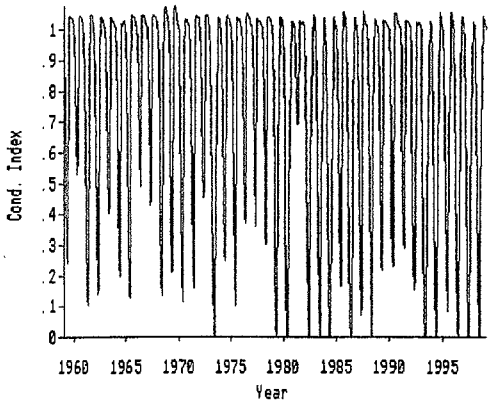
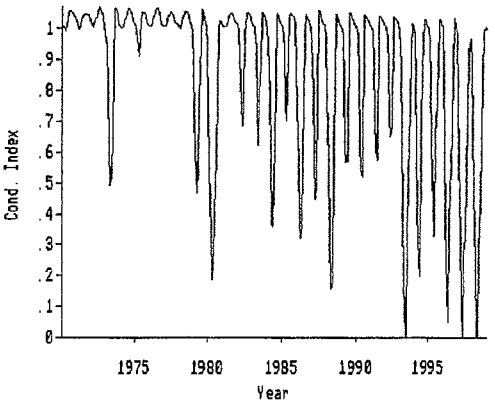


Figure 52. Forage intake rates (forage mass as a percent of body weight per day) for A) park elk herd, B) town elk herd, C) deer, D) beaver.

A)



B)



C)

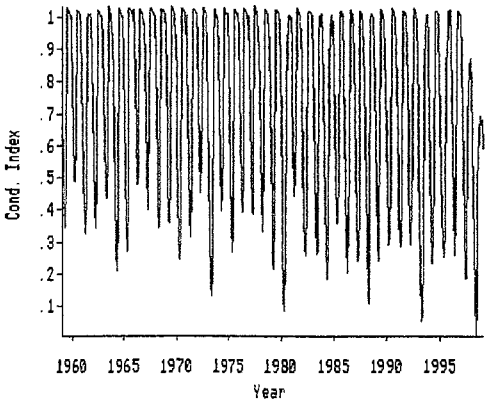
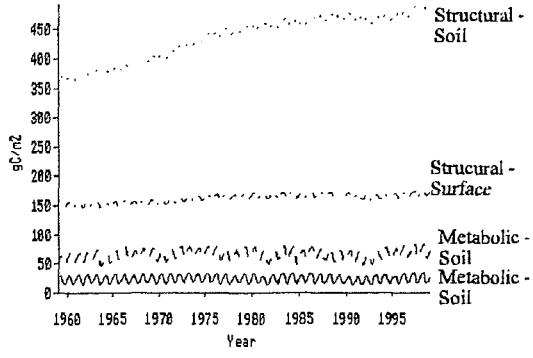
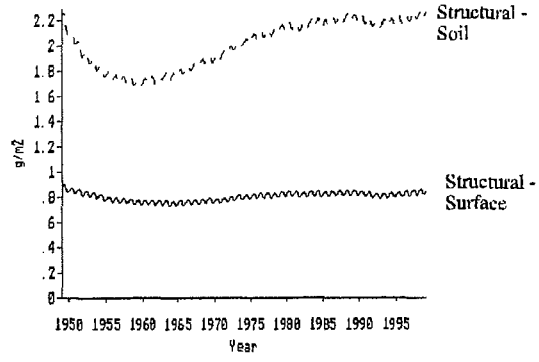


Figure 53. Condition indices of A) the park elk herd, B) the town elk herd, C) deer.

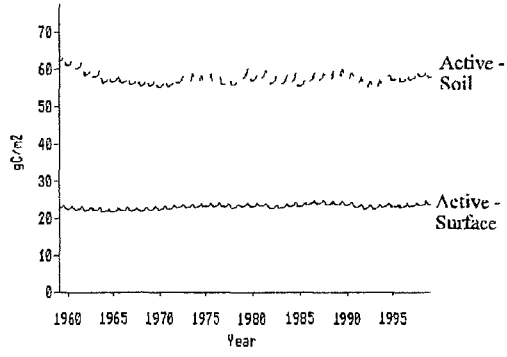
A)



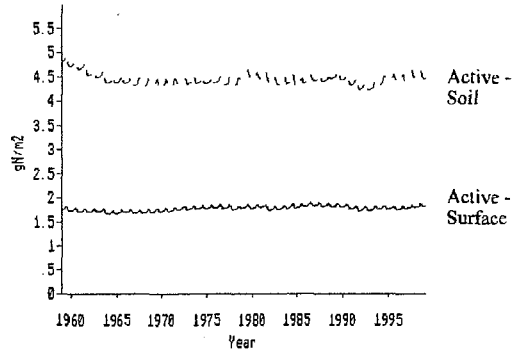
B)



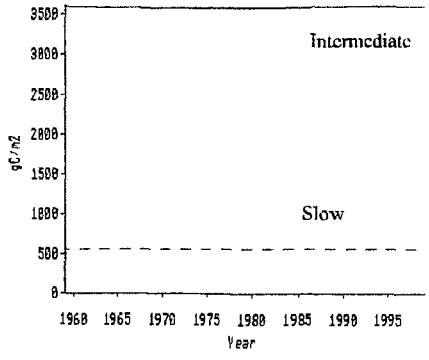
C)



D)



E)



F)

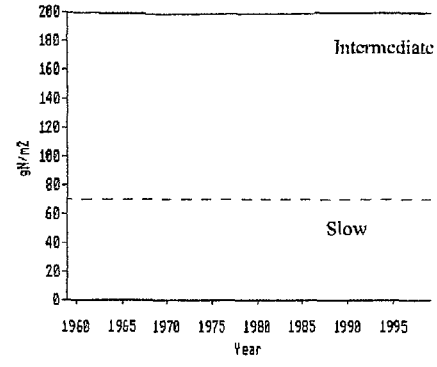
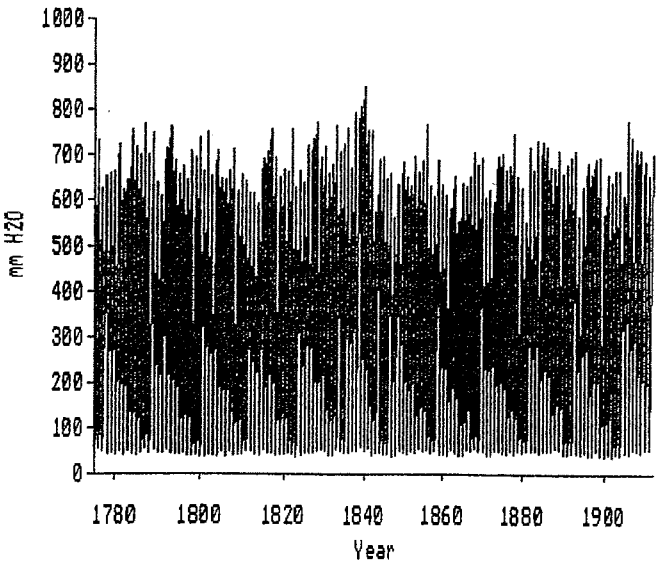


Figure 54. A) Litter carbon in surface metabolic and structural, soil metabolic and structural pools. B) Litter nitrogen in surface structural litter pool. C) Active soil organic matter carbon in surface and soil pools. D) Active soil organic matter nitrogen in surface and soil pools. E) Soil organic matter carbon in intermediate and soil turnover pools. F) Soil organic matter nitrogen in slow and intermediate turnover pools.

A)



B)

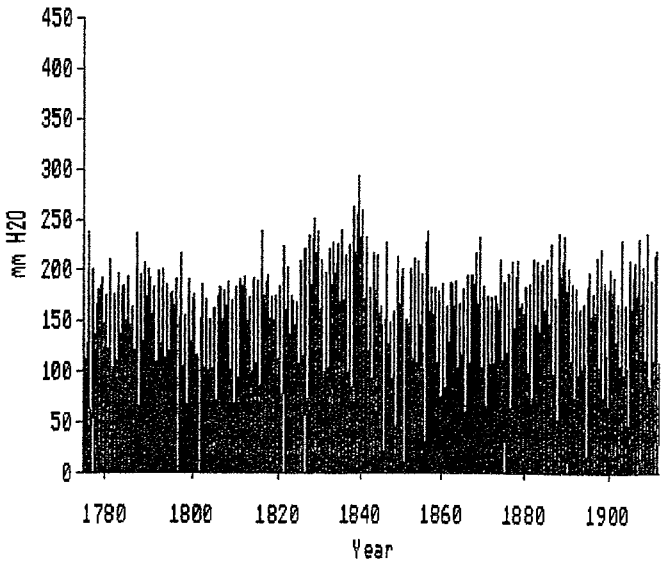


Figure 55. A) Mean annual precipitation over the domain, 1775-1911. based on climate reconstructed from tree ring data (Fritts et al. 1991b). B) Simulated mean snow water content.

Soil carbon and nitrogen

Soil litter (dead root) carbon in the structural (low N:C) pool increased gradually over the course of the simulation, but was beginning to level off (Figure 54a). This pattern was a result of the model coming into equilibrium with litter inputs. Structural surface litter increased very little over the period. Metabolic surface and soil litter carbon varied around steady-states, as decomposition rates balanced litter inputs. Structural N followed the pattern of structural C (Fig. 54b). Metabolic N varied widely compared to metabolic C. The active soil organic matter pools (mainly microbial biomass) attained steady-states, with turnover rates matching inputs (Figures 54c,d). The much larger intermediate and slow C and N soil organic matter pools also attained steady-states (Figures 54e,f), indicating there had been no long-term loss of soil carbon or nitrogen under the grazing regimes imposed during 1949-1998.

Summary

The control run provided a test of the model's capabilities to represent historical dynamics and spatial distributions of a wide range of ecosystem variables including climate, snowpack, hydrology, elk populations, plant production and offtake, herbivore diets and forage intake rates, and soil carbon and nitrogen. Realistic spatial patterns of precipitation were simulated. The snow model adequately represented snowpack dynamics over a wide range of elevations. Simulated streamflow patterns were in agreement with observations of high and low streamflow years. There was a good relationship between observed streamflow and observed water table depths, which permitted the parameterization of a link between the two to enable model estimations of water table depths from simulated streamflow. This run also served as the calibration run for the animal submodels. The calibrated model represented the observed population dynamics over the period, including the increase and gradual limitation due to density dependence. The declining calf:cow ratio was a good test of the key process involved in density dependence. There was a reasonable agreement between modeled and observed elk spatial distributions. Model predictions of diets and intake rates were in good agreement with data. Condition indices of herbivores showed reasonable dynamics. I sum, the control run provides confidence that the model is working well at the level of individual submodels, and at the level of interactions amongst the submodels.

MODEL EXPERIMENTS

1775-1911

The period before the reintroduction of elk included transitions from an ecosystem undisturbed by Euro-American colonists but possibly affected by Native Americans, to an ecosystem that was heavily exploited by early settlers. Beaver trapping occurred prior to 1850, market hunting and extirpation of elk occurred in the 1870s, followed by logging and heavy livestock grazing throughout the Estes Valley and the elk winter range inside the current park boundaries. Wolves were still present in 1894, but were extirpated well before 1917 (Stevens 1980). Simulation studies of this period were designed to examine the pre-settlement ecosystem, and the impacts of these initial disturbances.

There were no weather data available from this period except from Fort Collins for 1900-1911. Consequently, the weather data set that was reconstructed from tree-ring data was used. The resulting pattern of annual precipitation is shown in Figure 55. Reconstructed precipitation was in a range similar to that observed 1949-1998 (Figure 26), with the exception of the three wet years 1995-1997. Means and standard deviations were 679 mm $\pm$54 for 1775-1911 as compared to 669 mm $\pm$93 for 1949-1998, so the inter-annual variance in precipitation was markedly lower in the tree-ring data. There was no long-term trend or cycle evident in the tree ring data. Snow water content was 15% lower in 1775-1911 than in 1949-1998 (Figures 55, 26). Means and standard deviations for snow water content in March-April were 130 mm $\pm$72 for 1775-1911, in comparison to 153 mm $\pm$89 for 1949-1998.

The reconstructed undisturbed vegetation map was used in all of these runs (Figure 14). This map removed all human development, and restored a mesic, sub-irrigated grassland to the current site of Lake Estes and the Big Thompson floodplain. All willow habitats were assumed to have optimum water tables due to beaver activities. Willows were initialized to 40% cover throughout, with a population size class structure comparable to that observed in present day tall willow stands.

Human impacts on ungulates were represented in the model through the imposition of prescribed hunting regimes. Historical evidence indicates that elk were extirpated by 1879 (Guse 1966, Stevens 1980). The first settlers arrived in the Estes Valley in 1860. Market hunting was in full force through most of the 1860's. In the control run for this period it was consequently assumed that there was no interference with elk until 1860. Then, during the period 1860-1867, a hunting regime was prescribed which reduced elk numbers to a range of 500-700. This was then followed by a period 1868-1874 which reduced elk numbers to 100-300. During 1875-1911, hunting was assumed to have reduced elk numbers to zero. In the control run a single elk herd was represented, which had access to the combined area now occupied by the park and town. Little is known about mule deer, but they were not extirpated. To reduce confounding effects, deer were kept at or below 600-700 throughout the entire simulation period except in the experiment with no deer reductions. Beavers on the elk winter range inside the park were held at 450 throughout, which is a number below what Packard (1947b) estimated, but allows for the likely possibility that he overestimated the population. Beavers

were not simulated at other locations, but this will have little effect on outputs which are for the park winter range only. Wolves were assumed to be present as long as they could persist on the prey base.

Experimental runs (Table 21) included the following: a) a control run simulating undisturbed vegetation, but with overhunting and extirpation of elk as actually occurred; b) undisturbed conditions, with no hunting or extirpation of elk; one herd; c) undisturbed conditions with no hunting or extirpation of elk, but with two elk herds limited to the ranges now occupied by park and town herds, respectively; d) no hunting or extirpation of elk; one herd, no wolves present; e) no elk, without wolves or hunting of mule deer; f) no elk, deer, or wolves.

In the control run with the historic pattern of hunting, elk were extirpated as specified, and in response, deer numbers increased (Figure 56a), and wolves were eliminated due to lack of prey (Figure 57a). Without elk hunting, and with wolves (undisturbed conditions), total elk numbers varied between 1,500-3,500 (Figure 56b), and gradually increased throughout the simulation. It made little difference if the elk were simulated as one or two subherds (Figures 56b,c), in terms of the total number of elk. Distinguishing two subherds indicated the relative sizes of herds that would be expected in the two ranges. The park herd was held at 300-800 elk, while the town herd varied about 1,400-1,500 at first, increasing to approximately 1,600-2,000 in later years. Deer numbers were kept to <200 solely by wolf predation. Wolf numbers varied from 18-24 irrespective of whether there were one or two subherds (Figure 57b,c). Wolf numbers increased in response to the increase in elk numbers in later years.

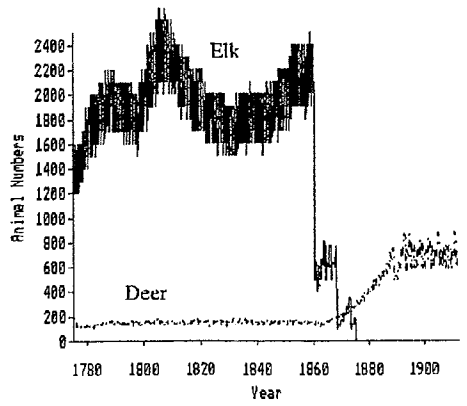
Without wolves, total elk numbers increased at first to about 3,800, then numbers exhibited a dynamic equilibrium at approximately 2,800 elk (Figure 56d), but with a declining long-term trend. The declining trend was likely a response to declining forage, due to heavy grazing. Comparing runs with and without wolves demonstrates that wolves, as parameterized here, could control the elk population, reducing it by 15-40% overall. Interestingly, elk numbers reached similar levels by the end of the runs (2,300 with wolves compared to 2,800 without), and the peak of nearly 2,300 with wolves in 1885 was actually greater than the value reached without wolves at the same time. The convergence of results in that time period was brought about by different mechanisms. With wolves, the elk herd was sometimes highly productive, with ample forage. Elk were in good body condition (Figure 58b,c). Without wolves, a large number of food-limited elk were supported on a declining range base, and elk were in poor body condition (Figure 58d). Elk numbers in Figures 56b,c could be viewed as "predator-limited" carrying capacity, while elk numbers in Figure 56d could be viewed as "food-limited" carrying capacity. Deer were kept at low numbers by competition with elk. Without elk, wolves, or deer hunting, deer increased to their food-limited carrying capacity, oscillating between 1,200-2,200 animals (Figure 56e).

When the historical hunting offtake was imposed, condition indices remained as they were with wolves until the hunting began. Then, condition indices increased due to declining competition for forage (Figure 58a). Elk condition indices remained higher in winter when wolves were limiting the population compared to when food was limiting the population (Figures 58b-d). Elk mortalities due to starvation were therefore likely to be far less with wolves present. Even summer maximum

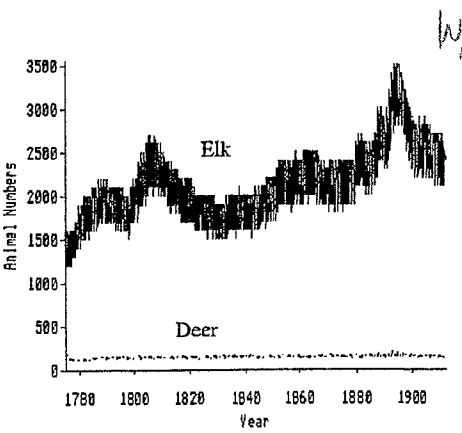
Table 21. Conditions for 1775-1911 model experiments. Run refers to panel letters in Figures 56-62.

Run	Elk Herds	Elk Removals	Deer Presence	Deer Removals	Beaver Numbers	Wolf Presence	Vegetation and Water Table Conditions
A	1	Yes	Yes	Yes	Held Constant	Yes	Natural
B	1	No	Yes	No	Held Constant	Yes	Natural
C	2	No	Yes	No	Held Constant	Yes	Natural
D	1	No	Yes	No	Held Constant	No	Natural
E	None	No	Yes	No	Held Constant	No	Natural
F	None	No	Yes	No	Held Constant	No	Natural

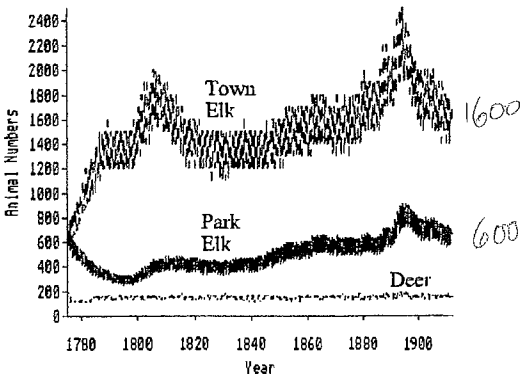
A)



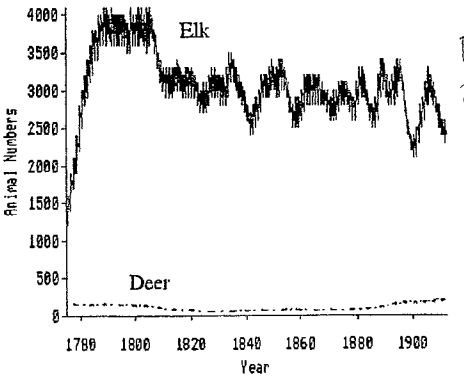
B)



C)



D)



E)

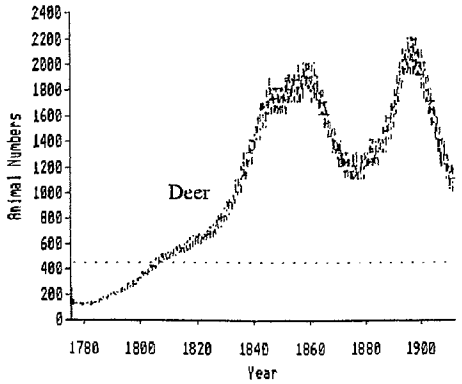
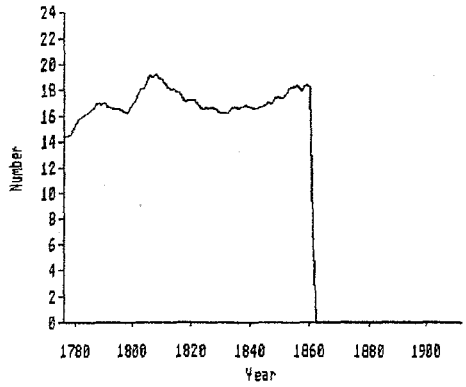
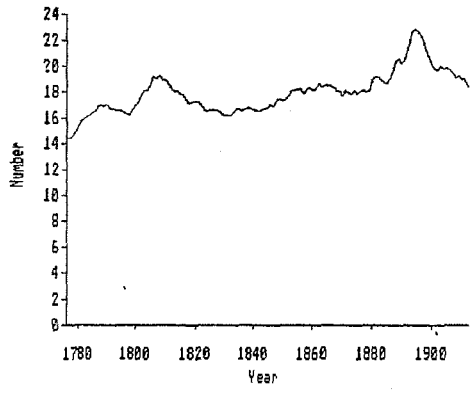


Figure 56. Herbivore populations in simulations of the period 1775-1911. A) Control run with elk culled to simulated market hunting and extirpation. B) No removal of elk, wolves present, a single elk herd. C) No removal of elk, wolves present, 2 elk herds. D) No wolves present. E) No elk, no wolves, deer not hunted.

A)



B)



D)

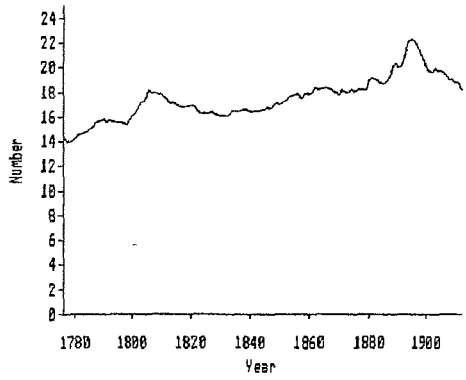
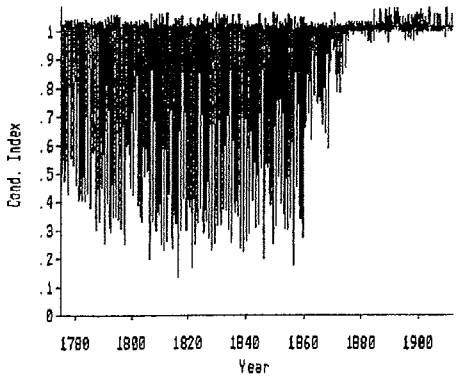
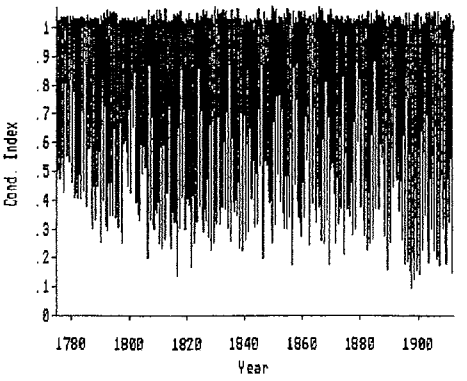


Figure 57. Wolf population dynamics in simulations of the period 1775-1911. A) Control run with elk culled to simulated market hunting and extirpation. B) No removal of elk, wolves present, a single elk herd. C) No removal of elk, wolves present, 2 elk herds.

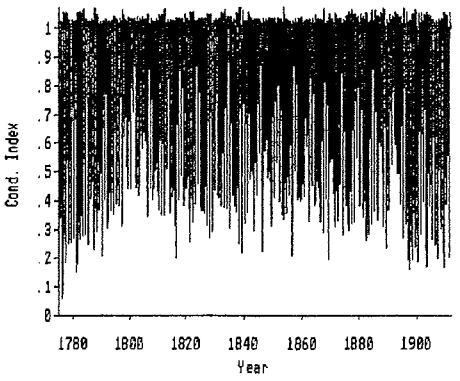
A)



B)



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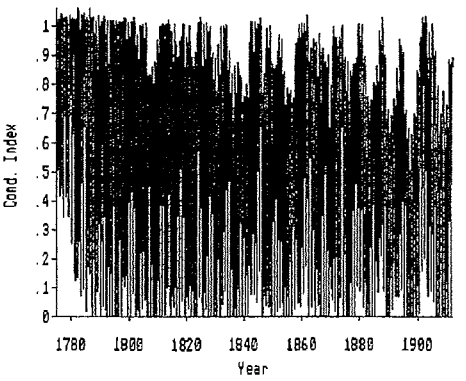


Figure 58. Elk condition indices in simulations of the period 1775-1911. A) Control run with elk culled to simulated market hunting and extirpation. B) No removal of elk, wolves present, a single elk herd. C) No removal of elk, wolves present, 2 elk herds. D) No wolves present.

condition indices were reduced without wolves, more so in the latter years of the simulation (Figure 58d).

Dryland herbaceous biomass increased when elk were hunted to historic levels (Figure 59a). Dryland herbaceous biomass (i.e., herbaceous layer biomass everywhere on the park elk winter range except in riparian willow and wet meadows) increased and then decreased slightly when elk were limited by wolves (Figure 59b). When two elk subherds were simulated (Figure 59c), dryland herbaceous biomass increased to higher levels, probably due to lower elk densities and grazing pressures on the park sub-herd winter range. Without wolves (Figure 59d), dryland biomass declined gradually throughout the period. Without elk present after 1875, herbaceous biomass attained values by 1910 that exceeded those simulated with wolves and two elk sub-herds. When elk and wolves were absent and deer were not reduced, dryland forbs declined markedly, due to increases in deer numbers and deer preference for forbs (Figure 59e). Without elk or deer, herbaceous biomass reached maximal levels (Figure 59f). Forb biomass reached levels comparable to grass biomass.

Mesic grass biomass decreased to lower levels when elk were controlled by wolves, than when they were not (Figures 60b,c,d). This counterintuitive result is due to the increase in willow cover with wolves (Figures 61b,c,d). As the willow increased, the space available for grasses declined. The model outputs are mean grass biomass on the entire grid-cells in which willow are present. Grass biomass density on portions of the grid-cells where there is no willow cover can be computed by dividing grass biomass density in the grid-cell by non-willow cover. For example, after 1860, this gives 160/(1-0.7) = 533 g m^{-2} with wolves, and 200/(1.-0.4) = 333 g m^{-2} without wolves. Thus, increased elk reduced mesic grass biomass density where there was no willow cover, but their impact on willow overshadowed that to produce the reverse result, to increase total mesic grass biomass in grid-cells with willow. With no elk, mesic herbaceous grass decreased to lower amounts (Figures 60a,e,f).

. With historic elk hunting, willow cover increased to the maximum level (Figure 61a). Willow cover increased to near-maximal levels when wolves were present (Figures 61b,c). This is the percent canopy cover in grid-cells of the willow vegetation type, not cover over the entire winter range. In contrast, without wolves, willow cover declined (Figure 61d). With no elk, but with abundant deer, willow cover increased to maximal values within several years (Figures 61e). With no elk or deer, willow also increased to maximal values (Figure 61f). The responses of willow in individual grid-cells (Figure 62) show that cover increased at all locations when wolves were present. With two elk herds, several of the cells were slightly more suppressed than with one elk herd (Fig. 61c). With elk extirpation, willow cover reached maximal values at all locations following extirpation (Figure 62a). With no wolves, willows at six of ten locations in the park were suppressed to near elimination within 40-50 years (Figure 62d). Willow cover at the other four locations increased, but not to maximal values. With no elk, willow cover reached maximal values at all locations in the first several years (Figures 62e,f).

When historic hunting patterns were introduced, aspen increased markedly following the extirpation of elk (Figure 61a). Aspen cover decreased even when wolves were present (Figures

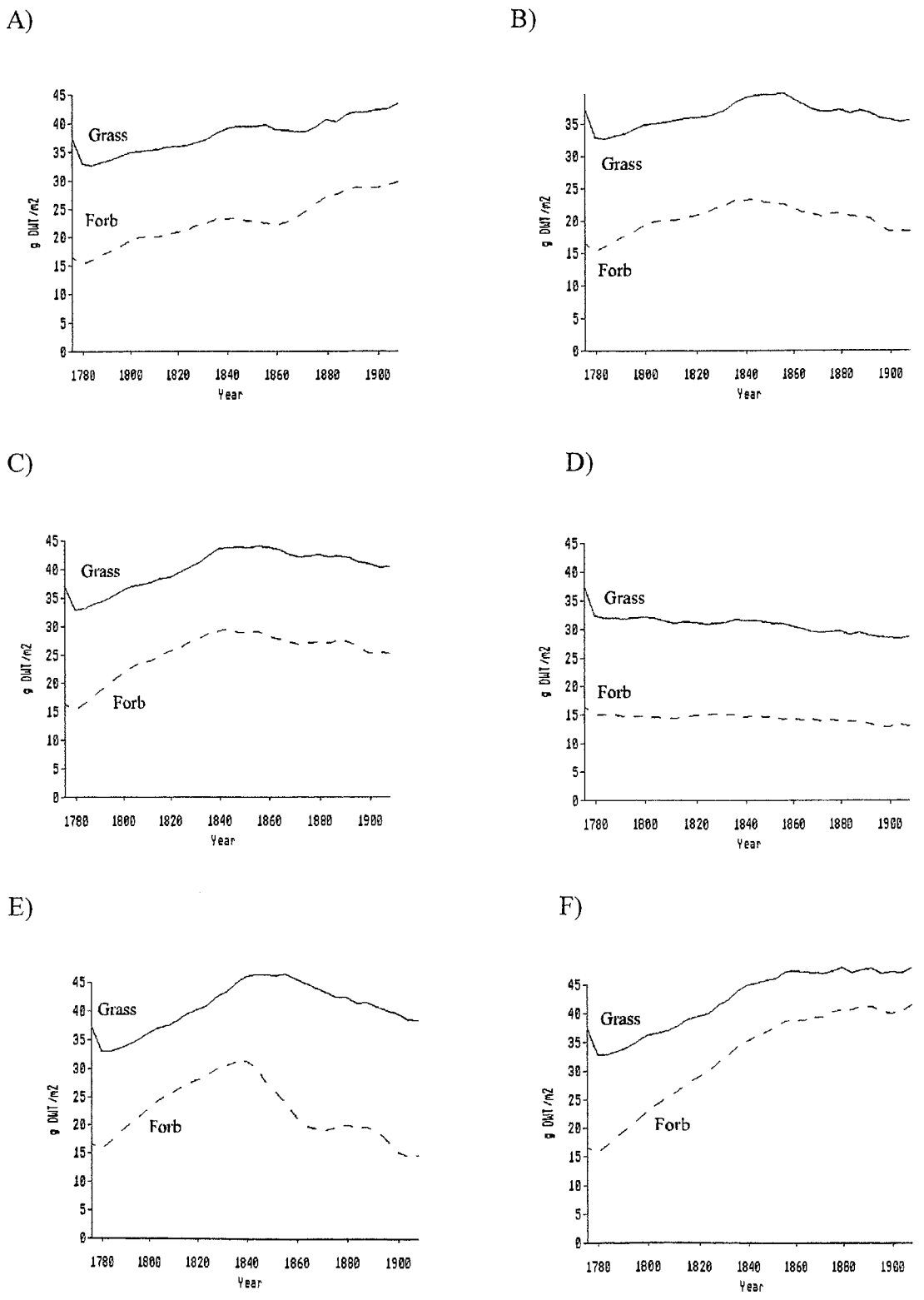
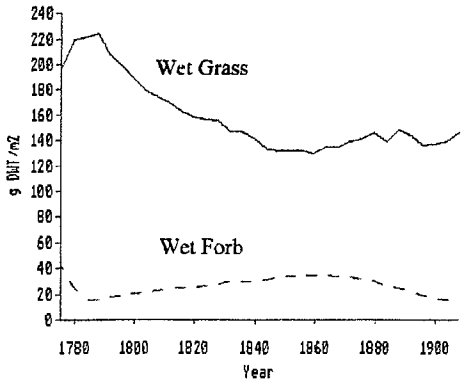
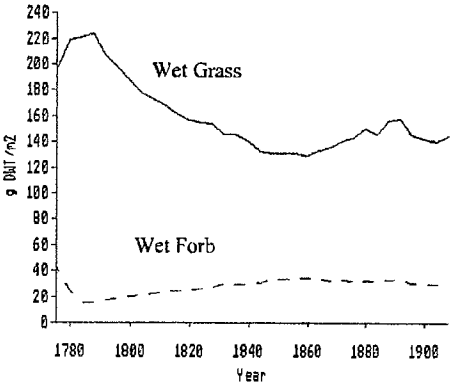


Figure 59. Dryland herbaceous peak aboveground biomass on what is presently the park elk winter range, in simulations of the period 1775-1911. A) Control run with elk culled to simulated market hunting and extirpation. B) No removal of elk, wolves present, a single elk herd. C) No removal of elk, wolves present, 2 elk herds. D) No wolves present. E) No elk, no wolves, deer not hunted. F) No elk or deer.

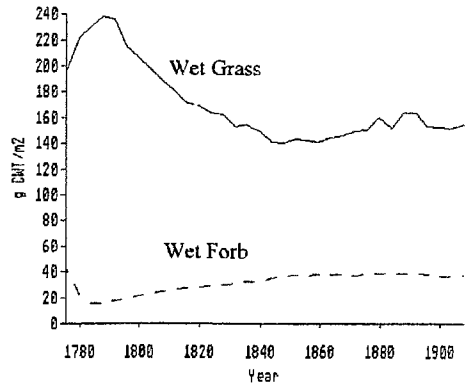
A)



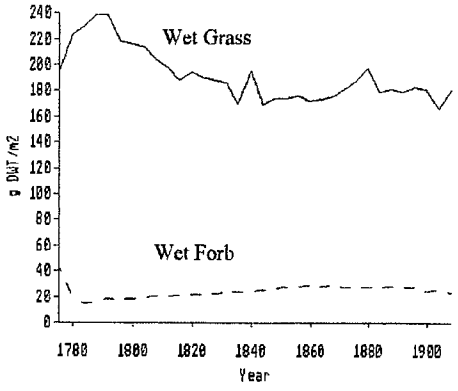
B)



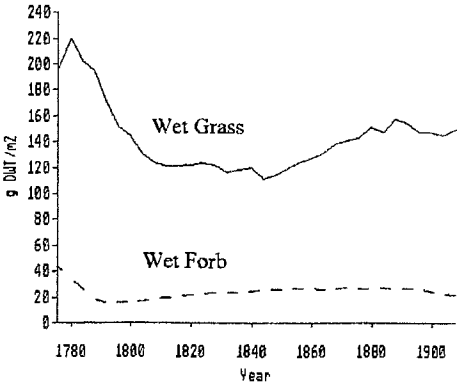
C)



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E)



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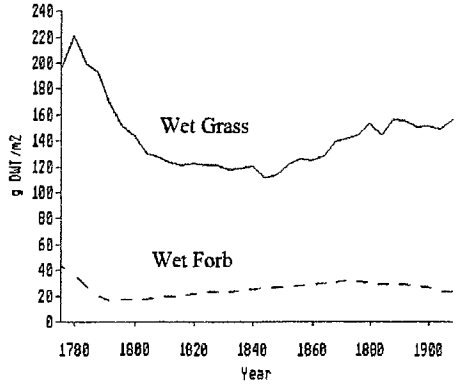


Figure 60. Mesic herbaceous biomass in simulations of the period 1775-1911. A) Control run with elk culled to simulated market hunting and extirpation. B) No removal of elk, wolves present, a single elk herd. C) No removal of elk, wolves present, 2 elk herds. D) No wolves present. E) No elk, no wolves, deer not hunted. F) No elk or deer.

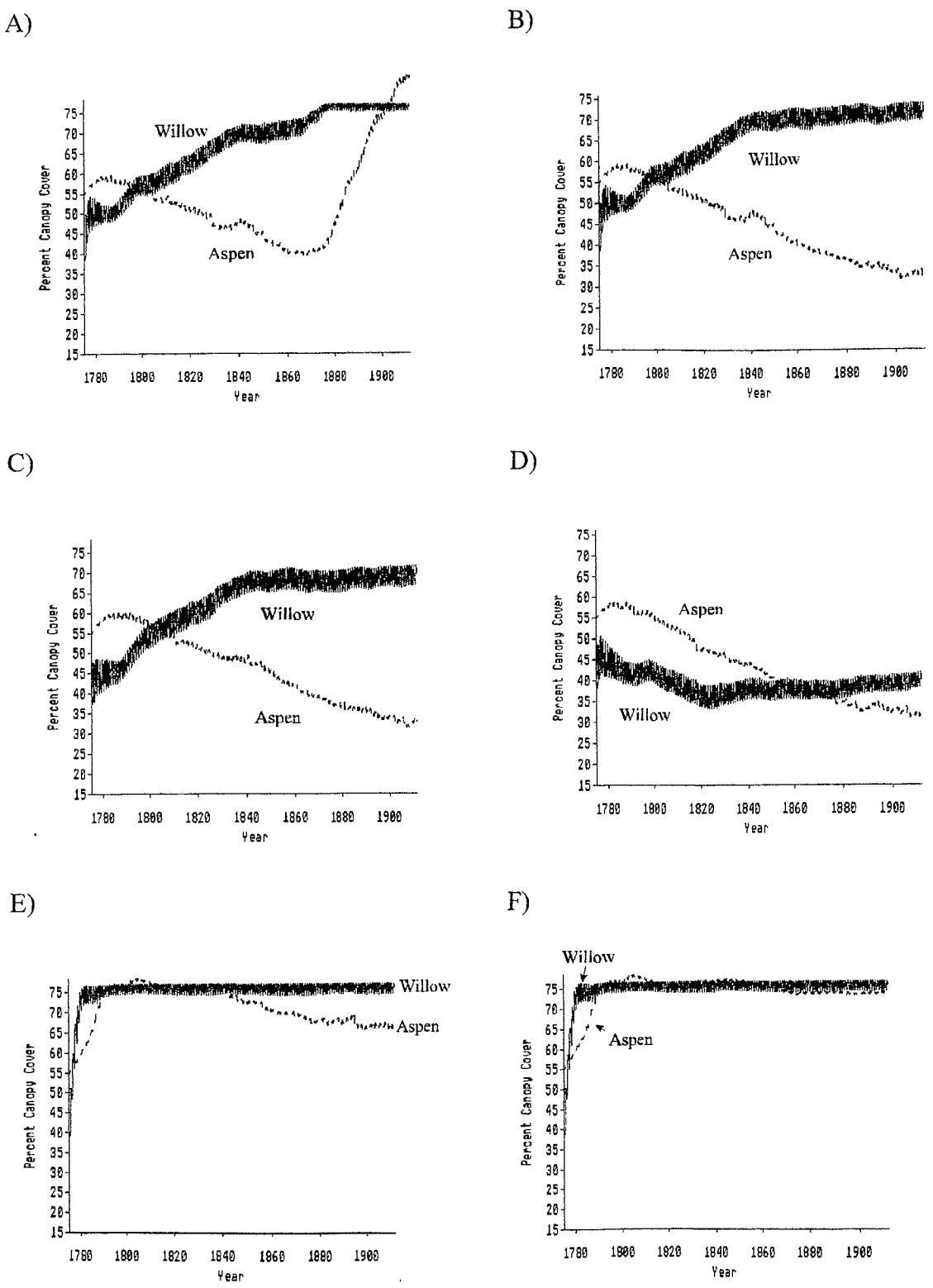


Figure 61. Willow and aspen cover in simulations of the period 1775-1911 reported as mean canopy cover within the grid-cells having that vegetation type. A) Control run with elk culled to simulated market hunting and extirpation. B) No removal of elk, wolves present, a single elk herd. C) No removal of elk, wolves present, 2 elk herds. D) No wolves present. E) No elk, no wolves, deer not hunted. F) No elk or deer.

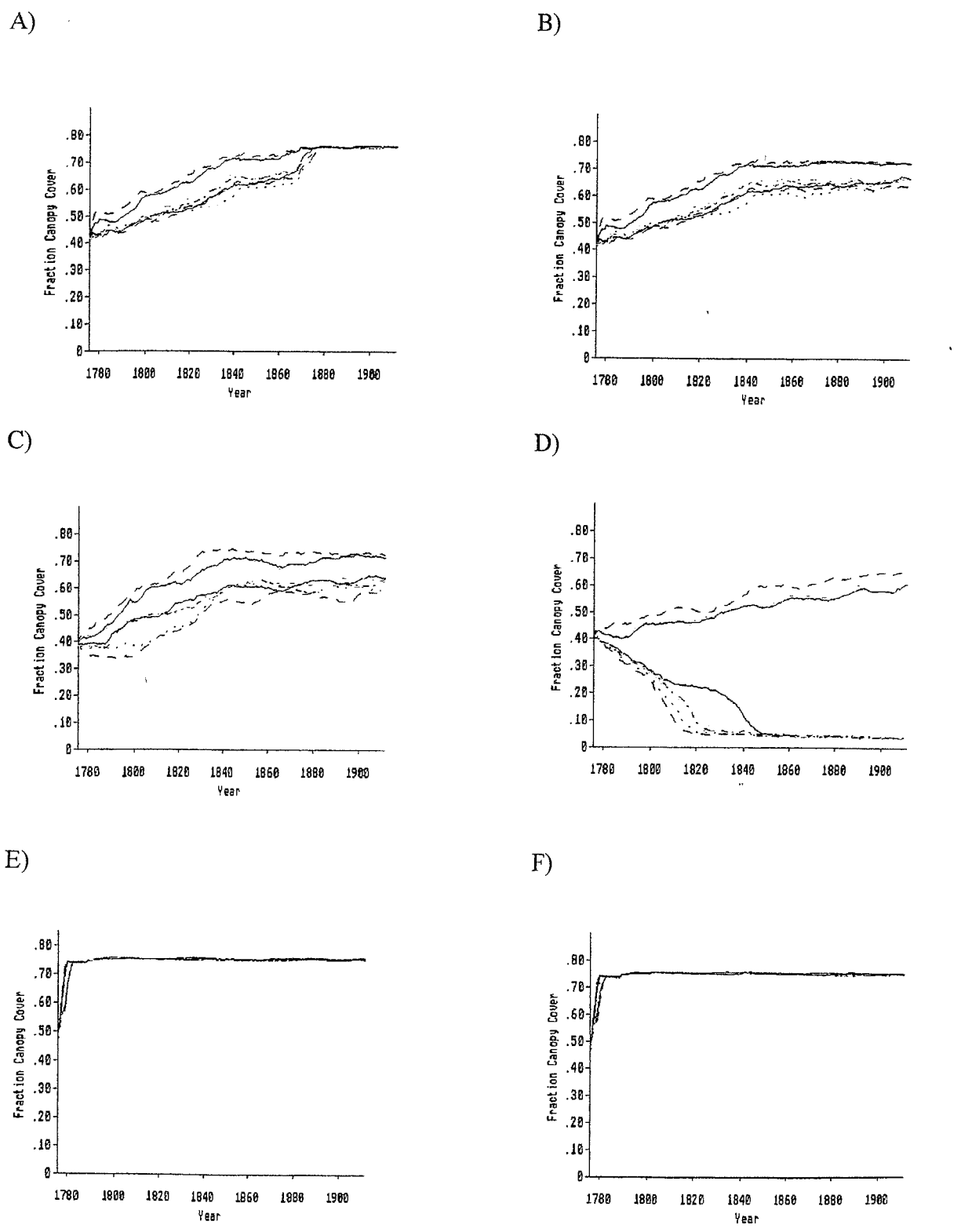


Figure 62. Willow cover in 10 individual grid-cells in simulations of the period 1775-1911. A) Control run with elk culled to simulated market hunting and extirpation. B) No removal of elk, wolves present, a single elk herd. C) No removal of elk, wolves present, 2 elk herds. D) No wolves present. E) No elk, no wolves, deer not hunted. F) No elk or deer.

61b,c). Similar to willow cover output, this is the canopy cover in grid-cells of the aspen vegetation type. These declines were due to browsing by elk, as can be seen by comparisons to runs without elk (Figures 61e,f). The aspen decline was not accelerated by lack of wolves (Figure 61d). This suggests that aspen cover at the inception of the park and elk reintroduction, could have been higher than that if there were no elk extirpation.

The distribution of herbivory on the elk winter range within the current park boundary can be assessed by plotting the fractions of grid-cells grazed or browsed to certain levels over time (Figure 63). Results are shown for two of the experimental runs, the control run with elk extirpation (e.g., Figure 56a), and the undisturbed run with 2 elk herds (i.e., Figure 56c). In the undisturbed run, the fraction of locations where dryland grasses were grazed 50-80% remained at <1% but increased to 5-6% briefly at about 1895 (Figure 63b). The fraction of locations grazed >80% was nil until late in the run, and then only increased to 1%. Most locations were grazed at 0-20%, and 5-15% of locations were grazed at 20-50% (Figure 63d). In contrast, when elk were extirpated, the fraction of locations grazed >50% remained <2% and the fraction grazed >80% was nil (not shown). Nearly all locations were grazed <20% (Figure 63e). In the undisturbed run, willow browsing at 50-80% offtake occasionally occurred on several percent of the landscape (Figure 63c). Most all willow were browsed at the 20-50% level (Figure 63a). When elk were extirpated after 1875, essentially all willow were browsed at negligible levels (Figure 63f).

To summarize the assessment of 1775-1911, it is very plausible for wolves and other predators to have maintained elk numbers below food limited carrying capacity, but still at moderately high numbers, maintained by increased productivity of the vegetation compared to current conditions. Increased cover of willow could be supported, but beaver activities would be critical to maintenance of high water tables. Aspen would have had a difficult time becoming established or surviving the predator-limited densities of elk and mule deer on the core, lower elevation portions of the winter range.

1912-1948

This period includes the inception of the park, the reintroduction of elk, and early elk conservation efforts. For most of the period, elk reductions were absent, or minimal. Hunting offtake was insignificant until 1941, and was 90-108 elk per year during the period 1941-1945 (Stevens 1980). The first significant management reduction did not occur until 1945, when 301 elk were removed (Stevens 1980). There were no reductions between 1945-1948, and hunting offtake was reduced to 20-80 per year. Thus, this was mainly a period of elk protection, with the first elk reduction management only occurring at the end of the period.

Beavers were likely recovering from their near elimination from the Estes Valley by trappers in 1890, and by 1925 there were abundant beavers in one area near the elk winter range (Warren 1926). By 1947 beavers were very abundant on the elk winter range, if not overabundant (Packard 1947b). Wolves were extirpated well before 1917 (Stevens 1980), and continued to be absent throughout this period.

Table 22. Conditions for 1912-1948 model experiments. Run refers to panel letters in Figures 65-75.

Run	Elk Herds	Elk Removals	Deer Presence	Deer Removals	Beaver Numbers	Wolf Presence	Vegetation and Water Table Conditions
A	2	Yes	Yes	Yes	As Observed	No	Current
B	None	No	Yes	Yes	As Observed	No	Current
C	2	No	Yes	No	As Observed	No	Current
D	2	No	Yes	Yes	As Observed	No	Current
E	2	No	Yes	No	As Observed	No	Current
F	2	No	Yes	No	As Observed	Yes	Natural

This was a period of considerable human land use change. Much of the elk winter range within the current park boundary was affected by human settlement, livestock grazing, haying, and resorts. Willow habitats were drained, and willow was removed to create pastures or hayfields. Water was diverted for irrigation. The town of Estes Park was settled, and much of the land in the Estes Valley was intensively used for livestock grazing.

It is unclear what land elk actually had access to in the early years following the elk reintroduction, but the total area available was certainly less than that available prior to settlement. Furthermore, livestock grazing and haying would have reduced forage biomass, effectively making a fraction of the land unavailable for elk foraging. As an approximation for this removal, I assumed that between 1912-1931, the elk were mainly restricted to the area east of the current park boundary. Although the park boundary in 1915 was considerably west of the current boundary, a Colorado State Game Refuge was created in 1919 along the east boundary, and probably included much of what is now within the current boundary, but outside the 1915 boundary. However, I assumed that elk did not have access to the core grasslands in Moraine Park and Horseshoe Park (west of the current boundary) as these were grazed by domestic stock or hayed. The total winter range was thus about 100 km^2, in contrast to the 165 km^2 available in 1775-1911. It was assumed that one primary elk herd occupied this area, with out-migration at a rate comparable to that simulated from the park to the town population in the 1980s. Emigrants could then use the area now known as the "town" elk herd range, but numbers were assumed to be held in check to <300 by hunting, poaching, or other human interferences.

Simulations were driven with weather data that were partly reconstructed based on data from Fraser, Colorado 1912-1931. Data from more stations were available after 1931, but data for many stations had to be reconstructed based on correlations to Estes Park data. The resultant annual precipitation over the study area (Figure 64) was 10% higher (737 mm $\pm$128) than in 1949-1998 (669 mm $\pm$93). Simulated snowpack (157 mm $\pm$99) was nearly the same as in 1949-1998 (153 mm $\pm$89).

Conditions are summarized in Table 22. In all runs except the undisturbed run with wolves, 12 elk were introduced in 1913 and another 14 were introduced in 1914. In actuality, 12 elk were introduced in 1913 of which 5 were bulls, and 24 2-year-old cow elk were introduced in 1914 (Guse et al. 1965). Undoubtably many did not survive. It is also known that the official park estimate was 30 survivors in 1915. The numbers 12 and 14 used in the model were simply chosen to result in 30 elk in 1915.

Deer were kept at the 600-700 level until the period 1927-1942, when the population was allowed to increased to 1,000-1,200 animals, consistent with estimates (Stevens 1980). All runs except the undisturbed run assumed that wolves were present.

In the control run for this period, elk increased to about 800 animals by 1934 (Figure 65a). In actuality, estimates put elk numbers at 300-500 in 1934 and 1935. The accuracy of these early ground counts is unknown. A model constraint was employed which reduced elk to 600, and elk numbers climbed back to 800 again by 1938, and again in 1942. While the simulations do not match

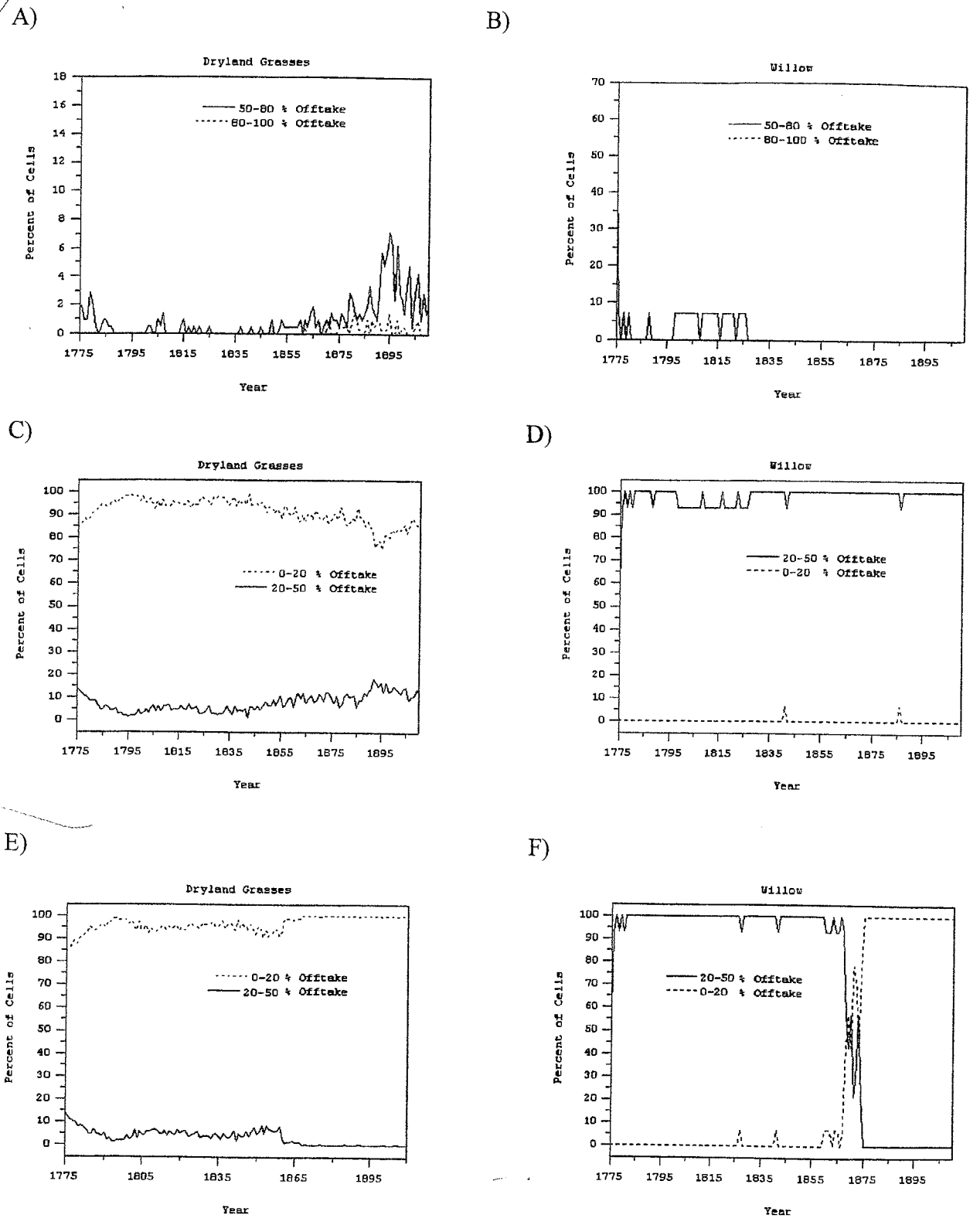
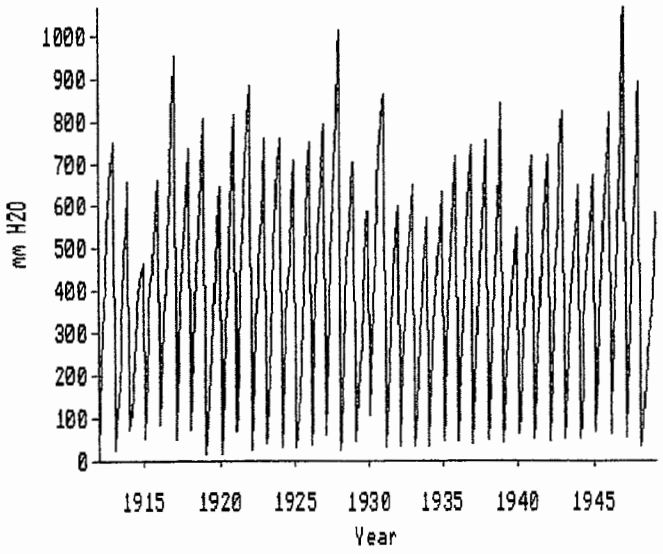


Figure 63. Offtake levels in A-D) the undisturbed 1775-1911 run and E-F) the 1775-1911 run where elk were hunted to extirpation by 1875. In the latter run, the percentage of cells of >50% offtake of grasses was <2% when elk were present. Willow offtake >50% was nonexistent.

A)



B)

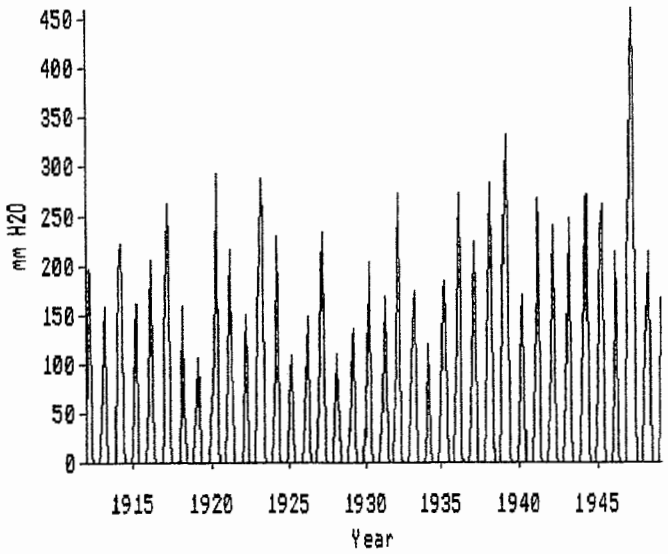
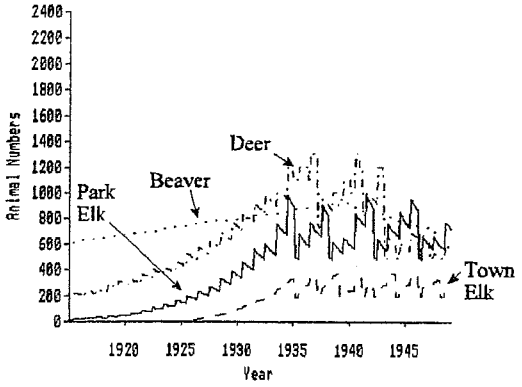
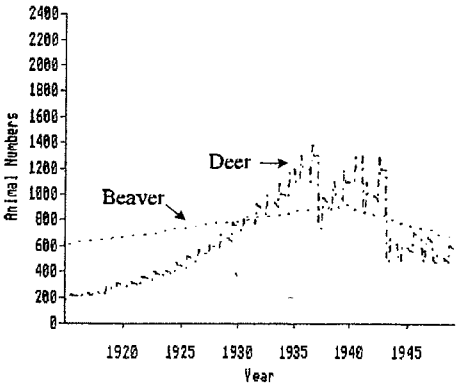


Figure 64. A) Annual precipitation in runs 1911-1948. B) Mean snow water equivalent as simulated.

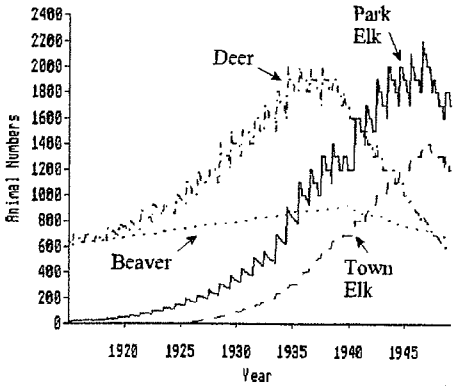
A)



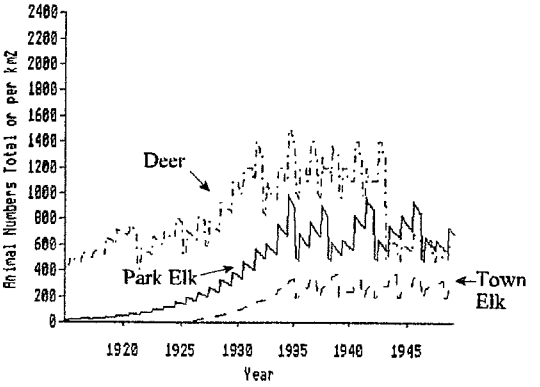
B)



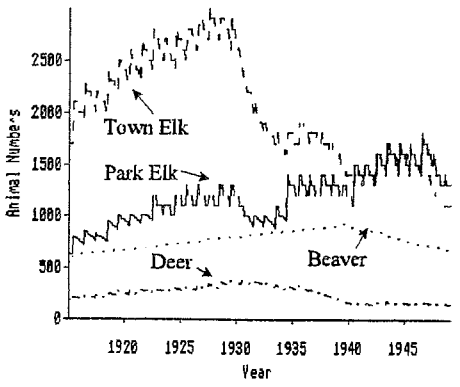
C)



D)



E) No wolves



F) wolves.

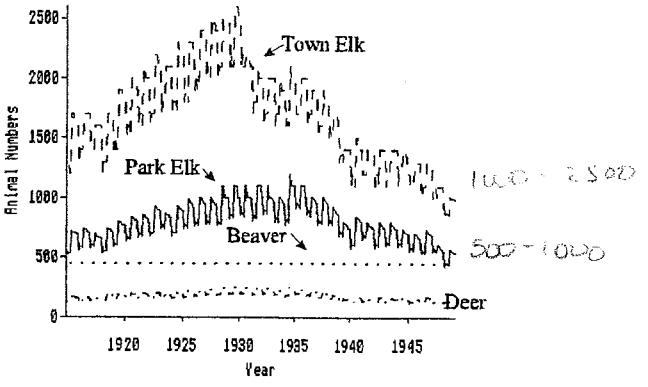


Figure 65. Herbivore populations in simulations 1912-1948. A) Control, observed removal rates. B) No elk. C) No elk removal. D) No beaver. E) Starting with elk at the end of the 1775-1911 undisturbed run, with no elk removal, and with no wolves. F) With wolves, plants and ungulates starting at levels at the end of the 1775-1911 undisturbed run. No wolves in any run except F).

observed counts exactly during 1934-1945, elk were kept within a similar range to the estimated values. There is uncertainty about how many animals out-migrated, how many were poached, and how many were missed during counts. Consequently, the results were judged to be adequate given the uncertainties.

In the simulation with no elk, deer and beaver numbers varied as prescribed (Figure 65b). In a simulation with no elk reductions, elk in the park herd increased to over 2,000 animals by 1945 (Figure 65c). This is not necessarily indicative of long-term food-limited carrying capacity, but is instead, typical of an initial eruption during the period before grazing reduces forage abundance (Caughley 1970,1976). Elk in the subpopulation outside of the protected area increased to 1,400, which was less than that of the park herd because of their later start. Ungulate population dynamics in a simulation with no beaver were essentially the same as in the control run (Figure 65d). A simulation with elk beginning at levels at the end of the 1775-1911 undisturbed run, and without wolves, resulted in an increase in the park subherd from 600 to 1,500 (Figure 65e). The town subherd increased to about 2,700 before declining markedly to approximately 1,500.

The undisturbed simulation began with the elk numbers simulated at the end of the undisturbed 1775-1911 run (Figure 65f), and with wolves present. In this run, elk also had access to the full winter range, as opposed to being precluded from the core winter range inside the park. Wolves held the park subherd to 500-1,000 elk. By 1948, the park subherd was at 500 elk, in contrast to 1,500 elk with no wolves (Figure 65e). The town herd increased to 2,500 and then declined to 1,200. Wolf numbers varied in response to the elk population, as they regulated their territorial spacing in response to prey density. Wolf numbers increased from 18 to 24, then decreased to 15 (Figure 66).

Elk body condition started out high in all simulations except the undisturbed run (Figure 67) due to initially low elk numbers. As elk numbers increased, late winter body conditions declined. Lower body conditions were reached earlier in the simulation with no reductions (Figure 67c) than in simulations with reductions. Removing deer or beaver had essentially no impact on elk. The reason for the decline in elk in the late 1930's in the undisturbed run could be seen in the low body conditions that were simulated, especially in 1939 (Figure 67f), and in the weather data. Annual precipitation in 1939 was low. This was preceded by higher than average snowpacks in 1937-1938 and 1938-1939 (Figure 64). The decrease in elk demonstrates that in an undisturbed system, elk could periodically have been reduced to low numbers due to the combined effects of weather and predation. This suggests that the original ecosystem exhibited non-equilibrial dynamics.

Willow cover increased to high levels in all runs where elk started out at zero, even with no reductions of elk (Figure 68c). The initial period when elk were absent or present at low numbers was sufficient for willow to reach tall stature. Once willow reach tall stature, it for the most part escaped herbivory. Subsequent conversion to short willow depended on the gradual mortality of old plants, and suppression of replacement plants. In the run beginning with moderate elk numbers (Figure 68e), the elk were capable of suppressing some of the willows, preventing them from escaping to the tall growth form. In the undisturbed run (Figure 68f), willow were initialized as tall plants, as was

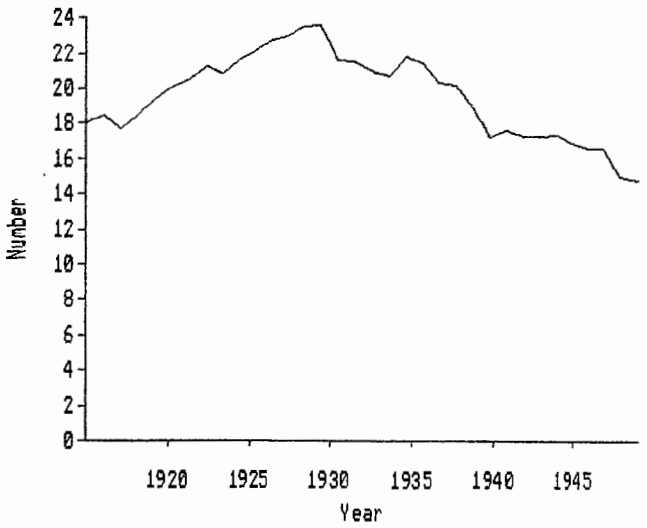
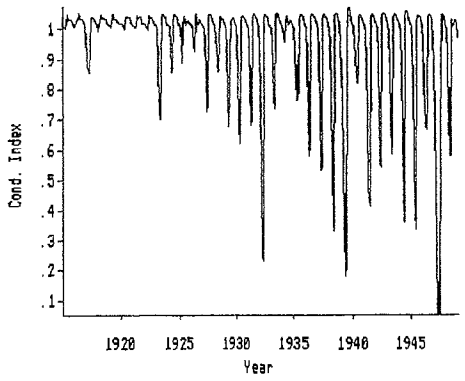
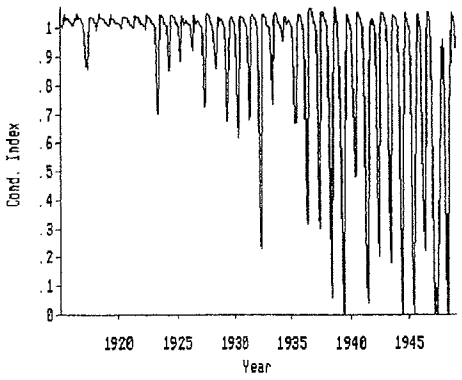


Figure 66. Wolf number in the undisturbed simulation as in Figure 63, with plants and ungulates starting with values from the undisturbed 1775-1911 run.

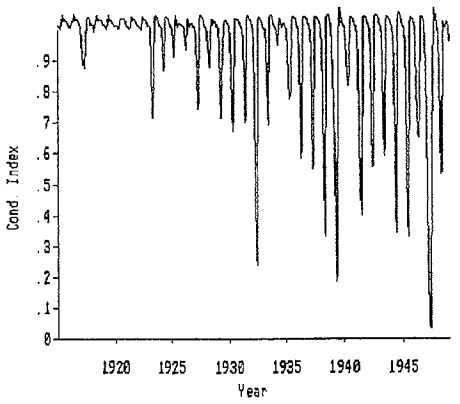
A)



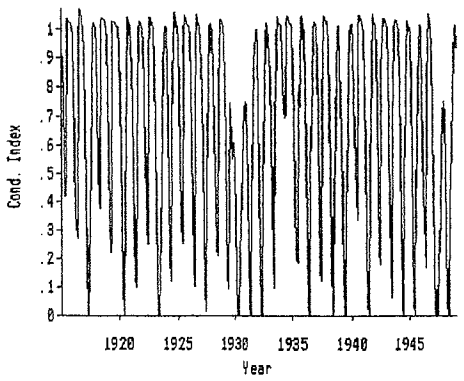
B)



C)



D)



E)

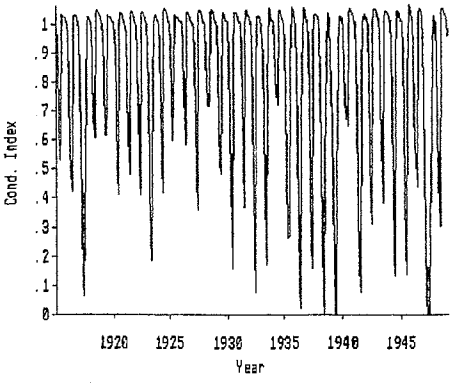


Figure 67. Elk condition in simulations 1912-1948. A) Control, observed removal rates. B) No elk removal. C) No beaver. E) Starting with elk at the end of the 1775-1911 undisturbed run, with no elk removal, and with no wolves. F) With wolves, plants and ungulates starting at levels at the end of the 1775-1911 undisturbed run.

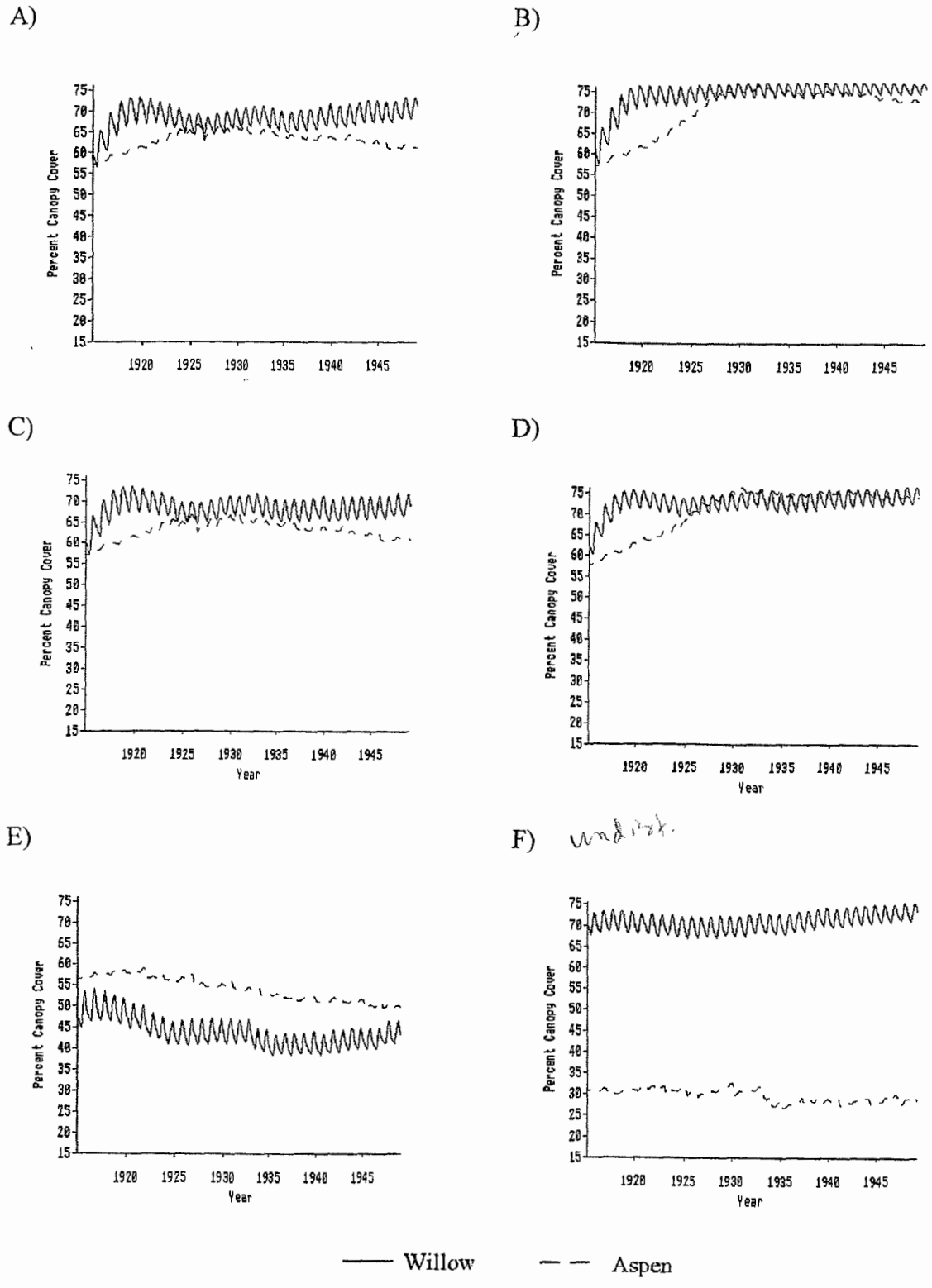


Figure 68. Willow and aspen in simulations 1911-1948 reported as mean canopy cover within the grid-cells having that vegetation type. A) Control, observed removal rates. B) No elk. C) No elk removal. D) No beaver. E) Starting with elk at the end of the 1775-1911 undisturbed run, with no elk removal, and with no wolves. F) With wolves, plants and ungulates starting at levels at the end of run with wolves 1775-1911.

simulated at the end of the 1775-1911 run. This allowed the willow to keep from being suppressed, even though elk were present. Elk were then held to low enough densities by wolves to prevent subsequent suppression. The responses of willow at individual locations are shown in Figure 69. In the run beginning with moderate elk numbers, willow declined to near extinction at some, but not all of the locations (Figure 69e).

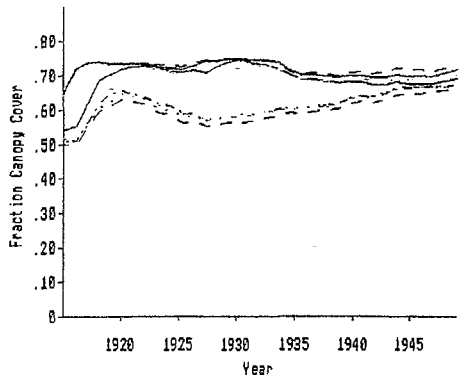
In the control run, aspen increased at first, up until about 1925-1930, then began to decrease (Figure 68a). With no elk, the decrease did not occur (Figure 68b). With no elk reductions, the decrease was accelerated (Figure 68c). Removing beaver also prevented the aspen decline (Figure 68d vs. 68a). Since aspen did not decline with beaver and no elk, the results suggest that the combination of elk and beaver was responsible for the decline in the control run. In the run beginning with moderate elk densities, aspen declined during most of the simulation (Figure 68e). In the undisturbed run, aspen remained steady at the low initial value, suggesting that in undisturbed conditions, aspen would be present at lower abundances, but at other locations, aspen would be sustained at higher abundances even in the presence of elk.

There were few differences among dryland herbaceous biomass amounts in the different scenarios during this period (Figure 70). With no elk reductions, grass was slightly lower, and forbs were moderately lower than in the control run (Figure 70c,e). In the undisturbed run, dryland herbaceous biomass remained relatively high (Figure 70f). Mesic herbaceous biomass, particularly grass, declined in all runs in which willow cover increased, as the willow displaced the grass (Figures 71a-d). Mesic herbaceous biomass remained constant in the runs beginning with moderate elk densities (Figures 71e,f). There was more mesic forb biomass in the undisturbed run than in most other runs.

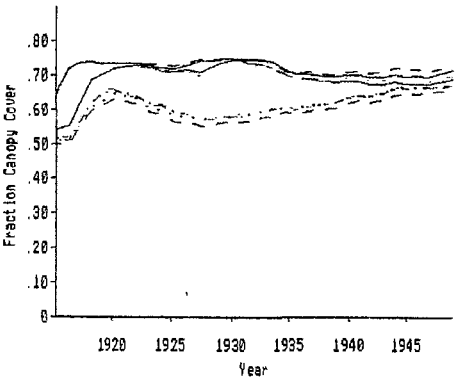
Part of the explanation for high willow resistance to herbivory in the previous runs could be that water tables were assumed to be kept high by beaver activities. To examine this possibility, comparable runs were conducted using current, more shallow, water table conditions. Current water table conditions had little effect on ungulate population dynamics (Figure 72) compared to undisturbed water tables (Figure 65). Current deeper water table conditions markedly reduced willow cover (Figure 73) compared to undisturbed high water tables (Figure 68). This demonstrates that any factor which lowers water tables, such as a reduction in beaver damming, draining of wetlands by humans, or diversion of water, could have contributed to a willow decline irrespective of elk. Under such conditions, removing elk would have alleviated the willow decline by about 15% (compare Figures 73a and b). Examination of the responses of individual grid-cells shows that cover declined at some but not all of the locations (Figure 74). The differences are highlighted in comparisons of responses with and without altered water tables (Figures 74 vs. Figure 69). Elk removal would have lessened, but not halted the willow declines at locations with lowered water tables (Figures 74a vs. 74b).

The frequency distributions of grazing and browsing intensities on the park winter range 1912-1948 are shown in Figure 75. In the control run, dryland grasses were nearly all grazed at a 0-20% offtake level (Figure 75a). Less than 5% was grazed at 20-50%. Willow were browsed at 0-20%

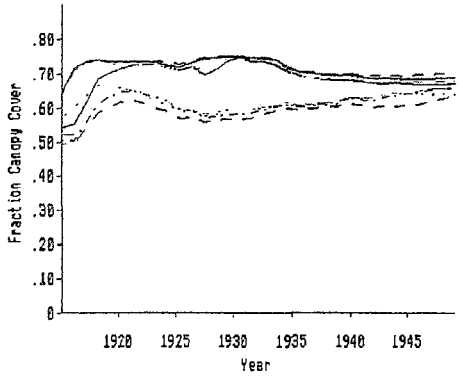
A)



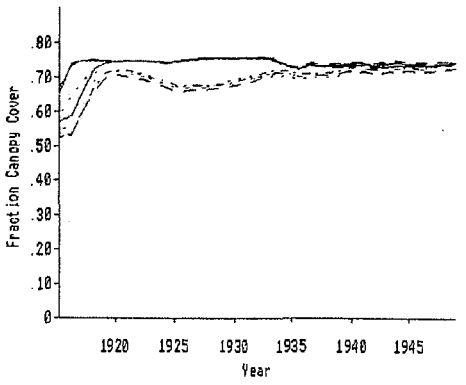
B)



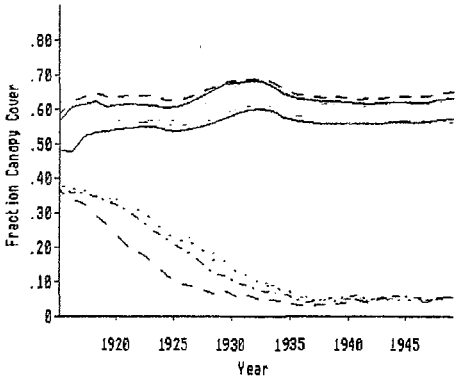
C)



D)



E)



F)

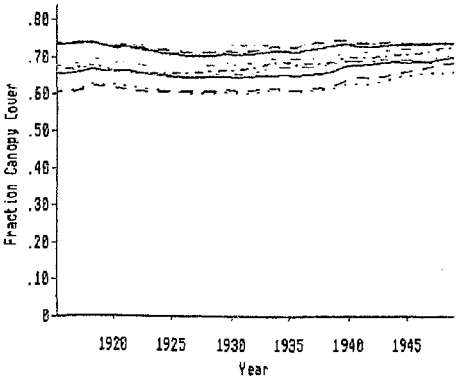


Figure 69. Willow cover in individual grid-cells in simulations 1912-1948. A) Control, observed removal rates. B) No elk. C) No elk removal. D) No beaver. E) Starting with elk at the end of the 1775-1911 undisturbed run, with no elk removal, and with no wolves. F) With wolves, plants and ungulates starting at levels at the end of the 1775-1911 undisturbed run.

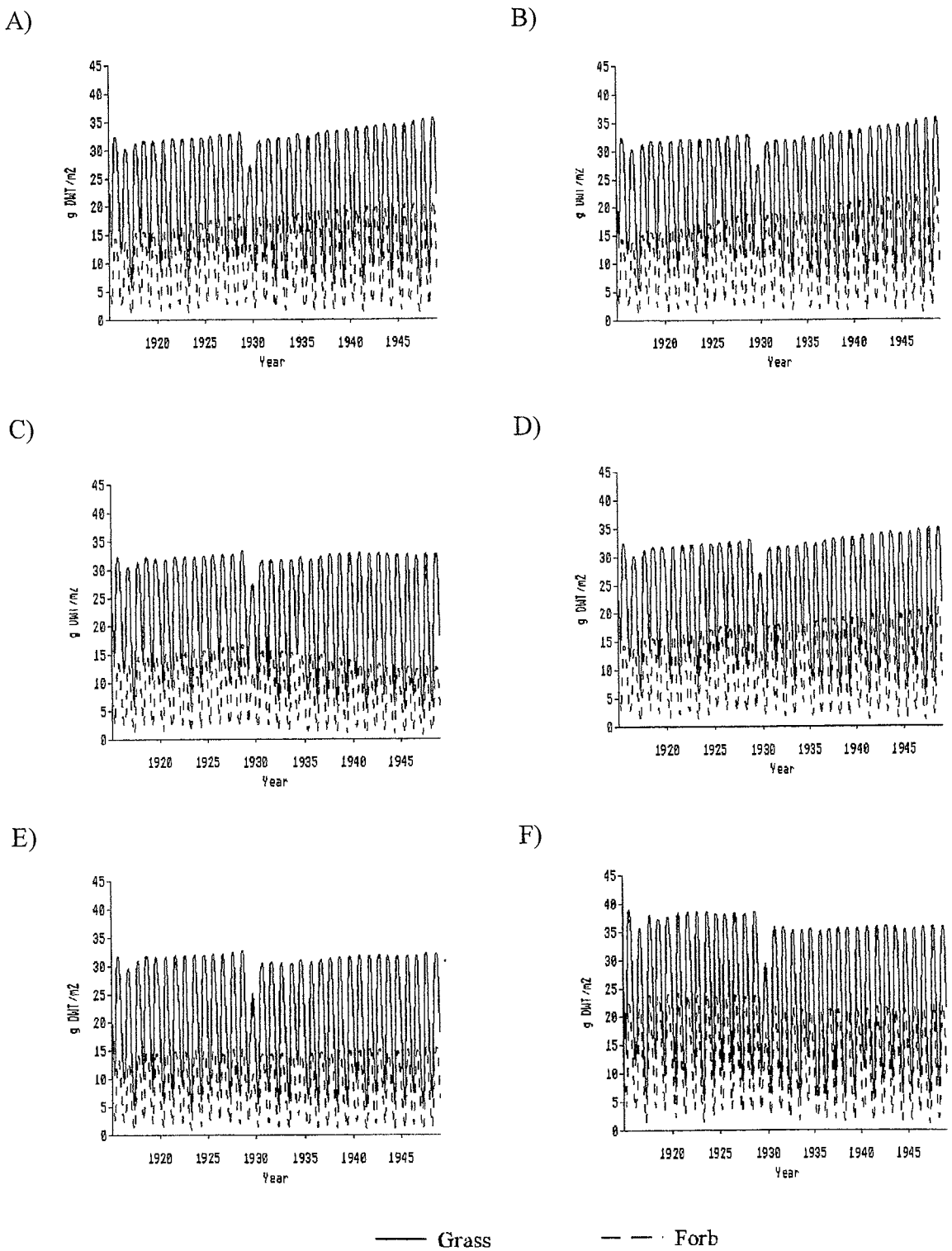


Figure 70. Dryland herbaceous biomass in simulations 1912-1948 A) Control, observed removal rates. B) No elk. C) No elk removal. D) No beaver. E) Starting with elk at the end of the 1775-1911 undisturbed run, with no elk removal, and with no wolves. F) With wolves, plants and ungulates starting at levels at the end of the 1775-1911 undisturbed run.

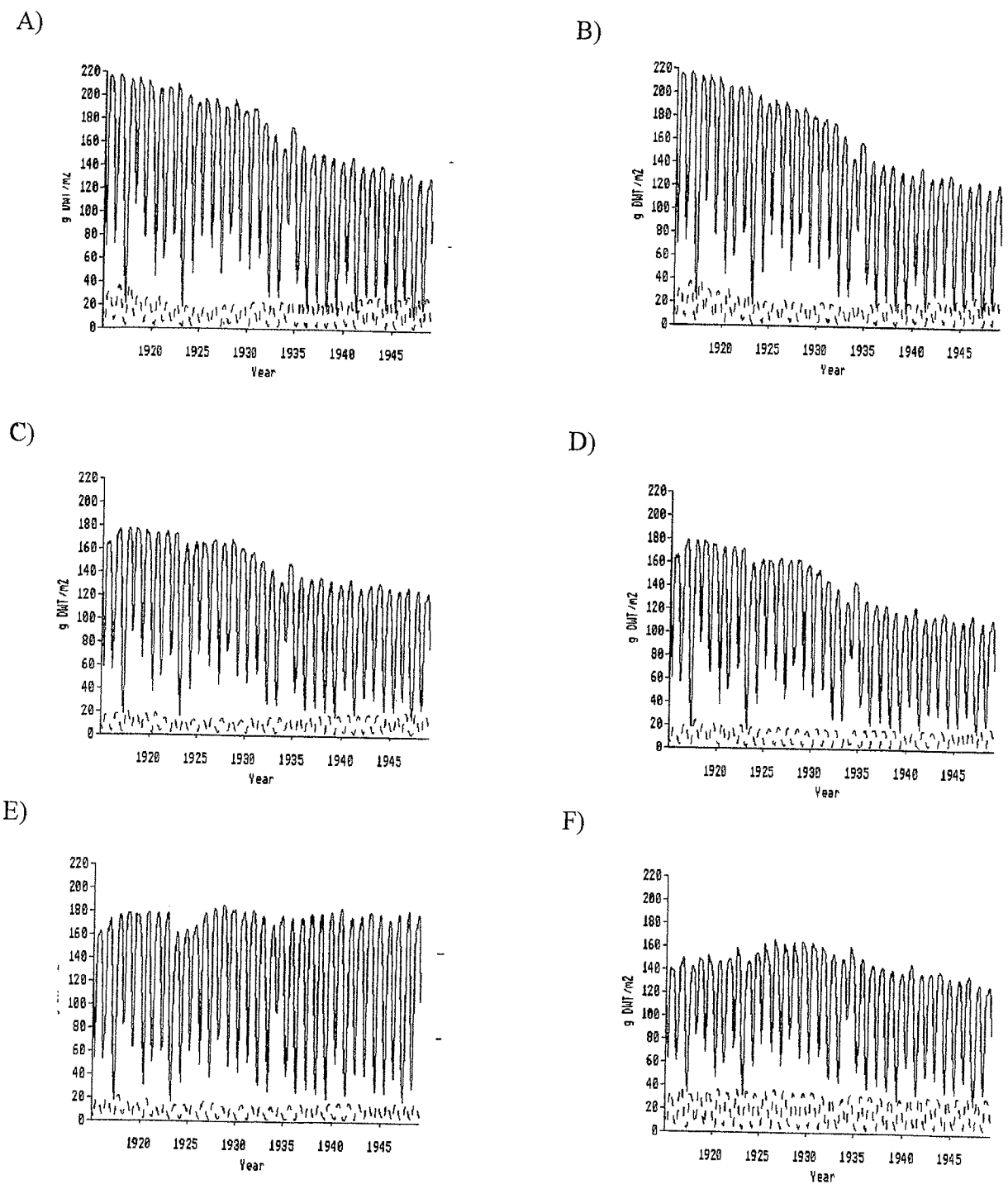
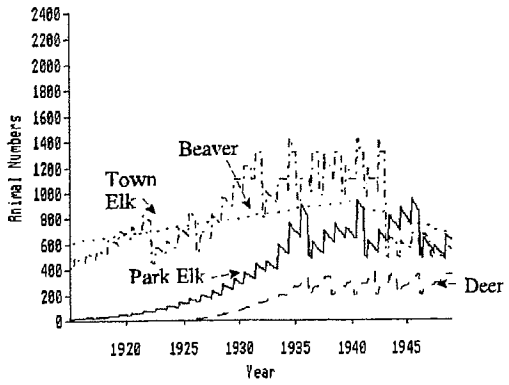
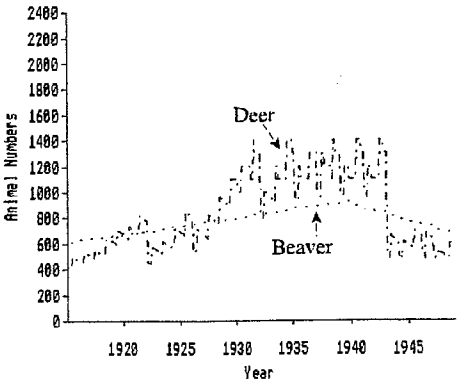


Figure 71. Mesic herbaceous biomass in simulations 1912-1948. A) Control, observed removal rates. B) No elk. C) No elk removal. D) No beaver. E) Starting with elk at the end of the 1775-1911 undisturbed run, with no elk removal, and with no wolves. F) With wolves, plants and ungulates starting at levels at the end of the 1775-1911 undisturbed run.

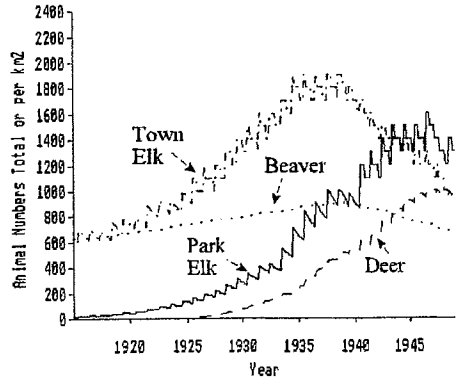
A)



B)



C)



D)

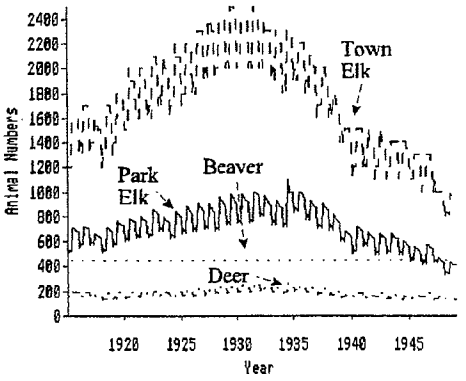
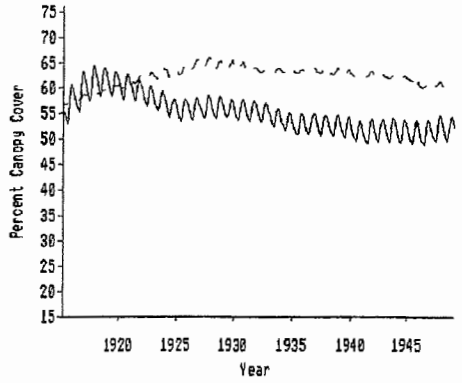
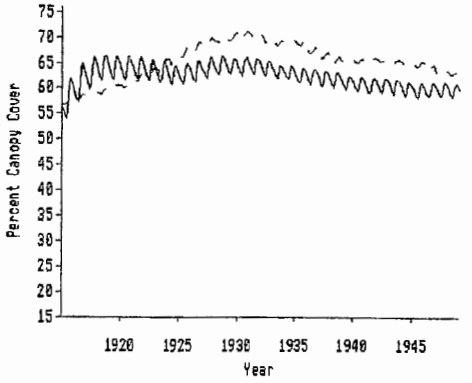


Figure 72. Herbivore populations in simulations 1912-1948, with current soil and water table conditions. A) Control, observed removal rates. B) No elk. C) No removal of elk. D) With wolves, starting with plants and ungulates as at end of the 1775-1911 run with wolves.

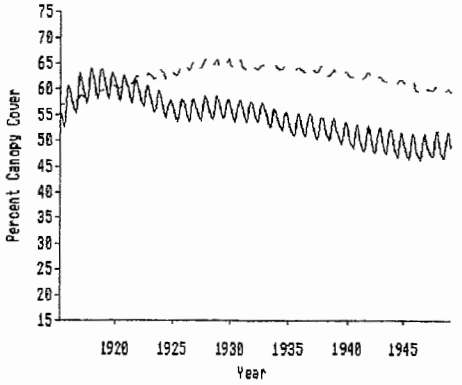
A)



B)



C)



D)

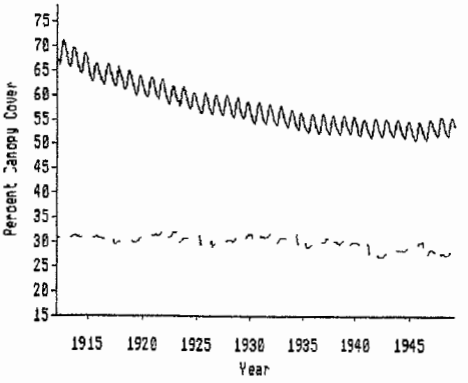
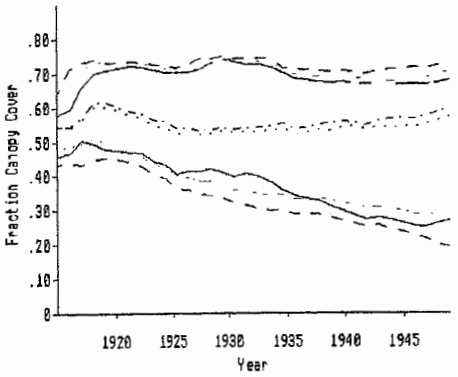


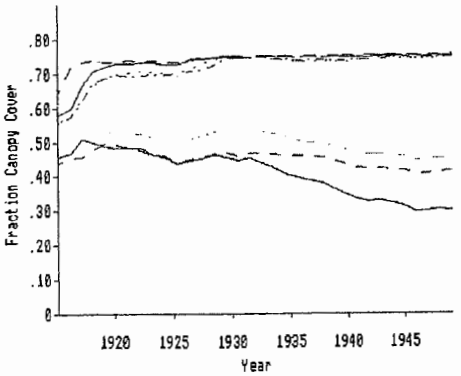


Figure 73. Willow and aspen in simulations 1911-1948, with current soil and water table conditions reported as mean canopy cover within the grid-cells having that vegetation type. A) Control, observed removal rates. B) No elk. C) No removal of elk. D) With wolves, starting with plants and ungulates as at end of the 1775-1911 run with wolves.

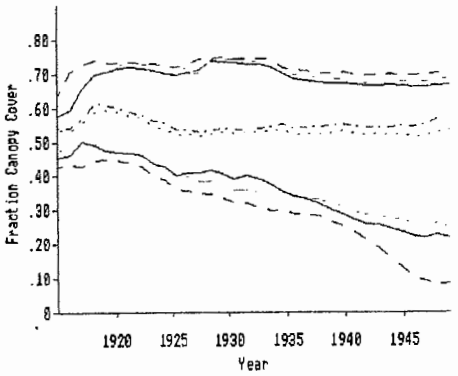
A)



B)



C)



D)

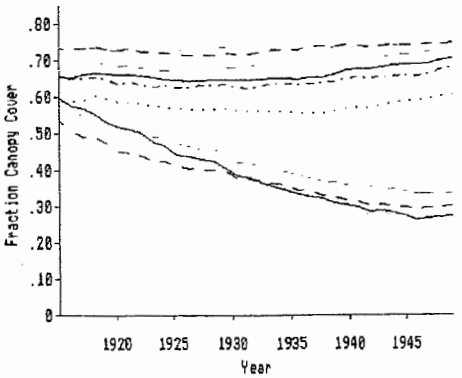
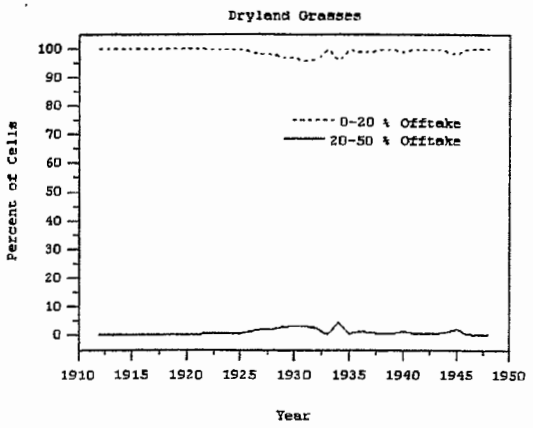
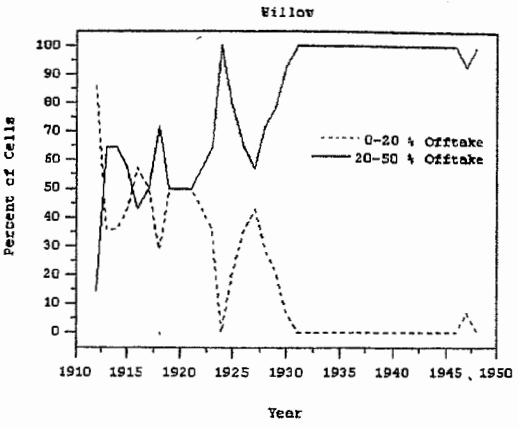


Figure 74. Willow cover in ten individual grid-cells in simulations 1912-1948, with current soil and water table conditions. A) Control, observed removal rates. B) No elk. C) No removal of elk. D) With wolves, starting with plants and ungulates as at end of the 1775-1911 run with wolves.

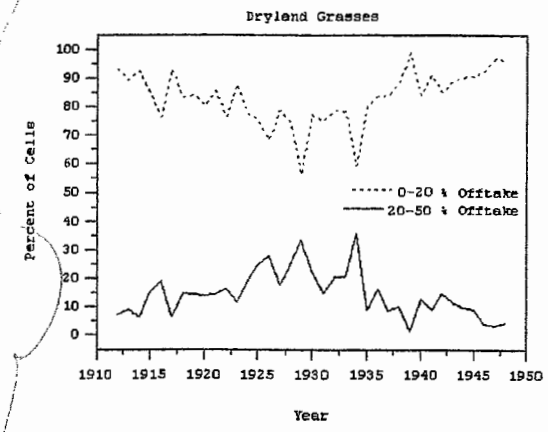
A) control



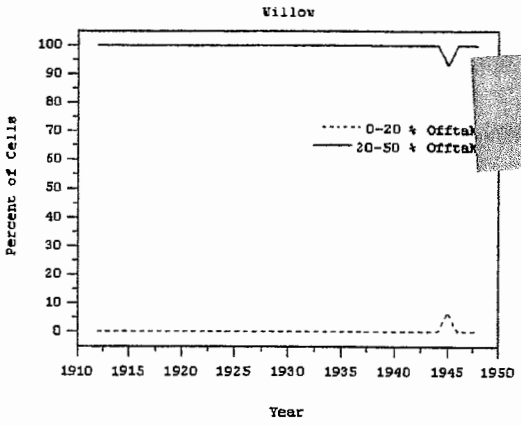
B) control



C) undist



D) undist.



E)

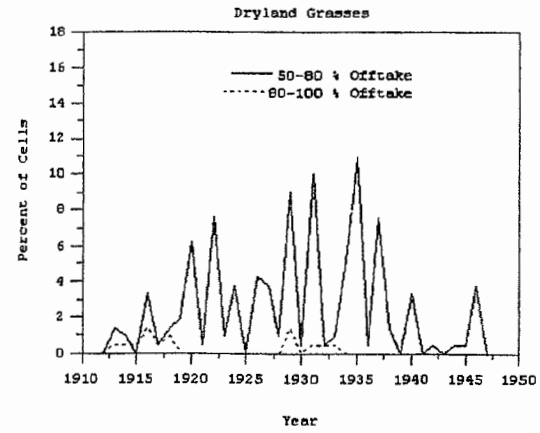


Figure 75. Offtake levels in A-B) the control run for 1912-1948, in which elk were initially absent, then reintroduced and C-E) the undisturbed run for in which elk were never extirpated, and with wolves continuously present. In the control run, <1% of cells had grasses with >50% offtake, and no cells had willow with >50% offtake. In the undisturbed run, no cells had willow with >50% offtake.

and 20-50% in the first part of the period, but by the 1930s, all willow were browsed at 20-50% (Figure 75b). In contrast, in the undisturbed run, dryland grasses were browsed at heavier intensities (Figure 75c,e). The temporal pattern of offtake intensity followed the temporal pattern of the park elk population (Figure 65f). As the park population increased from 500 to 1,000, the fraction o dryland grass locations grazed to 0-20% decreased while the fraction grazed at 20-50% increase (Figure 75c). With 1,000 elk, 20-40% of the dryland grasslands were grazed at 20-50%. As th population increased above approximately 600 elk, parts of the dry grasslands began to be grazed at 50-80% offtake (Figure 75e). At 800-1,000 elk, 8-10% of the grasslands were grazed at 50-80%. Willow, in contrast, were browsed at the 20-50% level throughout the run (Figure 75d).

The assessment of 1912-1948 revealed the importance of human disturbances both prior to and after 1912, in moving the system into what could be considered to be an alternate stable state. Livestock grazing, draining of wetlands, removal of elk and wolves, and compression of elevated numbers of beaver into reduced willow cover, all combined to reduce willow cover in Moraine and Horseshoe Parks further. Aspen declined as well, due to the combined effects of elk and beaver, but the initial presence of some of the aspen that declined in this period could have been a product of earlier elk extirpation.

1949-1998

Events during this period were described above in the Control Run section. Simulation experiments here were intended to investigate the effects of elk, elk management, and wolves. Conditions are summarized in Table 23. In these runs, two elk populations and ranges are simulated, the park and the town populations. Except for the undisturbed run, vegetation and water table conditions were those of current land cover, including lowered water tables in some of the willow locations. As a simplifying assumption, willow cover was initialized at 40%, with a population size class structure similar to current tall willow. Aspen was initialized based on the current woody cover map. Outputs are presented for the years 1959-1998, which omits the first 10 years (1949-1958) required for "spin-up" or model adjustment to initial conditions.

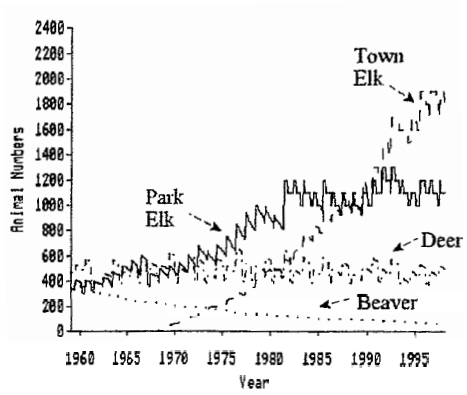
Population dynamics from the control run are presented again to facilitate comparisons to other experiments (Figure 76a). The first experiment was to allow elk populations to grow unchecked (Figure 76b). The park population grew to a food limited carrying capacity earlier than in the control run, and food-limited population sizes were slightly higher in the 1960s and 1970s than in the 1980s and 1990s. Food-limited carrying capacity of the park herd appeared to be in the range of 1,000-1,300 elk. The town population increased to a slightly higher level than in the control run (1,900 vs. 1,800) before declining. Without reductions, the deer population increased to 1,600 animals but then declined as the town elk herd grew in size, as a result of competition for food.

In the undisturbed vegetation/water table run with wolves, the park elk population was held to 300-500 (Figure 76c). The town population increased from 1,000 to 1,800, but then predation decreased the population to about 1,200. Wolf numbers varied between 14-17 throughout (not shown). Wolves held the deer population to less than 200 head.

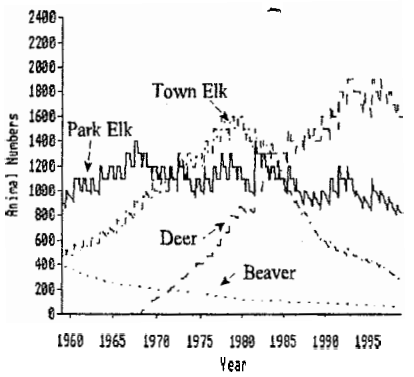
Table 23. Conditions for 1949-1998 model experiments. Run refers to panel letters in Figures 76-85. *Run E is like run A, but uses climate data from 1900-1949.

Run	Elk Herds	Elk Removals	Deer Presence	Deer Removals	Beaver Numbers	Wolf Presence	Vegetation and Water Table Conditions
A	2	Yes	Yes	Yes	As Observed	No	Current
B	2	No	Yes	No	As Observed	No	Current
C	2	No	Yes	No	As Observed	Yes	Natural
D	None	No	Yes	Yes	As Observed	No	Current
E*	2	Yes	Yes	Yes	As Observed	No	Current
F	2	Yes (keep numbers 400-600)	Yes	Yes	As Observed	No	Current

A)

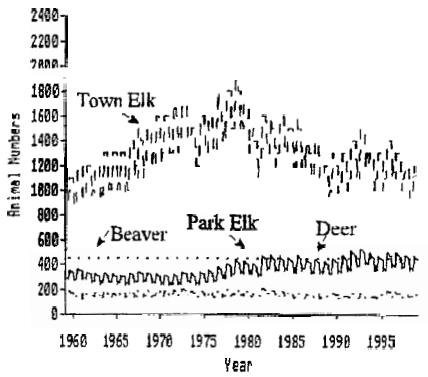


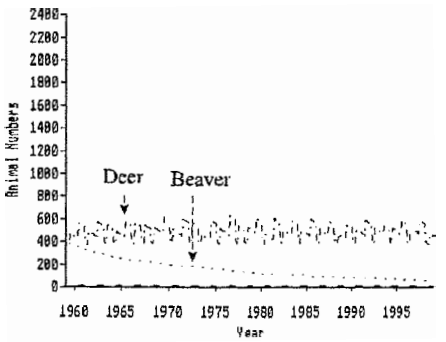
B)



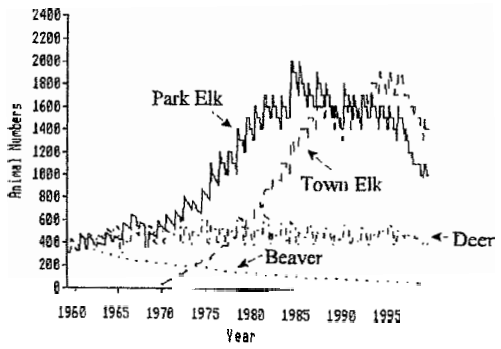
C) As used in the Undist.

D)





E)



F)

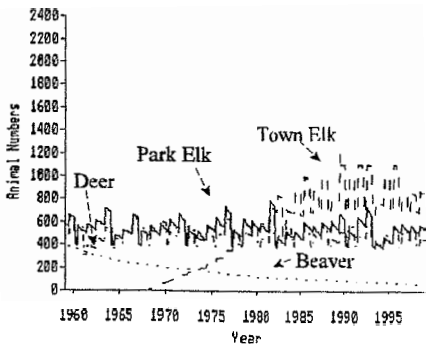
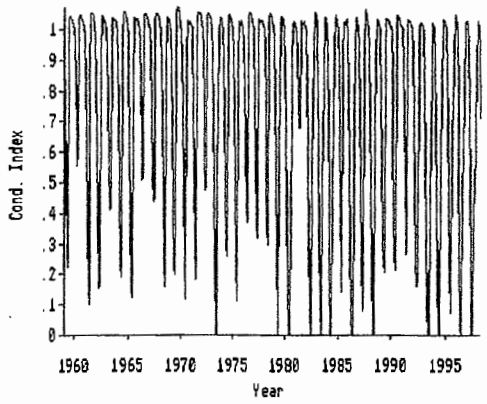
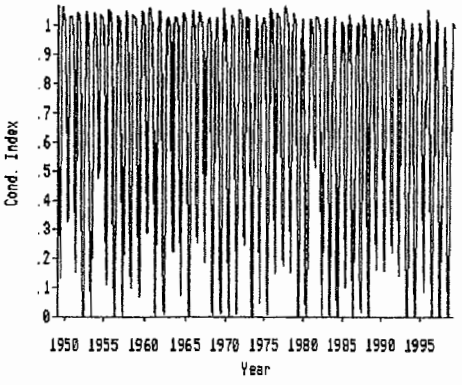


Figure 76. Animal population responses to different conditions during the period 1959-1998. A) Control run (observed conditions), B) no elk or deer removal, C) undisturbed conditions, with undisturbed vegetation, soils with elevated water tables, and wolves, D) no elk, E) control, but using the climate of 1900-1949, F) elk removals to 600-800.

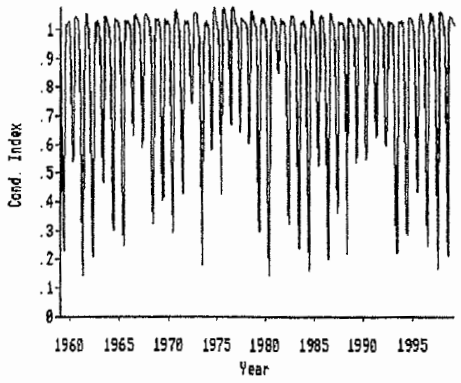
A)



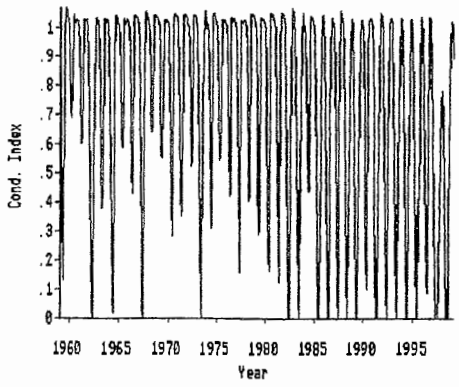
B)



C)



D)



E)

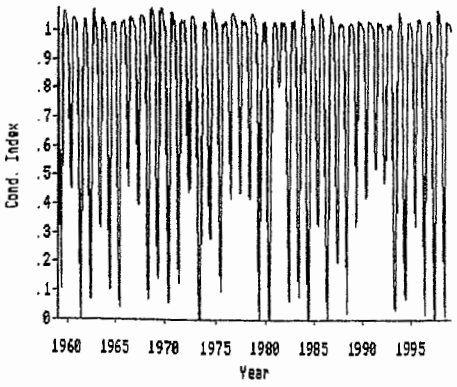


Figure 77. Park elk herd body condition responses to different conditions during the period 1959-1998. A) Control run (observed conditions), B) no elk removal, C) undisturbed conditions, with undisturbed vegetation, soils with elevated water tables, and wolves, D) control, but using the climate of 1909-2948, E) elk removals to 600-800.

In simulations with no elk (Figure 76d) and with elk reduced to 400-600 in the park and to 800-1000 in the town (Figure 76f), population dynamics behaved as prescribed.

A simulation was conducted using the same elk reduction rates and the same vegetation and water tables as the control run, but with the climate of 1900-1949 (Figure 76e). The purpose of this run was to see if climatic differences could have contributed to differences in ecosystem dynamics between these two periods. The park elk herd increased to higher levels (>1,800) than with actual climate, indicating that the climate of 1949-98 was more stressful to elk than that of 1900-1949. By the end of the simulation, the elk population declined to <1,200 head, similar to that of the control run. The primary difference in climate was higher precipitation in the 1920s than in the 1970s (Figures 26,64). There were also years of low snowpack in the 1920s.

Elk body condition in the run with no elk reductions was lower in winter than in the control run, throughout the simulation (Figures 77a,b). In the undisturbed run, body condition was maintained at a higher level, with the exception of several severe winters (Figure 77c). In the simulation driven by 1912-1948 climate, body condition was higher under the climate of the 1920s than the 1970s, but lower under the climate of 1935-1945 than climate of 1985-1995 (Figures 77a,d). When elk were reduced to 600-800, body condition was higher than in the run with no reductions (Figure 77e,b). Condition was similar to that of the control run until the 1970's, when reductions were ceased in the control run. Condition was slightly higher with reductions in the 1970s-mid 1980s, and notably higher with reductions from the late 1980s onwards.

When elk and deer were not reduced, there was about 10% less grass and 30% less forb biomass on drylands than in the control run by the end of the period (Figure 78b vs. 78a). In the undisturbed run, there was about 8% more grass and 5% more forb biomass than in the control run by the end of the period (Figure 78c). With no elk, there was about 10% more grass and 25% more forb (Figure 78d). Using 1900-1949 climate resulted in slightly less grass biomass, and about 10% less forb biomass by the end of the run, most likely due to the higher elk numbers. Reducing elk to 600-800 increased grass biomass about 5% and forb biomass about 10% relative to the control (Figure 78f).

Dryland grass root biomass on drylands remained steady with no elk reductions, as in the control, but forb biomass declined relative to the control (Figure 79b). In the undisturbed run, both grass and forb root biomass increased throughout the simulation (Figure 79c). The increases were comparable when there were no elk (Figure 79d). Root biomass with 1900-1949 climate was very similar to the control (Figure 79e). Reducing elk to 600-800 caused grass and forb roots to increase at a rate very similar to that of the undisturbed run (Figure 79f).

In mesic herbaceous communities (willow, aspen, and sub-irrigated meadow), grass production was little different between the control run and the run with no elk or deer reductions, however forb biomass decreased compared to the control (Figure 80b). These outputs are reported in terms of g per m^2 of grid-cell area rather than per m^2 of non-willow covered area. As willow cover decreased, herbaceous biomass increased due to the increased area without competition from willows.

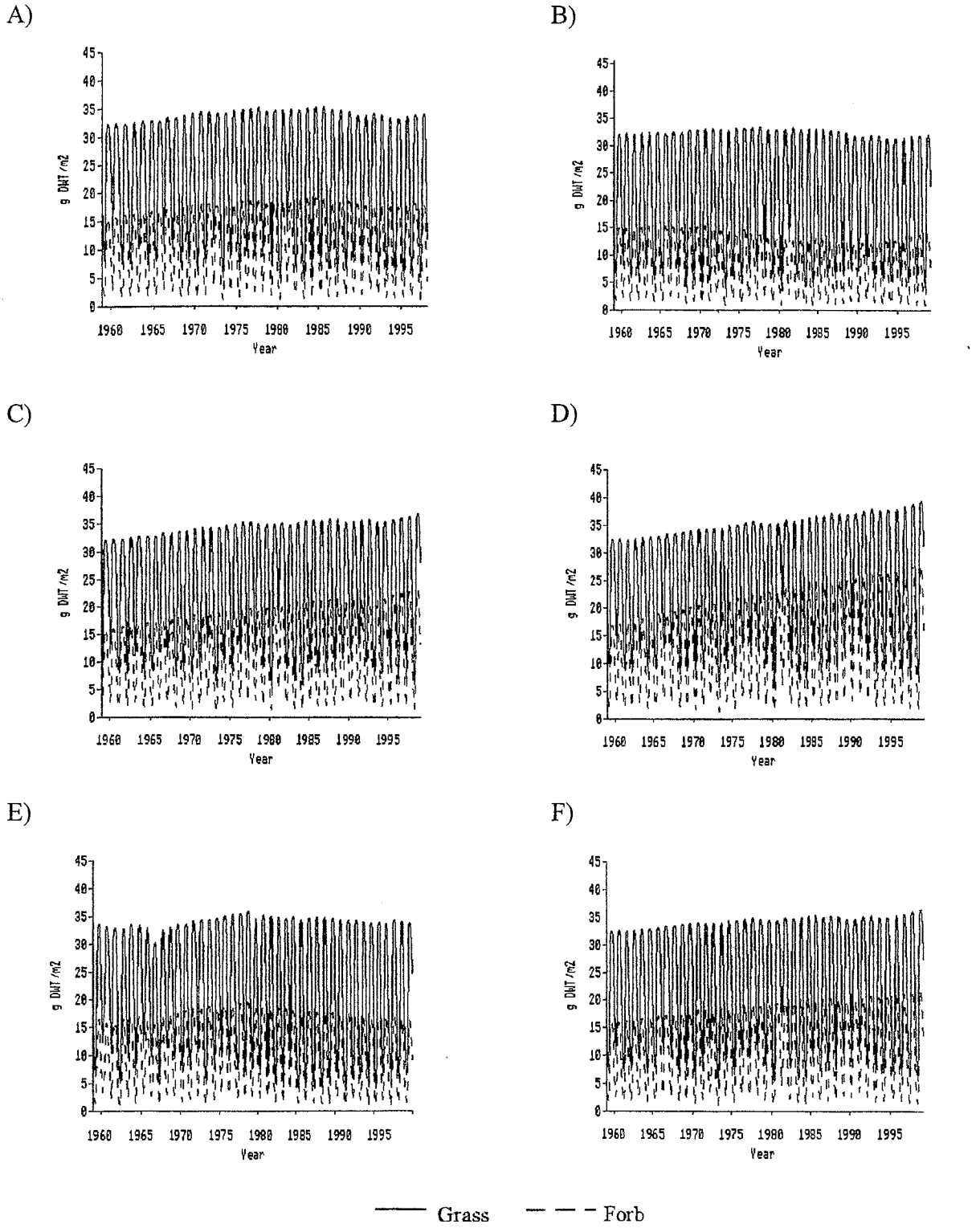


Figure 78. Dryland herbaceous aboveground biomass responses to different conditions during the period 1959-1998. A) Control run (observed conditions), B) no elk removal, C) undisturbed conditions, with undisturbed vegetation, soils with elevated water tables, and wolves, D) no elk, E) control, but using the climate of 1900-1949-1949, F) elk removals to 600-800.

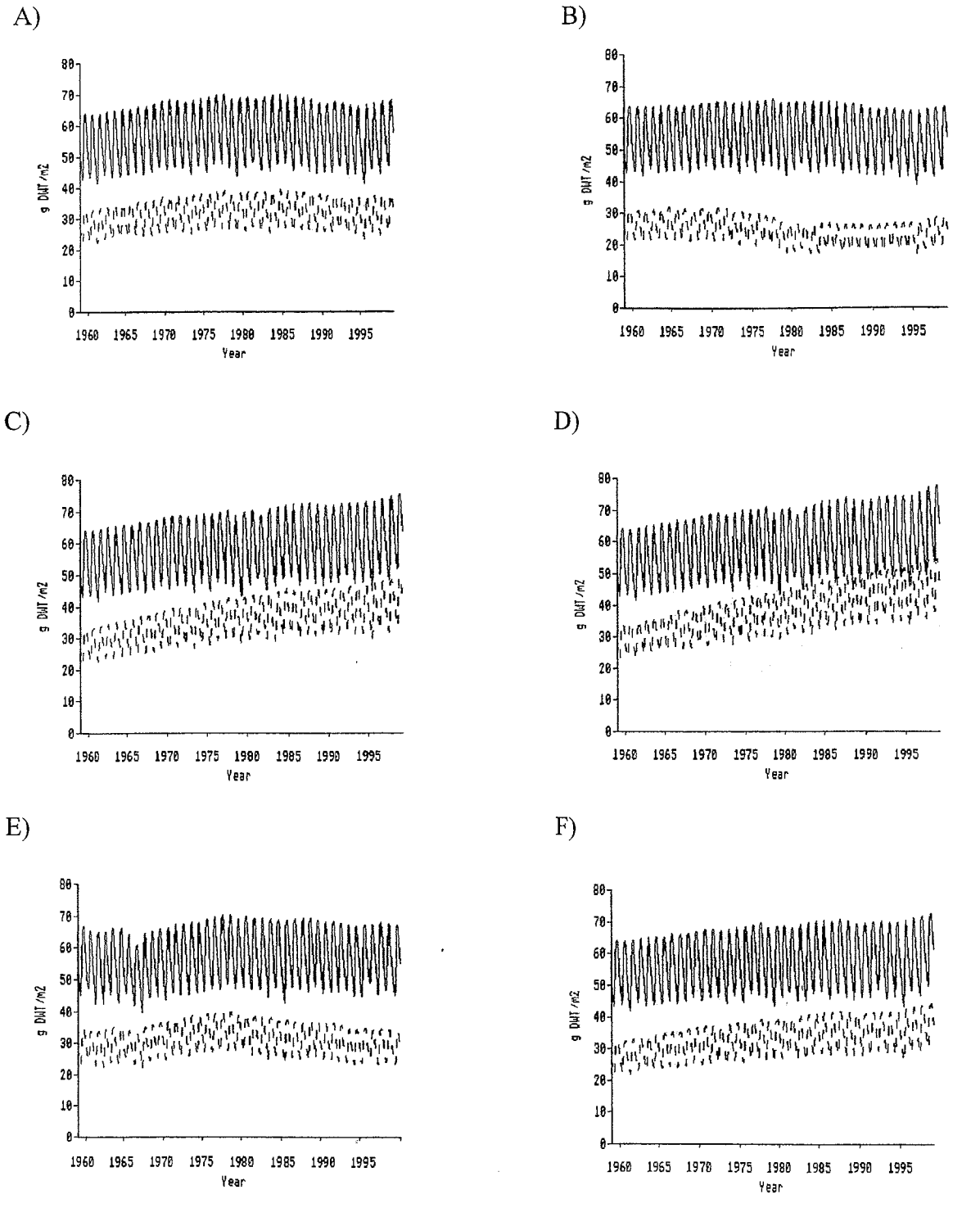
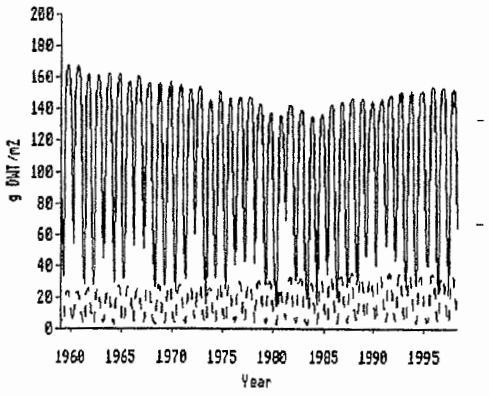
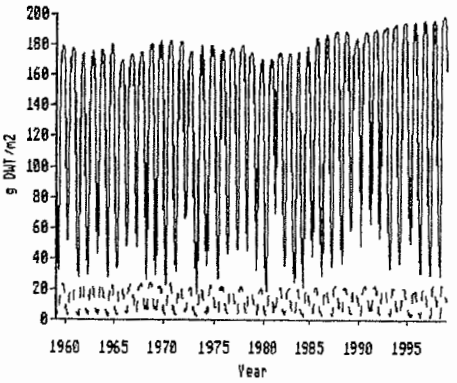


Figure 79. Dryland herbaceous root biomass responses to different conditions during the period 1959-1998. A) Control run (observed conditions), B) no elk removal, C) undisturbed conditions, with undisturbed vegetation, soils with elevated water tables, and wolves, D) no elk, E) control, but using the climate of 1909-2948, F) elk removals to 600-800.

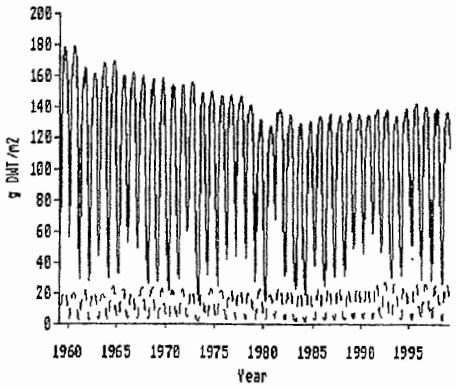
A)



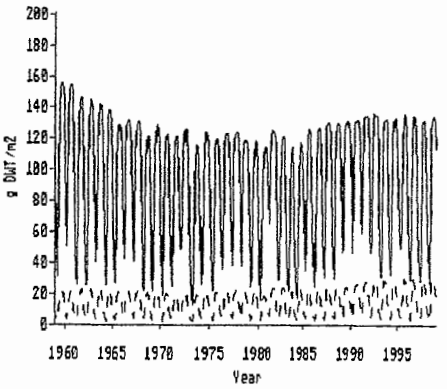
B)



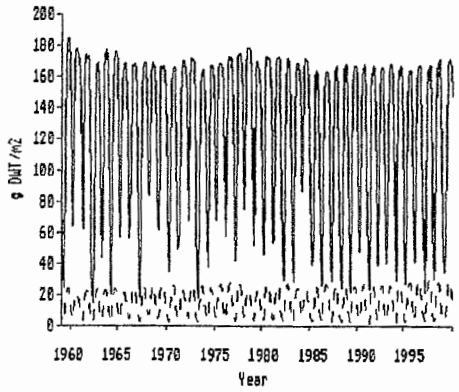
C)



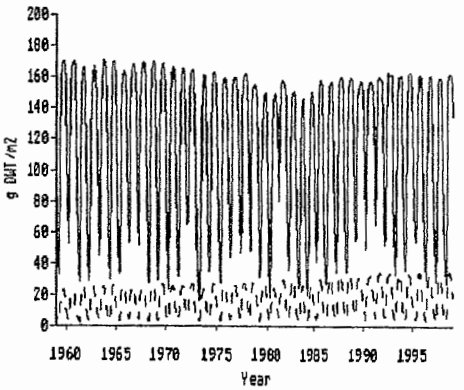
D)



E)



F)



—— Wet Grass — — — Wet Forb

Figure 80. Mesic herbaceous aboveground biomass responses to different conditions during the period 1959-1998. A) Control run (observed conditions), B) no elk removal, C) undisturbed conditions, with undisturbed vegetation, soils with elevated water tables, and wolves, D) no elk, E) control, but using the climate of 1909-2948, F) elk removals to 600-800.

Willow decreased with no elk reductions (Figure 81b), while it remained constant in the control (Figure 81a). Since willow cover decreased while grass biomass remained constant over the total land surface, grass biomass density in the openings between willow must have declined.

In the undisturbed run, mesic grass biomass declined (Figure 80c), due entirely to the increase in willow cover (Figure 81c). Forb biomass remained approximately comparable to the control, indicating that forb biomass per area of non-willow cover increased. With no elk, mesic grass biomass declined more than in the control or even the undisturbed run (Figure 80d). This again, is due mainly to higher willow cover with no elk than in the control. Willow cover rapidly increased from 40 to 60% in the spin-up years 1949-1958 with no elk (Figure 81d). Grass biomass may additionally have decreased slightly below that of the undisturbed run due to increased forb abundance.

Climate had little effect on mesic herbaceous biomass (Figure 80e). It was slightly higher with 1900-1949 climate than with 1949-1998 climate, while forb biomass was slightly less. The increase in herbaceous biomass was likely due to slightly lower willow cover with 1900-1949 climate (Figure 81e), which could have been due to drier conditions and a greater number of elk (Figure 76e).

When elk were reduced to 400-600, mesic herbaceous biomass was essentially the same as in the control (Figure 80f). Willow cover increased when elk were reduced, however (Figure 81f). The combined grass and willow responses suggest that grass biomass was more dense in openings between willows when elk were reduced.

Responses of willow in individual grid-cells indicated that without elk reductions, willow would have declined to very low abundances sooner, and a small number of locations would attain >50% willow cover (Figure 82b). In contrast, all willow locations in the run with undisturbed water tables and vegetation attained cover >60% (Figure 82c). Without elk, however, cover in three locations declined, due to lower water tables in those locations, compared to the undisturbed run. Comparison of the run with no elk to the control run (Figures 82a,d) shows the relative effects of elk and water tables. Reducing water tables had a negative effect on willow cover at three of the locations, but cover at those locations declined to lower values with elk than without elk. Elk also suppressed cover at two locations to about 50%, while without elk, cover increased to maximal values at all locations where water tables were not lowered.

Aspen cover declined by about 15% in the control simulation (Figure 81a). With no elk reductions, the decline occurred earlier, during the spin-up period before 1959 (Figure 81b). For the purposes of the experiment, aspen was initialized to the same value in 1949 as in the undisturbed run as in the control. By 1959, the first date shown on the graphs, aspen cover was lower with no elk removal than in the control. In the undisturbed run with wolves, aspen cover also declined due to elk herbivory (Figure 81c). With no elk, aspen increased (Figure 81d). With 1900-1949 climate, aspen declined early on, during 1949-1958, but values at the end of the run were similar to the control. When elk were reduced to 600-800, aspen actually declined to lower levels than in the control (Figure 81f), due to the fact that prior to 1965 elk were reduced to lower numbers by reductions in the control run than by reductions to 600-800 (Figure 76).

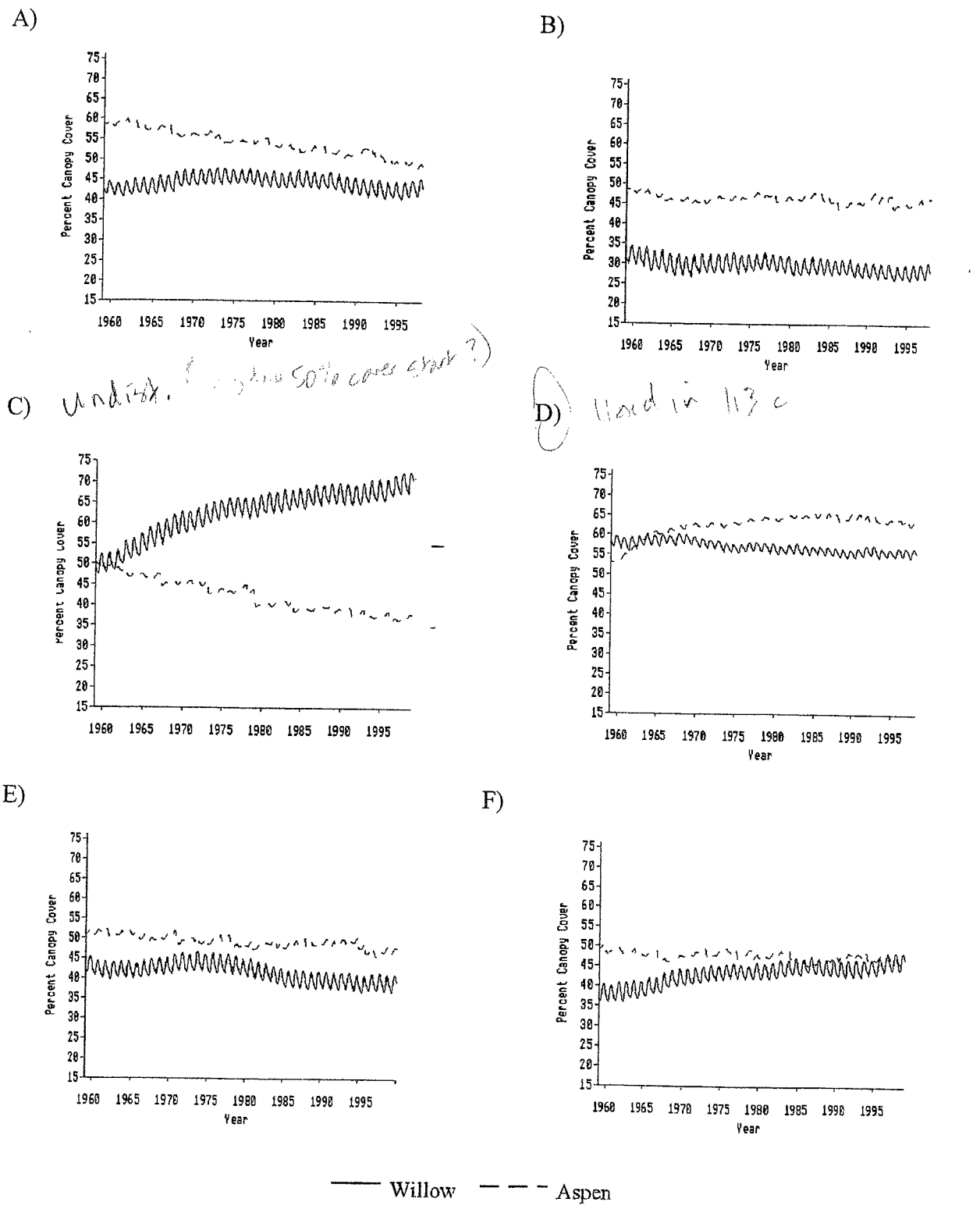


Figure 81. Willow and aspen cover responses to different conditions during the period 1959-1998 reported as mean canopy cover within the grid-cells having that vegetation type. A) Control run (observed conditions), B) no elk removal, C) undisturbed conditions, with undisturbed vegetation, soils with elevated water tables, and wolves, D) no elk, E) control, but using the climate of 1909-2948, F) elk removals to 600-800.

Five additional experiments were conducted to examine effects of water table, deer and beaver on willow and aspen. The effect of change in water table can be ascertained by comparing Figures 83a and 84a to Figures 81a and 82a. Using undisturbed water tables led to an increase in willow compared to the control run which used current water table conditions. The effect of the converse, of switching to current water table conditions in the otherwise undisturbed run, can be seen by comparing Figures 83d and 84d to Figures 81c and 82c. The switch led to markedly lower willow covers, with lower values being simulated in seven of the ten locations. The effect of deer can be seen by comparing Figure 83b to 83c, and Figure 84b to 84c (i.e., runs with deer only compared to runs with no animals). Deer had no effect. The effect of beaver can be determined by comparing Figure 83c (no animals) to Figure 81d (no elk). Beaver had a negligible impact on willow, but did reduce aspen by approximately 10%. Interestingly, in the simulation with wolves and current water table conditions (Figure 83d), aspen stabilized at a higher value than in the undisturbed run with wolves (Figure 81c).

The effect of wolf predation on willow and aspen was demonstrated by contrasting the undisturbed run with a run with no reductions, no wolves, and undisturbed water tables (Figure 81c vs. 82c). Even though water tables were high, if elk were not reduced, willow cover declined due to elk herbivory (Figures 83e, 84e). A similar contrast was made under current water table conditions (Figure 83d vs. 81b). The size of the park elk herd was markedly lower in the run with current water table conditions (Figure 83f) than in the undisturbed run (Figure 76c), most likely because the town herd segment was less productive with current water table and land cover than with natural land cover, which then caused the wolves to more intensively prey upon the park segment.

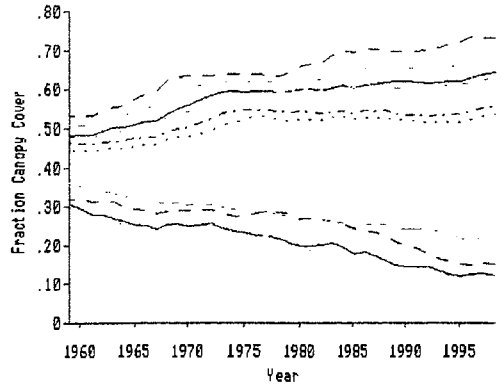
Soil organic nitrogen was very little affected by elk abundance (Figure 85). These outputs are averaged over the entire winter range, however, so the means are affected by areas which are grazed lightly or not at all. By the end of the runs, there was 3 g m^{-2} less nitrogen in the intermediate SOM pool in the no-reductions run than in the no-elk run. Compared to the large size of the pool, this was a very small amount.

In the control run, 10-50% of dry grassland sites were grazed 20-50% and 8-16% of dry grassland sites were grazed 50-80% between 1975 and 1998 (Figure 86a). A small fraction (1-2%) of grasslands were grazed in excess of 80%. In years when there was little grazing in the 50-80% range, grazing intensity shifted to the 20-50% range (Figure 86c). In the early years approximately 10% of willow locations were browsed in the 20-50% range, while the rest were browsed <20%. Beginning in the late 1970s, there were several years when 30-35% of willow locations were browsed at 50-80%.

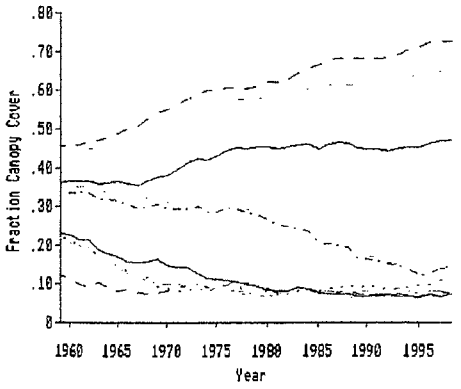
In the undisturbed run, 2-10% of dry grasslands were grazed at the 20-50% offtake level, while the remainder were grazed at 0-20%. There was no grazing in excess of 50%. A small fraction (<10%) of willow were infrequently browsed at 0-20%, and nearly all browsing was in the 20-50% offtake range.

The spatial distribution of grazing impacts on dryland herbaceous vegetation can be visualized

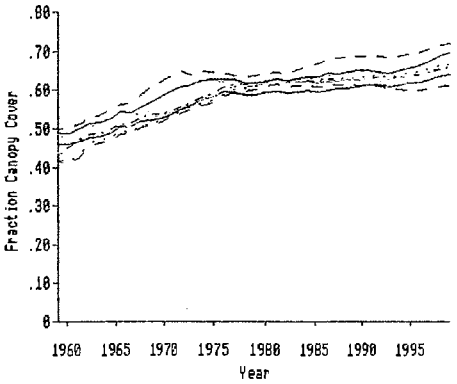
A)



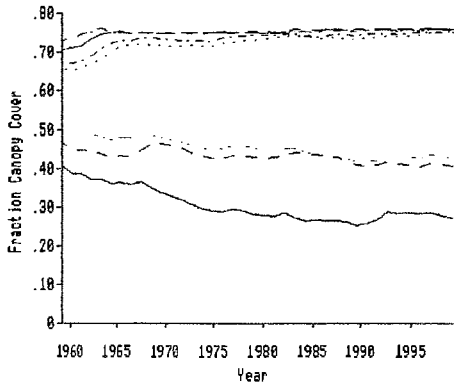
B)



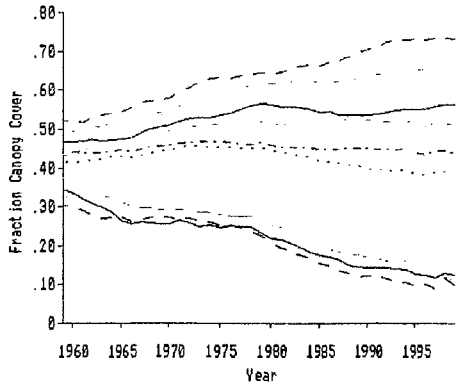
C)



D)



E)



F)

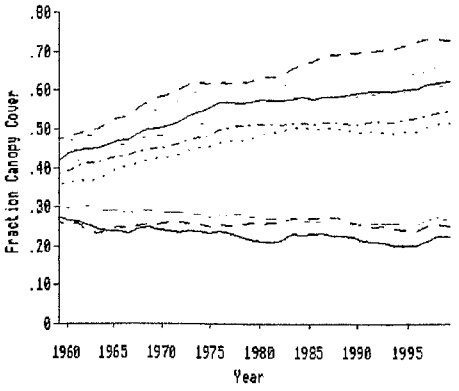


Figure 82. Willow cover in individual grid-cells under different conditions during the period 1959-1998. A) Control run, B) no elk removal, C) undisturbed conditions, with undisturbed vegetation, soils with elevated water tables, and wolves, D) no elk, E) control, but using the climate of 1909-2948, F) elk removals to 600-800.

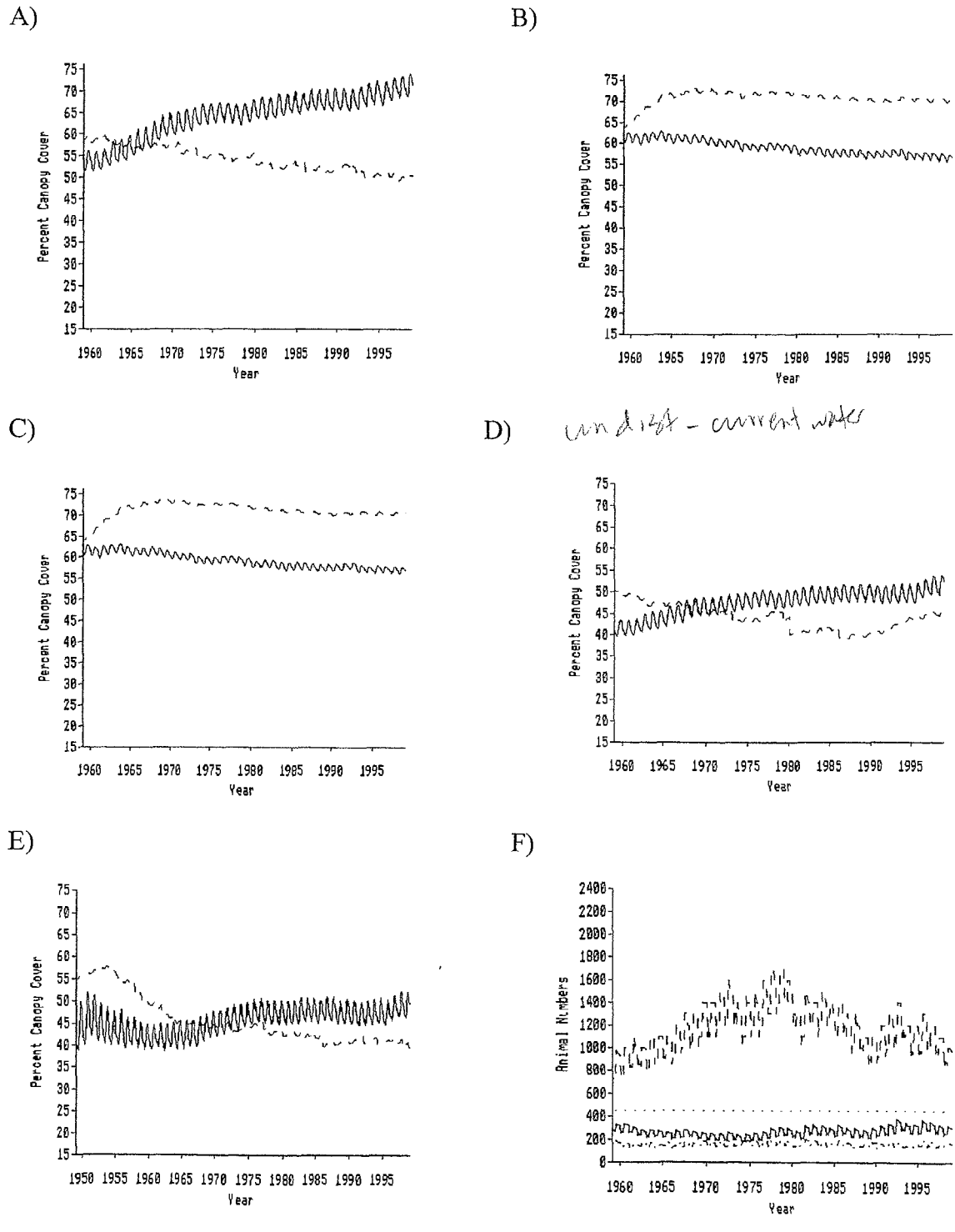
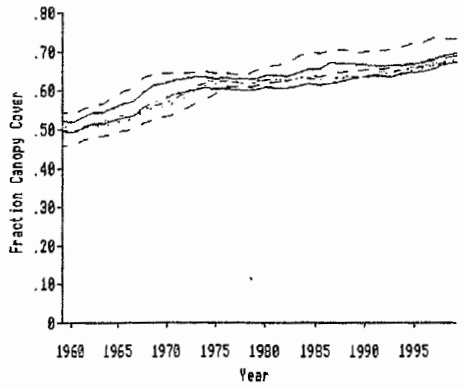
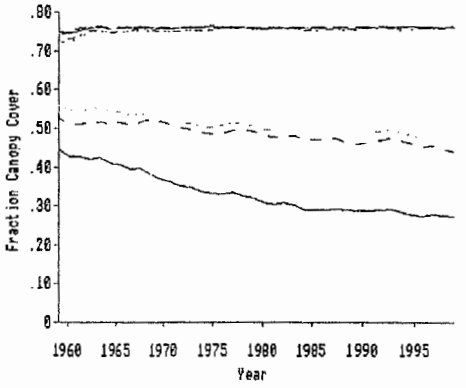


Figure 83. Willow and aspen cover responses to different conditions during the period 1959-1998 reported as mean canopy cover within the grid-cells having that vegetation type. A) Like the control run, but with undisturbed soil conditions. B) Deer only (no elk or beaver). C) No herbivores at all. D) With wolves, and current soil and water table conditions. E) No elk removal, no wolves, undisturbed soil and water table. F) Animal populations as in D.

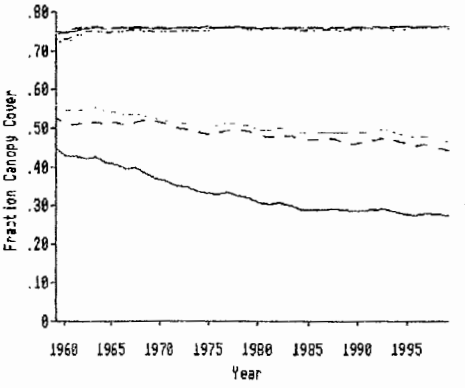
A)



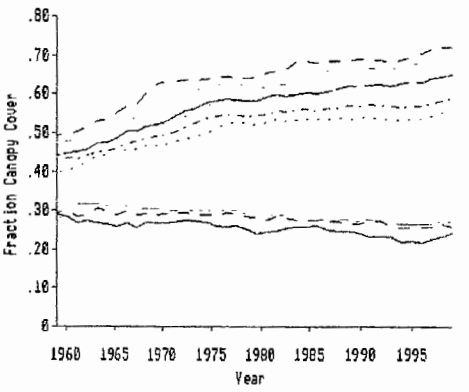
B)



C)



D)



E)

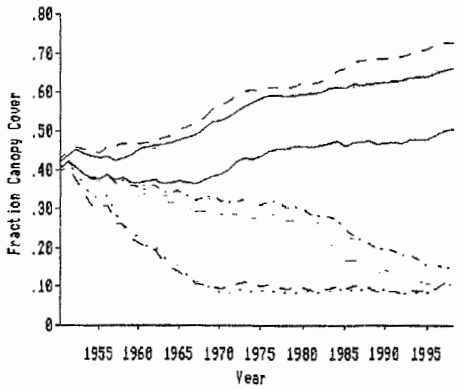


Figure 84. Willow cover in individual grid-cells under different conditions during the period 1959-1998. A) Like the control run, but using pre-disturbance soil conditions. B) Deer only (no elk or beaver). C) No herbivores at all. D) Like the undisturbed run, but with current soil and water table conditions. E) No elk removal, no wolves, undisturbed soil and water tables.

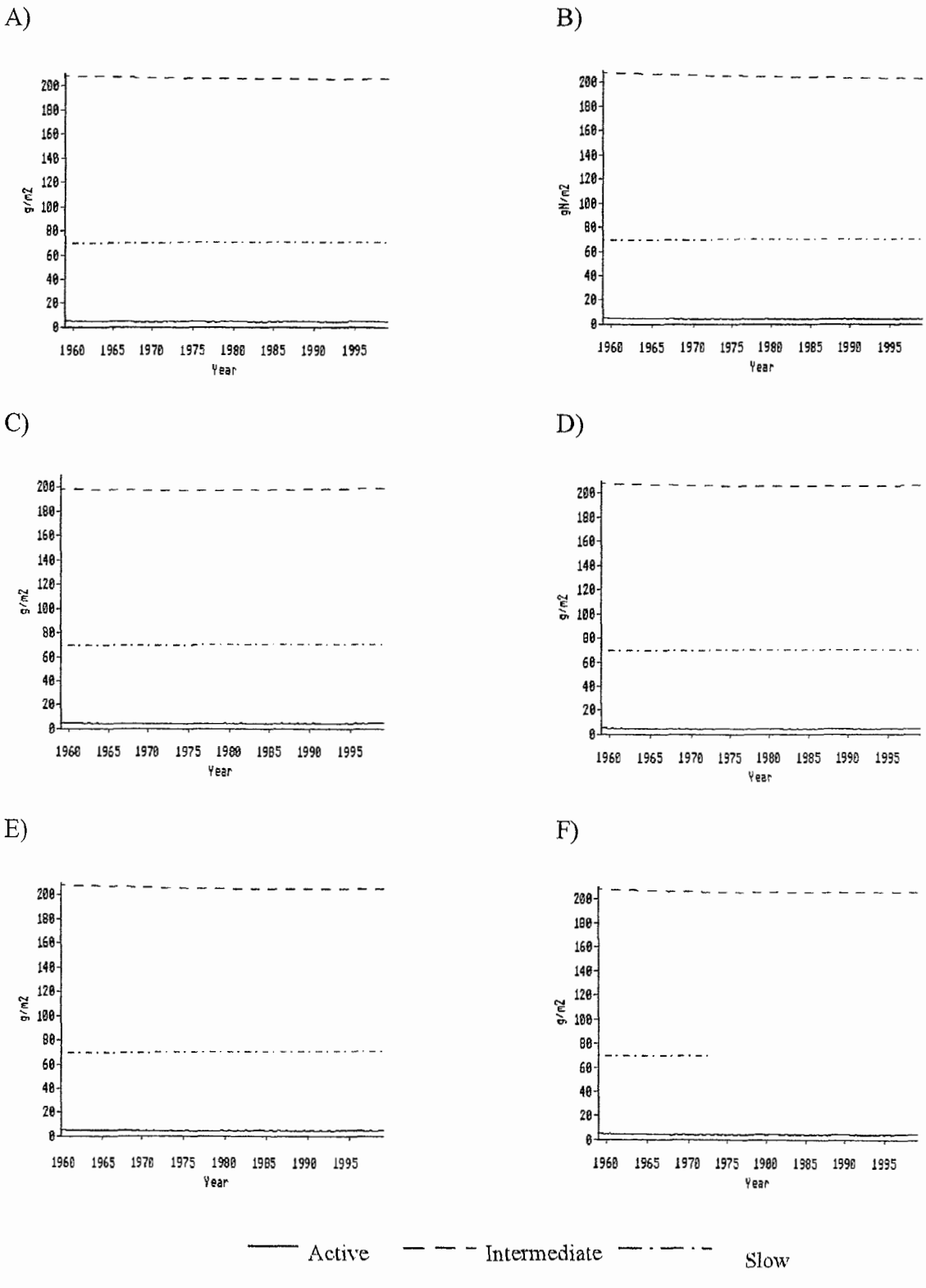
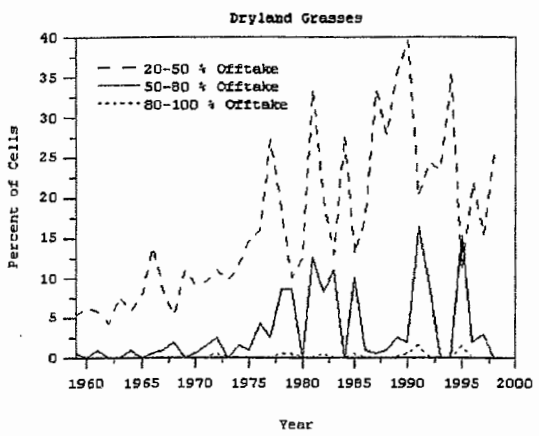
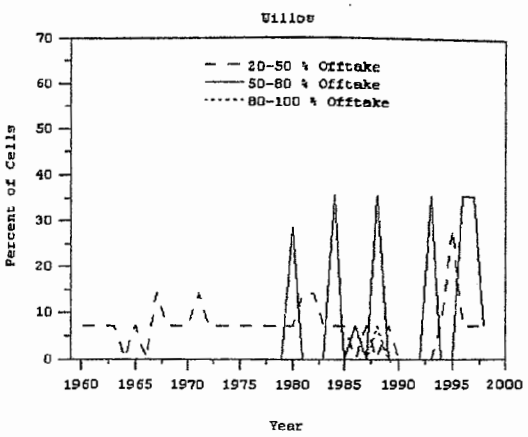


Figure 85. Soil organic nitrogen pools under different conditions during the period 1959-1998. A) Control run (observed conditions), B) no elk removal, C) undisturbed conditions, with undisturbed vegetation, soils with elevated water tables, and wolves, D) no elk, E) control, but using the climate of 1900-1949, F) elk removals to 600-800.

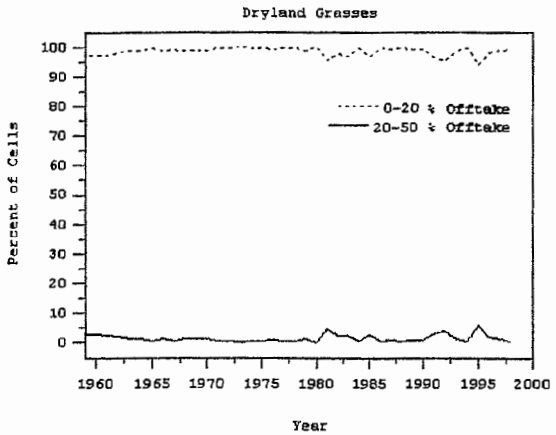
A)



B)



C) undist.



D) undist.

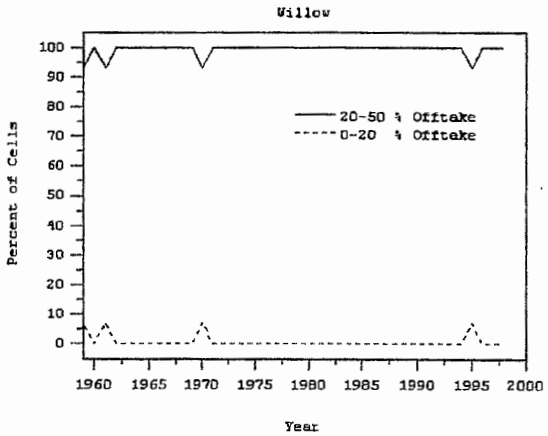


Figure 86. A) and B) are offtake percentages for the control run, showing the percentage of grid-cell cells with >50% offtake. C) and D) are offtake percentages for the undisturbed run 1949-1998 with wolves, and vegetation and animals starting at values at the end of the 1912-1948 undisturbed run. In the undisturbed run, there were < 1% of cells with >50% offtake of grass or willow, throughout.

from the spatial distributions of root biomass in dryland herbaceous vegetation. In a comparison between the control run and the undisturbed run, reductions in root biomass can be seen throughout the core winter range (Figure 87). The ratio of roots in the control to roots in the undisturbed run (Figure 87a) shows where the relative impacts were highest. Reductions of 20-30% were common. Reducing elk to 400-600 still caused reductions in root biomass relative to the undisturbed run. Most of the reductions were in the 10-15% range, with a few locations in the 15-20% range (Figure 87b). The ratio of roots in the control to roots in the no-elk scenario (Figure 88a) is of interest because it shows what might be expected in exclosure experiments. In some areas roots were reduced by 30-40% compared to no elk, but in many areas the reduction was only 5-15%. The ratio of roots in the control to roots under reductions to is of interest because it shows the effect of reductions to that level compared to the actual situation (Figure 88b). Root biomass in the control was 85-100% of that with elk reductions in most places. In a few areas, roots in the control were 75-85% of roots in the elk reduction scenario.

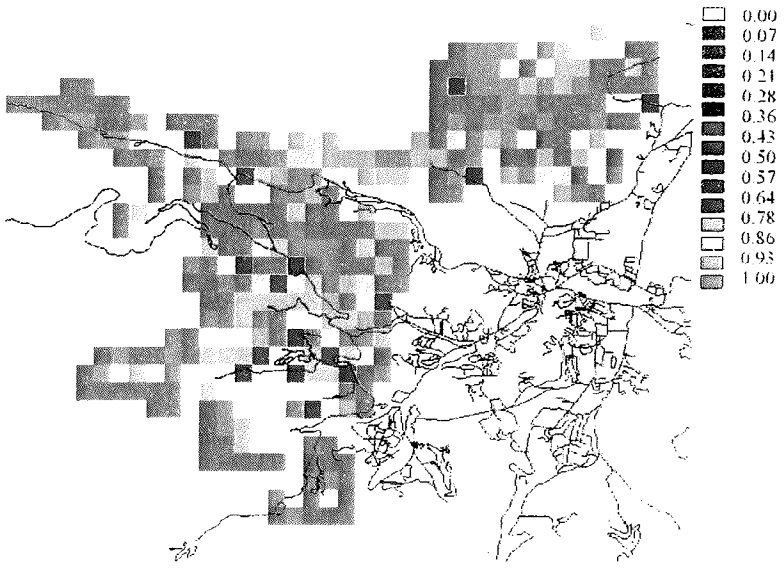
The temporal trends and ranges of spatial variability in dryland root biomass are shown in Figure 89. In the control run, root biomass increased and then decreased as elk numbers increased. In the run with elk reductions to 400-600, the increase continued, and in the undisturbed run the increase continued at a higher rate. The differences in minima between the 3 runs are small, but the differences in maxima are large, leading to intermediate differences in the averages. Another consequence was that the range of difference between the minima and maxima was greater in the undisturbed run and elk reduction run than in the control run.

The model experiments for 1949-1998 showed that following cessation of controls, the elk population attained a food-limited carrying capacity with elk numbers being higher than in the undisturbed conditions with wolves. Experiments also showed significant competitive interactions between elk and deer. Elk body condition behaved as expected, declining to lower values when there were more elk. There was a slight negative effect of elk on dryland herbaceous plants on average, but localized effects could have been greater. Mesic herbs were more affected by changes in willow cover brought about by elk browsing than by direct grazing impacts. Elk browsing negatively affected willow cover, but the primary cause of willow reductions was a lowering of water tables. Aspen abundance was reduced by elk in both the control run and the run with undisturbed conditions.

Factorial Experiment on Plant Responses to Elk, Beaver, and Water Tables

A factorially designed experiment was conducted in which elk and beaver densities were varied in all possible combinations, to assess their relative effects on plants. Elk numbers in the park population were set at 0, 250, 500, 750, 1000, 1,250, 1,500, 1,750 and 2,000. The size of the park elk range is 96.25 km^2, so these numbers convert to densities of 0, 2.6, 5.2, 7.8, 10.4, 13.0, 15.6, 18.2, and 20.8 elk km^{-2}. Beaver numbers in the park elk winter range were set at 0, 200, 400, and 600. The size of the beaver habitat was kept constant at 425 ha, so these numbers convert to densities of 0, 0.47, 0.94, and 1.41 beaver ha^{-1}. These beaver densities span a realistic range. Assuming there are six beavers per colony, then 400 beavers is equivalent to 6.4 ha per colony, 200 beavers is equivalent to 12.8 ha per colony, and 600 beavers is equivalent to 2.4 ha per colony. Elk in the town

A)



B)

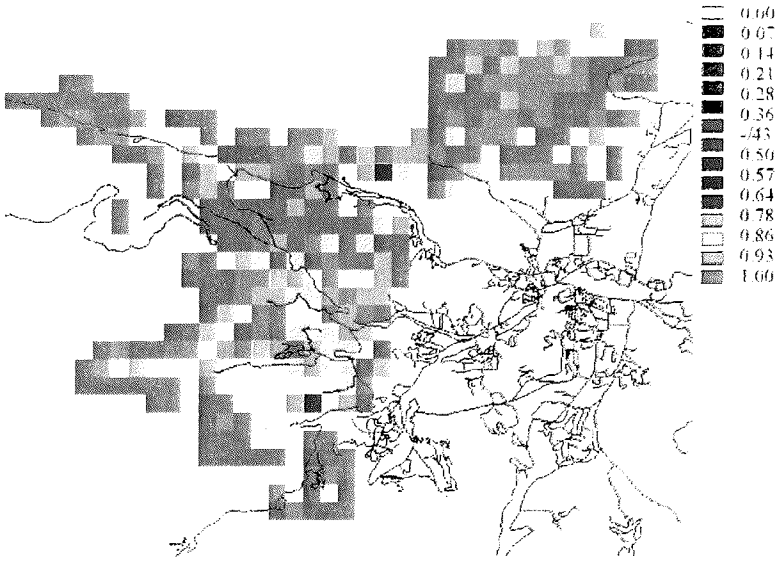
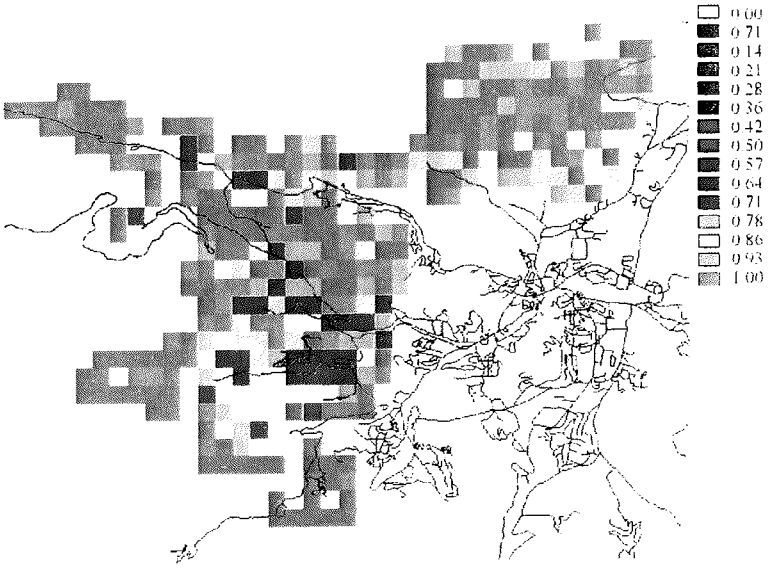


Figure 87. A) Ratio of dryland herbaceous root biomass in the last 10 years of the control simulation 1949-1998 to that in the undisturbed run with wolves. B) Ratio of root biomass with elk culled to 400-600 to that in the undisturbed run. Only cells with >15 g m^{-2} in the undisturbed simulation are included.

A)



B)

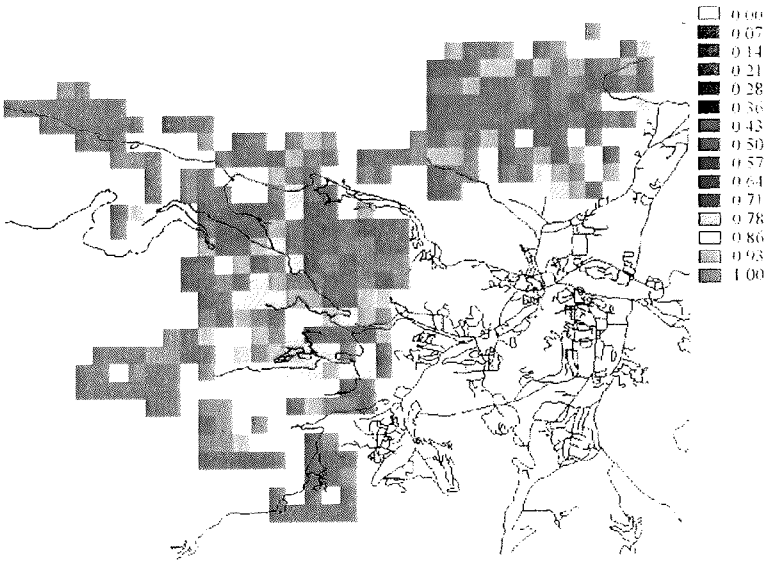
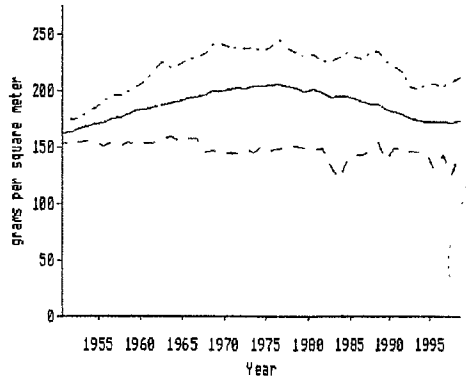
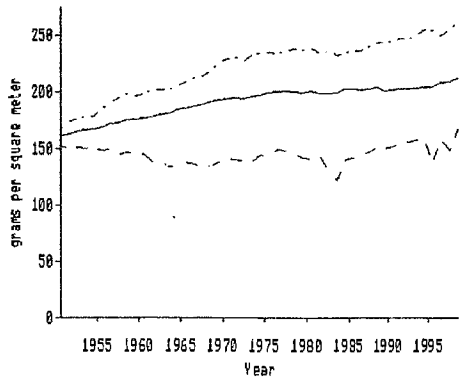


Figure 88. A) Ratio of dryland herbaceous root biomass in the last 10 years in the control simulation to that in the the no-elk simulation. B) Ratio of root biomass in the control simulation to roots in the simulation with elk culled to 400-600. Only cells with >15 g m^{-2} in the undisturbed simulation are included.

A)



B)



C)

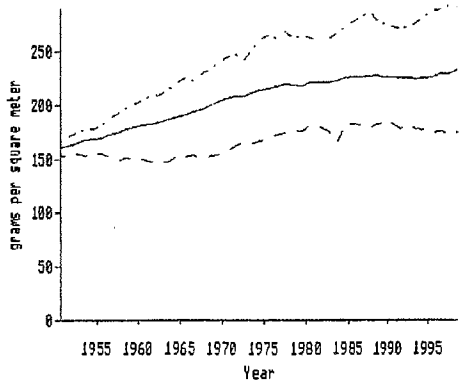


Figure 89. Herbaceous root biomass on the park elk range in July in grassland vegetation types only. A) The control run. B) Culling to 400 when park elk population reaches 600. C) The undisturbed run with wolves. Minimum, maximum, and average values among grid-cells are shown, illustrating the range of spatial variation.

population were set at 800, and deer were set at 400 in all runs. The simulations were otherwise configured like the control run for 1949-1998.

A response surface of willow cover generated from the results shows that elk and beaver can both have negative effects, but beaver effects are negligible at low elk densities (Figure 90). Willow cover with no elk or beaver was 60%. Increasing beaver had little impact on willow below 400 elk. Beaver started to have effects in the range of 400-800 elk. At most values below 450 beavers (the number assumed in the undisturbed run) and 600 elk, a high cover of willow was maintained. In the range of predator-limited elk carrying capacity (400-800 elk), less than 450 beavers had little impact on willow, and 450-600 beaver had a moderate effect. Above 800 elk, increasing beaver density had negative effects on willow cover. At 1,200 elk (roughly their food-limited carrying capacity), >100 beaver had significant negative effects on willow.

Aspen cover was highly sensitive to elk number in the low range of 0-400 elk (Figure 91). Above 500 elk, there were little added effects of increasing beaver or elk. The residual aspen cover was likely in stands above the core winter range, and away from beaver habitat (stream channels). With few elk (0-200), increasing beaver numbers from zero to 200 had a substantial negative effect on aspen, most likely in stands in beaver habitat. There was little added effect of beaver in excess of 200.

As elk numbers were increased, mean annual herbaceous production declined linearly (Figure 92a). Beaver had little impact on upland vegetation, so only responses to elk are presented here. Each increment of 100 elk resulted in a decrease of about 0.8 g m^{-2} yr^{-1}. Percentage-wise, this is about 1.2% per 100 elk. Similar responses were observed in peak shoot biomass and root biomass (Figures 92b,c). As elk numbers were increased, offtake rate exhibited a non-linear response, beginning to plateau at densities above 1,000. This corresponds to the range at which food begins to limit the elk population. Offtake as a fraction of production increased nearly linearly, except at the two highest elk densities where a non-linear response was beginning to develop (Figure 93a). Interestingly, in the range of food-limited carrying capacity (1,000-1,500), offtake was only 13-18% of forage production. Of course, these are only averages across the entire park herd winter range, and localized impacts and offtake rates would be much greater. As fraction offtake increased, mean production declined almost linearly (Figure 93b). This curve represents something different from the often reported grazing optimization curves (McNaughton 1983c, Detling 1988) in that this is neither a plot of the response of a single plant or of a stand of plants to grazing, nor is it a plot of the way different stands being grazed at different intensities respond to grazing. It is an average response across a large area, in which there are many implicit heterogeneities. At some locations neutral or positive responses could have been simulated, particularly where grazing intensities were low. As elk numbers increased, the area experiencing negative responses increased, overshadowing the neutral or positive responses in lightly grazed areas.

Upland shrub production also declined with increasing elk number (Figure 94). Offtake responded non-linearly, reaching a plateau above 1,500 elk. At a given elk density, there was a range of variability of offtake rates due to differences in beaver numbers. This is likely due to a dietary shift in elk brought about by increasing beaver density.

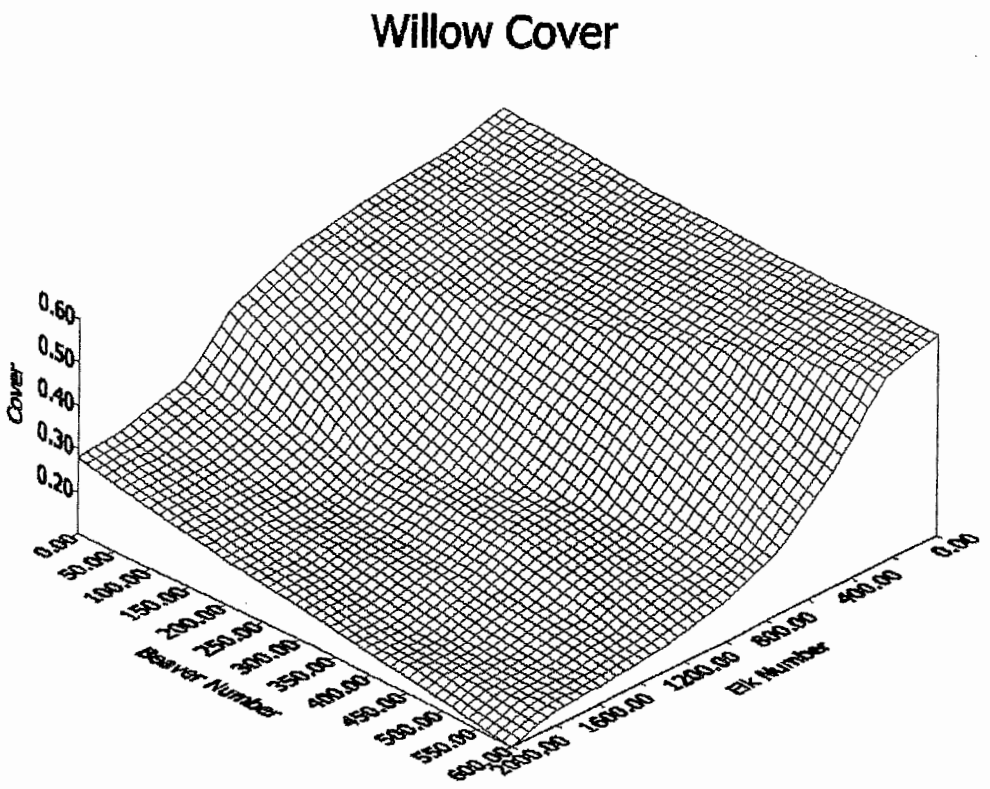


Figure 90. Response surface of willow cover on the elk winter range to elk and beaver numbers after constant stocking for 50 years.

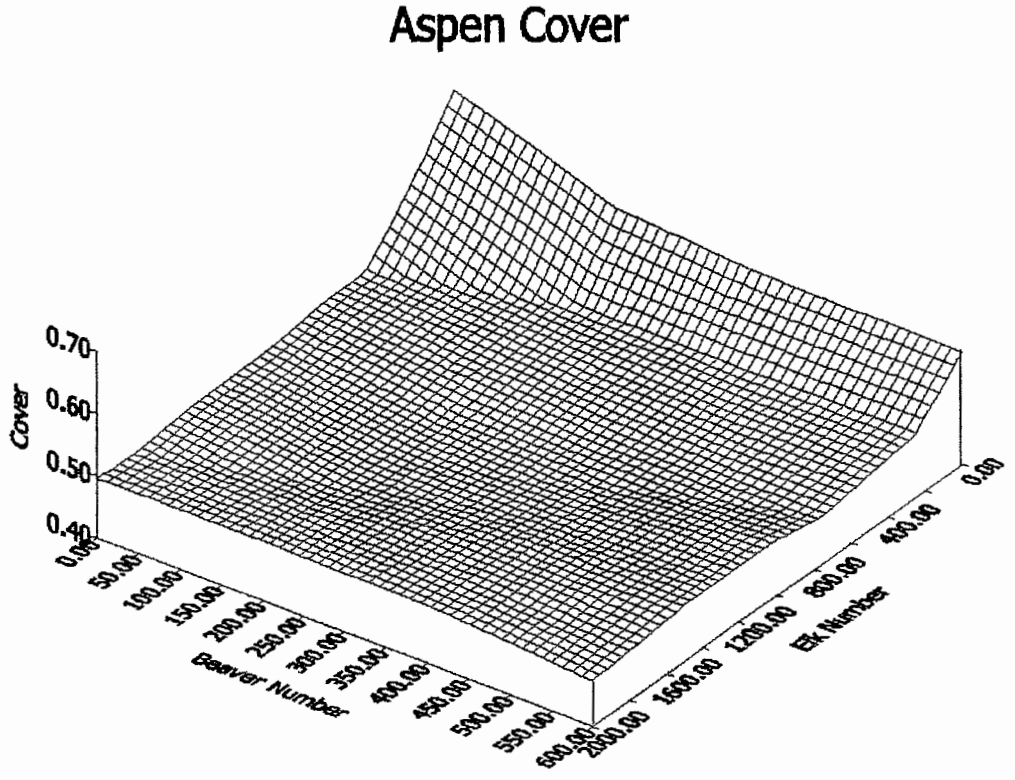


Figure 91. Response surface of aspen cover on the elk winter range to elk and beaver numbers after constant stocking for 50 years. Note the scaling of the z axis may exaggerate the response.

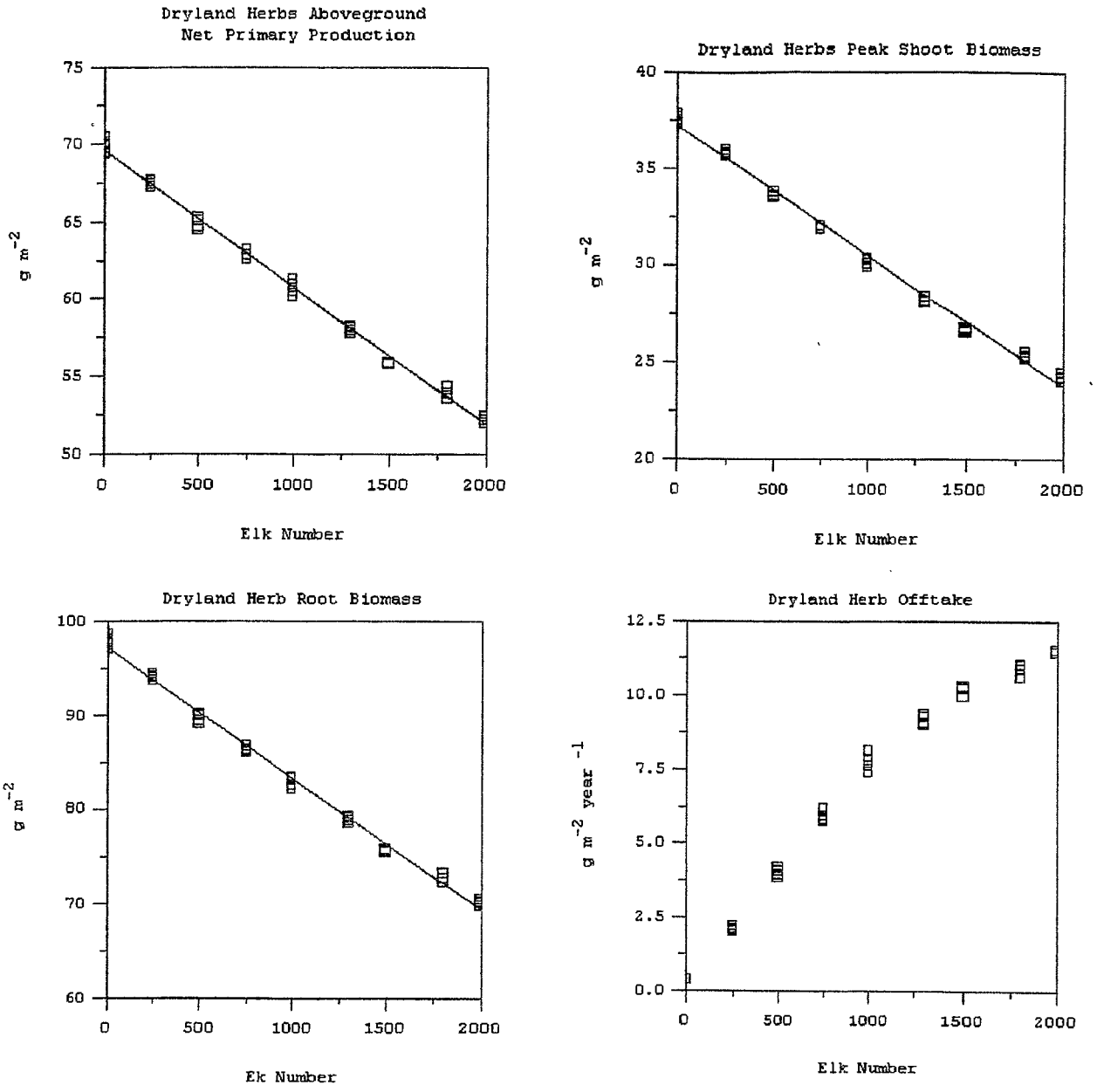


Figure 92. A-C) Responses of dryland (upland) herbs to elk number after constant stocking for 50 years. D) Offtake of herbaceous biomass by elk. Multiple points at each elk density represent runs with different beaver densities in the factorial experiment.

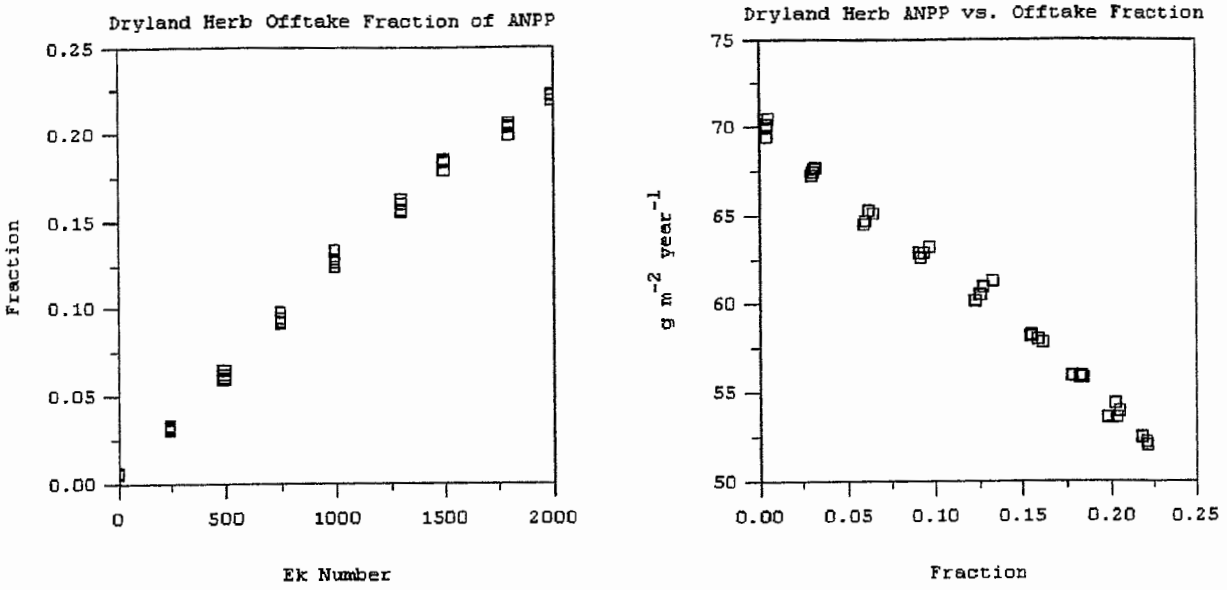


Figure 93. A) Fraction of dryland herb ANPP consumed by elk vs. elk number after constant stocking for 50 years. B) Dryland herb aboveground net primary production vs. fraction of ANPP consumed. Multiple points at each elk density represent runs with different beaver densities in the factorial experiment.

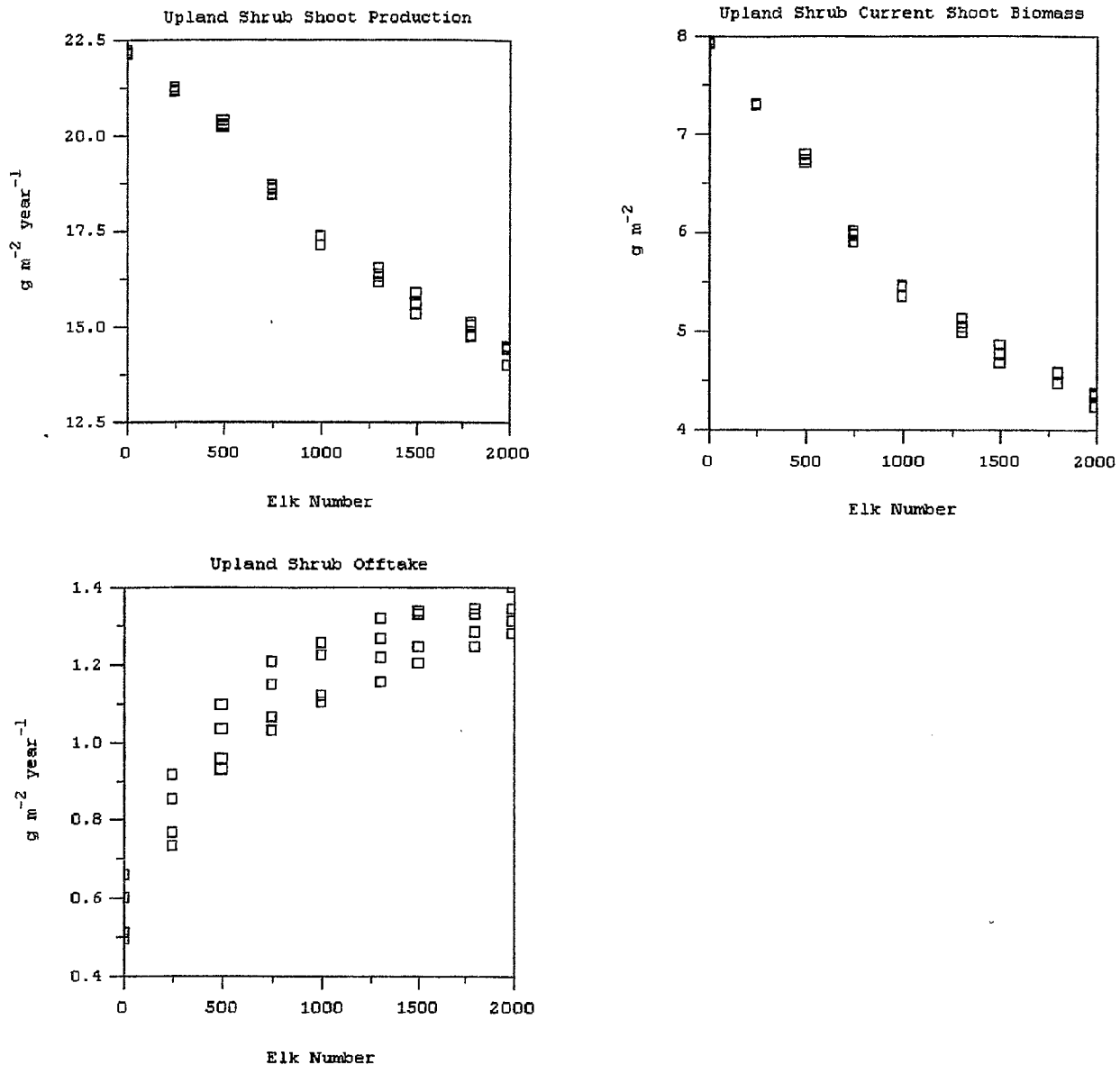


Figure 94. Responses of upland shrubs to elk number, constant stocking rate for 50 years. Multiple points at each elk density represent runs with different beaver densities in the factorial experiment.

As elk density increased, surface litter biomass declined slightly (Figure 95a). With 1,500 elk there was on average 6% less litter than with no elk. Soil litter declined as well (Figure 95b). With 1,500 elk there was on average 4% less soil litter than with no elk. Soil carbon decreased, but the percentage decline was very low (Figure 95c). With 1,500 elk, the decrease was only 1%. This would likely be undetectable in field sampling. The decrease in soil nitrogen was of a comparable magnitude (Figure 95d).

Elk and Vegetation Management Scenarios

Alternative elk management and vegetation fencing scenarios were simulated by running the model for 50 years using weather randomly selected from data for the period 1949-1998. Conditions are summarized in Table 24. All runs began with current conditions, including current herbivore numbers, willow sizes and densities, and water table depths. There were three elk reduction treatments. The park elk herd either was never reduced, reduced to 600-800, or reduced to 200-400. Beavers were assumed to start at current levels, and then gradually be restored to historic levels (450) over a 25-year period. In the no-reductions treatment, deer were not reduced. In the elk reduction experiments, deer were reduced or hunted to 400-600. The three elk reduction treatments were repeated with and without fencing of all willow and aspen on the park elk herd winter range. Deer and elk were excluded from all willow and aspen grid-cells in the park for a 25-year period. Beavers were not excluded. All willow cells in the park, but not all aspen cells, were suitable beaver habitat.

Precipitation and snow water for the simulations are shown in Figure 96. The range of variability was consistent with what was observed in 1949-1998 (Figure 26). There were no serious droughts, but there were occasional drier than normal years. There was one very wet year. Snowpack varied markedly, as it did in 1949-1998. There were years with 100-125 mm snow water equivalent, and there were years with 200-350 mm snow water equivalent.

With no reductions of the park or town herds, the park elk population fluctuated between 800-1,100 animals, consistent with the range previously estimated to be the food-limited carrying capacity (Figure 97a). The town population increased at first to 2,400, then varied between 1,400-2,000. The initial increase was consistent with that of a classic ungulate irruption following introduction to a new habitat (Caughley 1970, 1976). The population initially increased to a high level as it exploited new food sources. Then, as the forage production declined due to grazing, a lower dynamic equilibrium was reached between forage production and ungulate population growth rate. The deer population was suppressed to 200-600 throughout most of the simulation due to competition from elk. There was never any deer offtake.

Fencing all of the willow and aspen reduced the food-limited carrying capacity of the park population by approximately 30-40% (Figure 97b). At the end of 2024, the population was 750 without fences and 450 with fences. Since fences were not simulated in the town elk winter range, the town herd was not affected by the fencing.

Reducing the park elk herd to 600-800 or 200-400 resulted in the population dynamics shown

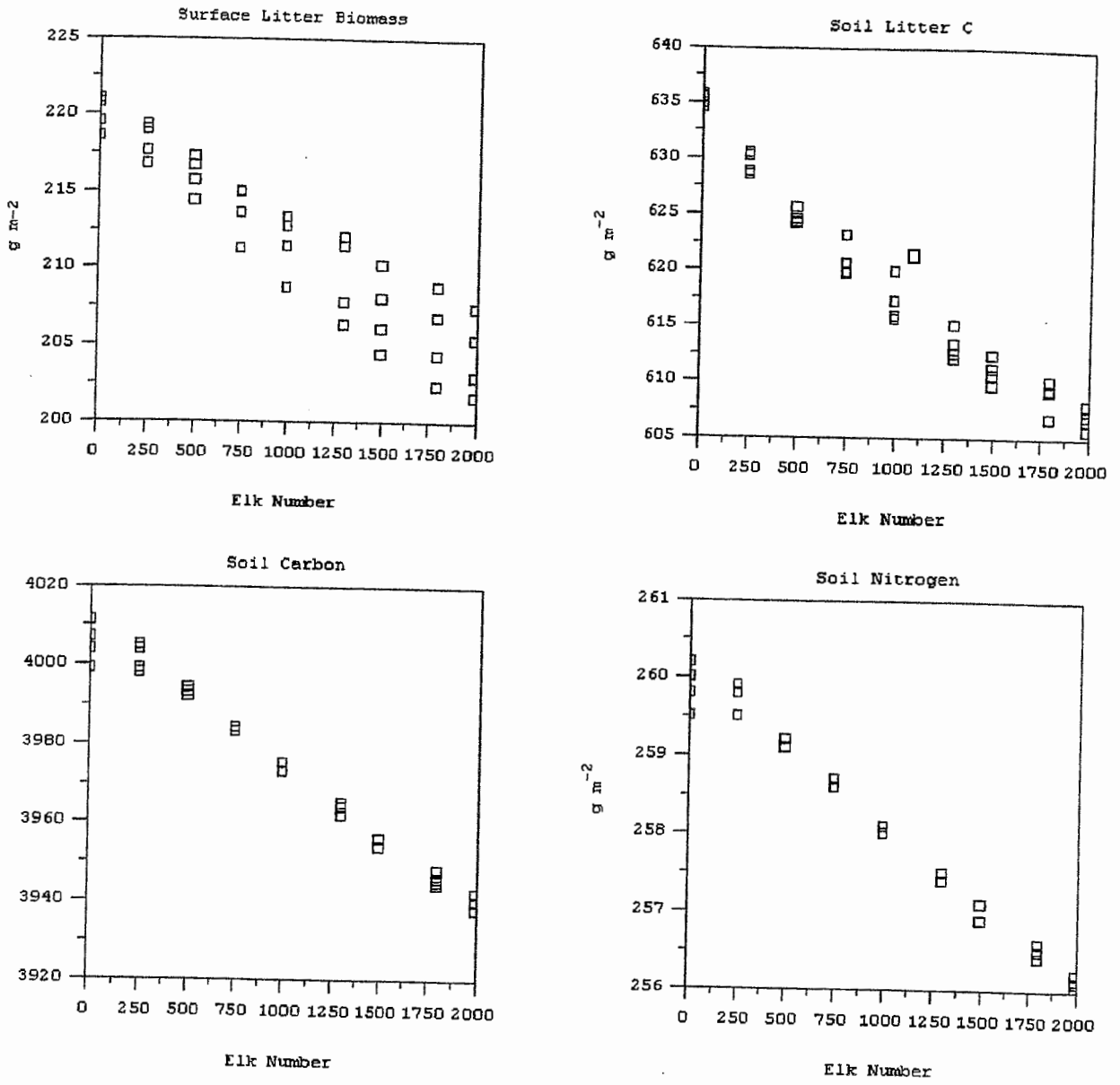
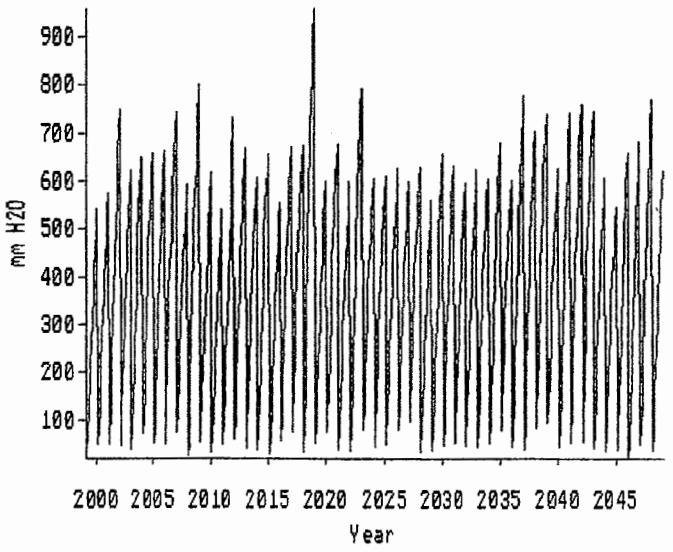


Figure 95. Responses of litter, soil carbon, and soil organic nitrogen to elk number after constant stocking for 50 years. Multiple points at each elk density represent runs with different beaver densities in the factorial experiment. Note scaling of y axes.

Table 24. Conditions for future management scenario model experiments. Run refers to panel letters in Figures 97-109. Vegetation and water table conditions are as current conditions in all runs.

Run	Elk Herds	Elk Removals	Deer Presence	Deer Removals	Beaver Numbers	Wolf Presence	Fencing of Willow and Aspen
A	2	No	Yes	Yes	Prescribed	Yes	No
B	2	No	Yes	Yes	Prescribed	Yes	Yes
C	2	to 600-800	Yes	Yes	Prescribed	Yes	No
D	2	to 600-800	Yes	Yes	Prescribed	Yes	Yes
E	2	to 200-400	Yes	Yes	Prescribed	Yes	No
F	2	to 200-400	Yes	Yes	Prescribed	Yes	Yes

A)



B)

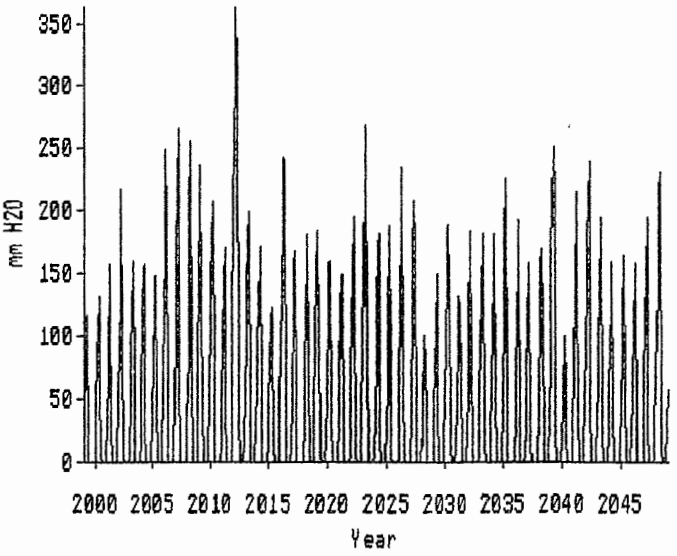
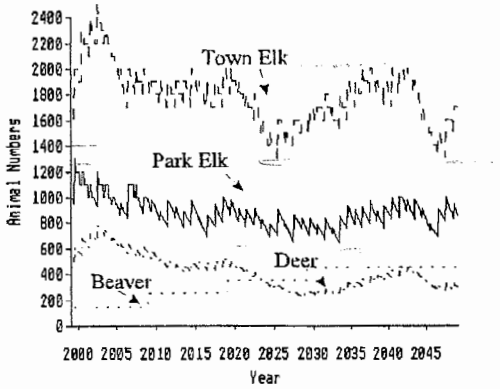
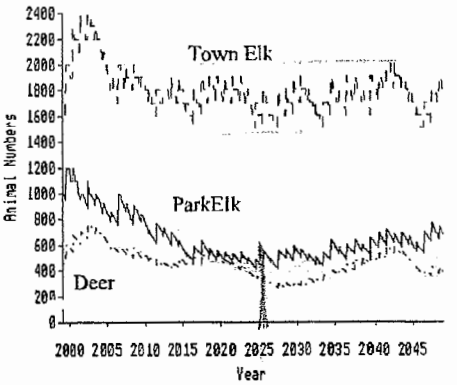


Figure 96. A) Annual precipitation in the future management scenarios. B) Snow water equivilent in the future management scenarios. Weather drawn at random from data for 1949-1998.

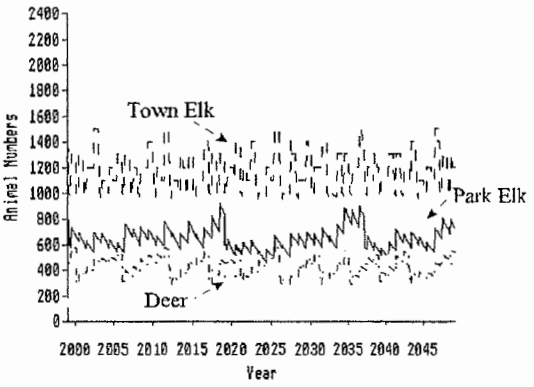
A) no action



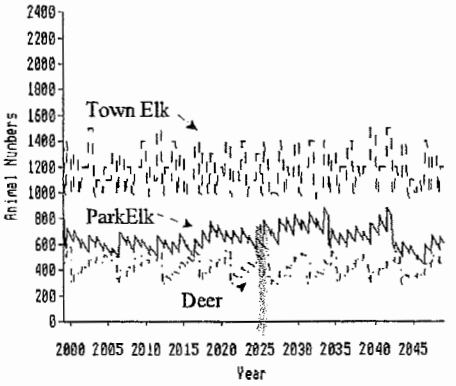
B) fence all willow/aspen for 25 years



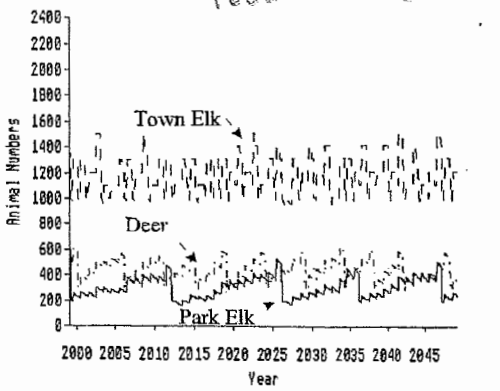
C) cull to 600-800 1000-1300 (town)



D) Cull to 600-800 and fence all 1000-1300 (town)



E) Cull to 200-400 1000-1300 (town)



F) Cull to 200-400 and fence all 1000-1300 (town)

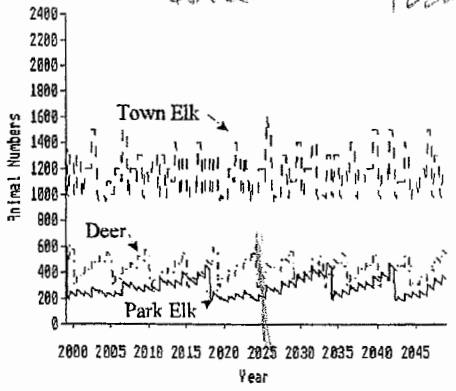


Figure 97. Elk, deer, and beaver population dynamics under different management scenarios. Beaver population dynamics are prescribed, and the same in all runs. A) No elk removals. B) No elk removals, but fence all willow and aspen for first 25 years. C) Cull elk to 600-800. D) Cull elk to 600-800, and fence all willow and aspen for first 25 years. E) Cull elk to 200-400. F) Cull elk to 200-400 and fence willow and aspen for first 25 years. Town elk were culled to 1000-1300 in runs C,D,E,F.

in Figures 97c-f. Note that the town population was kept to 1000-1300 in these runs (C-F) for intercomparability. Fencing had a small effect on elk population dynamics when elk were reduced. With no fencing, the park elk herd grew to the 800 maximum by 2013, while with the fence, the population did not reach the 800 maximum until after the fences were removed, in 2034. When reduced to 200-400, the fencing reduced the rate of elk population growth slightly. The first reduction was required in 2013 without fencing, and in 2018 with fencing.

Elk body condition in the winter was low when elk were not reduced (Figure 98a). Reducing elk to 600-800 raised winter body conditions moderately, while reductions to 200-400 raised body conditions markedly (Figures 98c,e). Fencing caused slight decreases in body condition (Figures 98b,d,e). With no reductions, the end of winter minima (at March 30) were on average 0.25 and 0.21 without and with fencing, respectively. Comparable values with reductions to 600-800 were 0.31 and 0.29. With reductions to 200-400, the unfenced and fenced values were 0.42 and 0.36. In harsh winters, the effect of fencing was more pronounced in the 200-400 elk reduction scenario. The minimum ends of winter condition indices were 0.15 and 0.16 without elk reductions, 0.17 and 0.16 when elk were reduced to 600-800, and 0.17 and 0.21 when elk were reduced to 200-400.

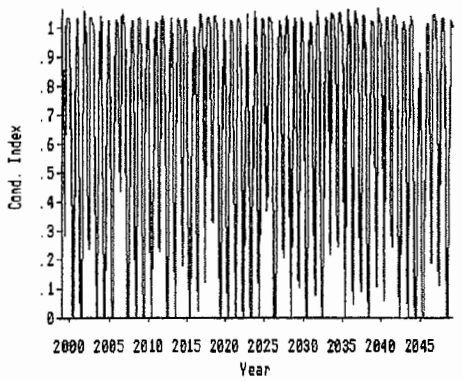
Dryland herbaceous biomass remained essentially constant when elk were not reduced (Figure 99a). However, when elk were reduced to 600-800, biomass increased slowly, over the entire period (Figure 99c). Reducing elk to 200-400 caused a faster rate of biomass increase, and biomass was still increasing after 50 years. Fencing had no discernable effects on dryland herbaceous biomass (Figures 99b,d,f).

With no fencing, and no elk reductions, mesic grasses and forbs remained constant (Figure 100a). Reducing elk to 600-800 had little effect on mesic herbs (Figure 100c). Reducing elk to 200-400 led to a decrease in mesic grass (Figure 100d), as a result of an increase in willow cover, while forbs increased. Fencing led to reduced amounts of mesic grass biomass, due to increases in willow during the fencing period (Figures 100 b,d,f). Fencing had little effect on mesic forb biomass per area of grid-cell. However, since willow cover increased, forb biomass density on non-willow covered areas increased markedly under fencing.

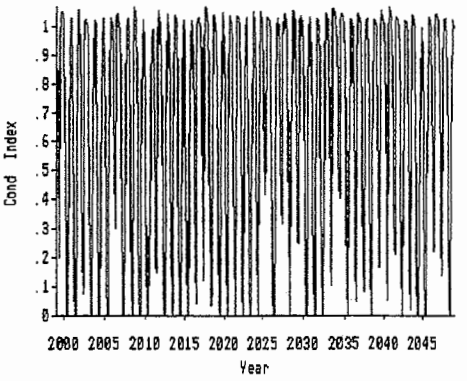
Aspen cover increased at first in all simulations (Figure 101), probably reflecting growth of established trees. After several years, however, aspen cover declined to similar levels irrespective of reductions. Only fencing halted the aspen decline. During the years when aspen were protected by fencing, cover increased markedly. However, when the fence was removed, aspen began to decline once again, in all elk reduction treatments.

Willow cover continued to decline when elk were not reduced (Figure 101a). Willow increased slightly when elk were reduced to 600, and markedly increased when elk were reduced to 200-400 (Figures 101c,e). Fencing resulted in a large increase in willow cover irrespective of reductions (Figures 101b,d,f). After the fence was removed, willow began to decline when elk were not reduced and when reduced to 600-800. In contrast, when elk were reduced to 200-400 willow cover remained at a high level after the fence was removed.

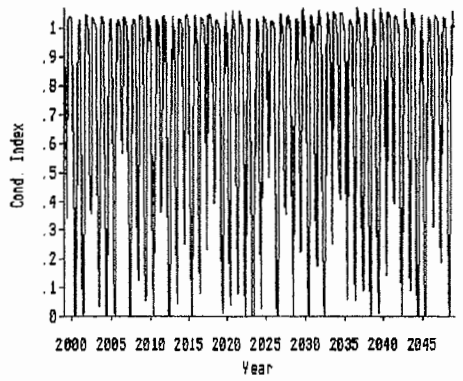
A)



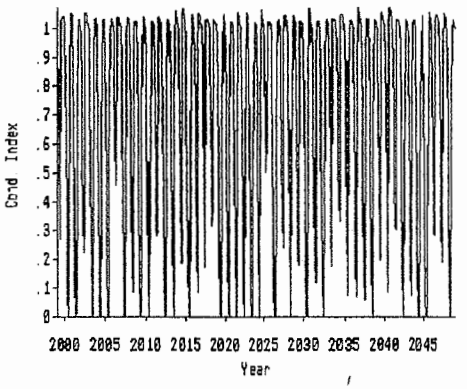
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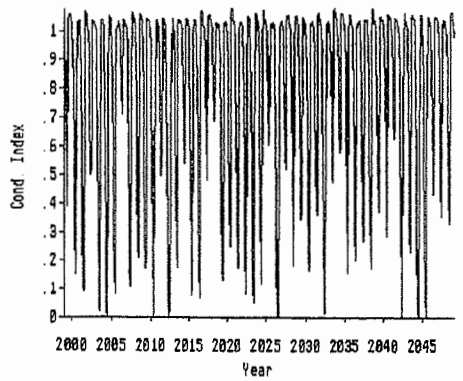
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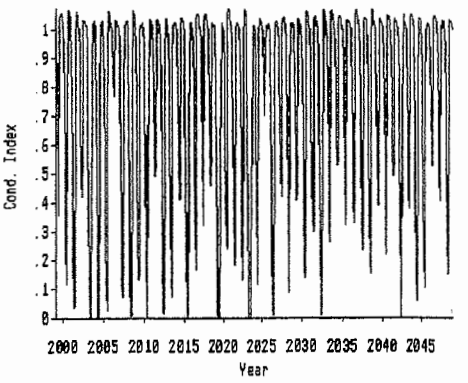


Figure 98. Responses of the body condition of the park elk herd to alternative management scenarios. A) No elk removals. B) No elk removals, but fence all willow and aspen for first 25 years. C) Reduce elk to 600-800. D) Reduce elk to 600-800, and fence all willow and aspen for first 25 years. E) Reduce elk to 200-400. F) Reduce elk to 200-400 and fence willow and aspen for first 25 years.

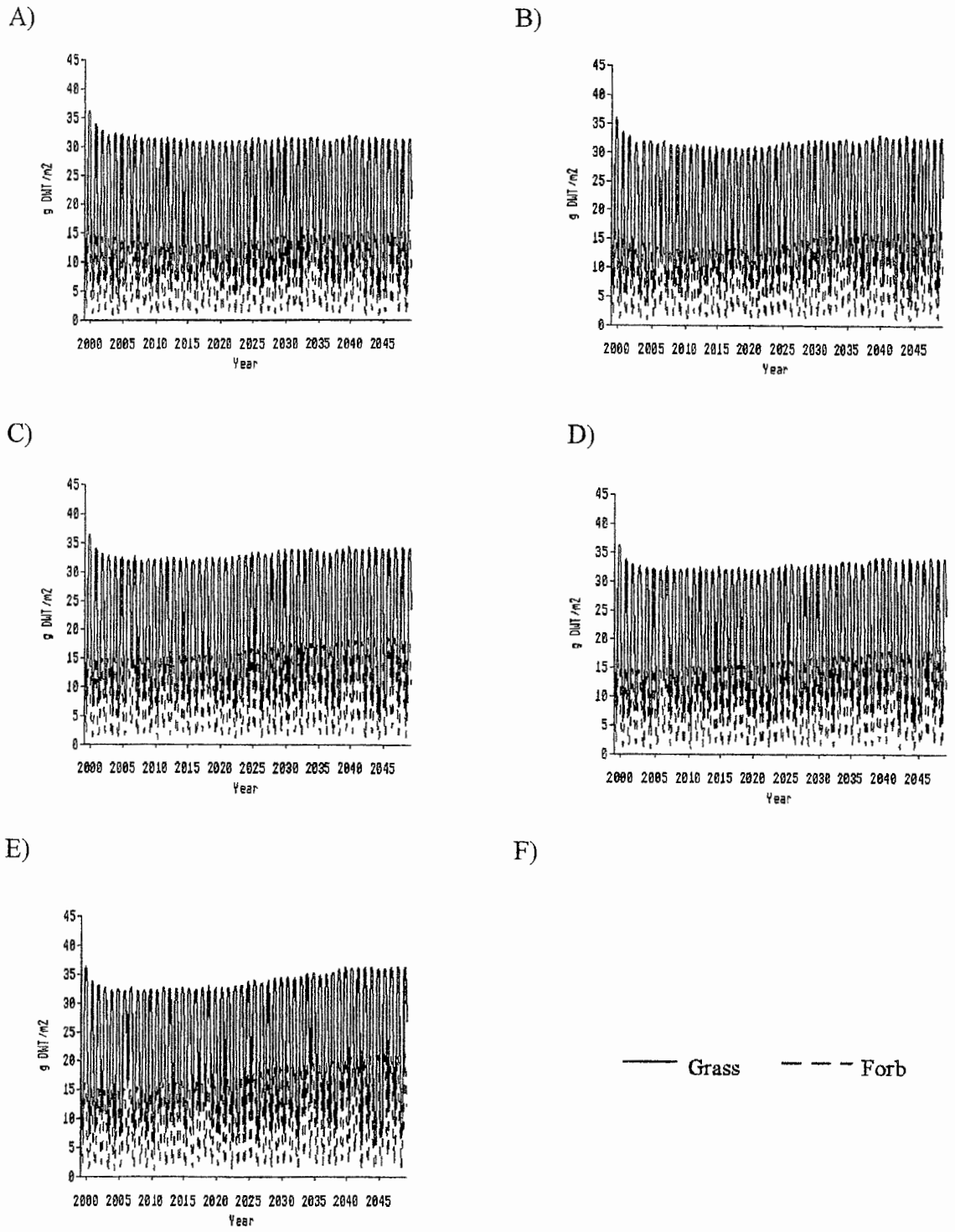


Figure 99. Responses of dryland herbaceous aboveground biomass (grasses and forbs) to alternative management scenarios, using randomly selected weather from 1949-1998, for 50 years. A) No elk removals. B) No elk removals, but fence all willow and aspen for first 25 years. C) Reduce elk to 600-800. D) Reduce elk to 600-800, and fence all willow and aspen for first 25 years. E) Reduce elk to 200-400. F) Reduce elk to 200-400 and fence willow and aspen.

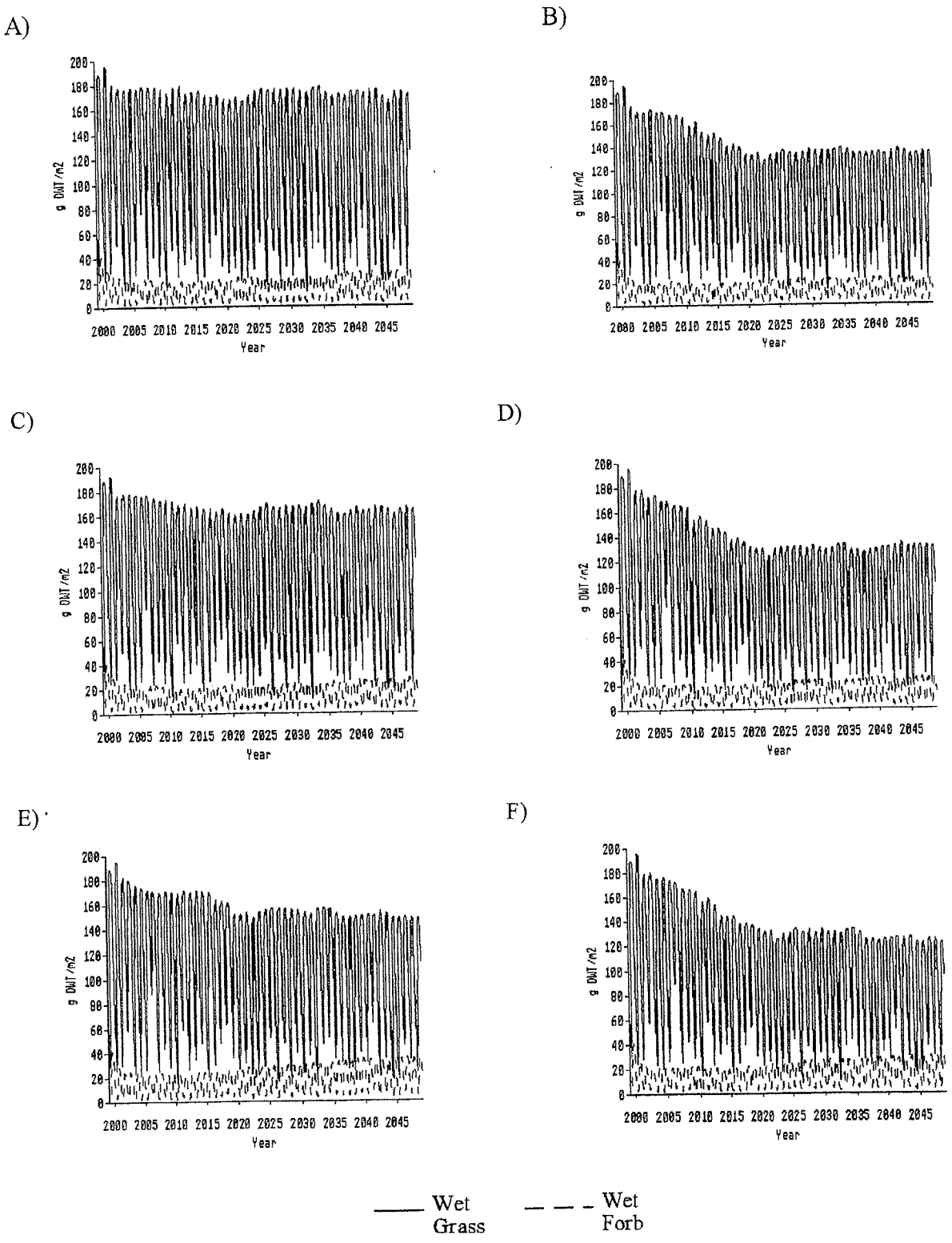


Figure 100. Responses of mesic herbaceous aboveground biomass (grasses and forbs) to alternative management scenarios. A) No elk removals. B) No elk removals, but fence all willow and aspen for first 25 years. C) Reduce elk to 600-800. D) Reduce elk to 600-800, and fence all willow and aspen. E) Reduce elk to 200-400. F) Reduce elk to 200-400 and fence willow and aspen for first 25 years.

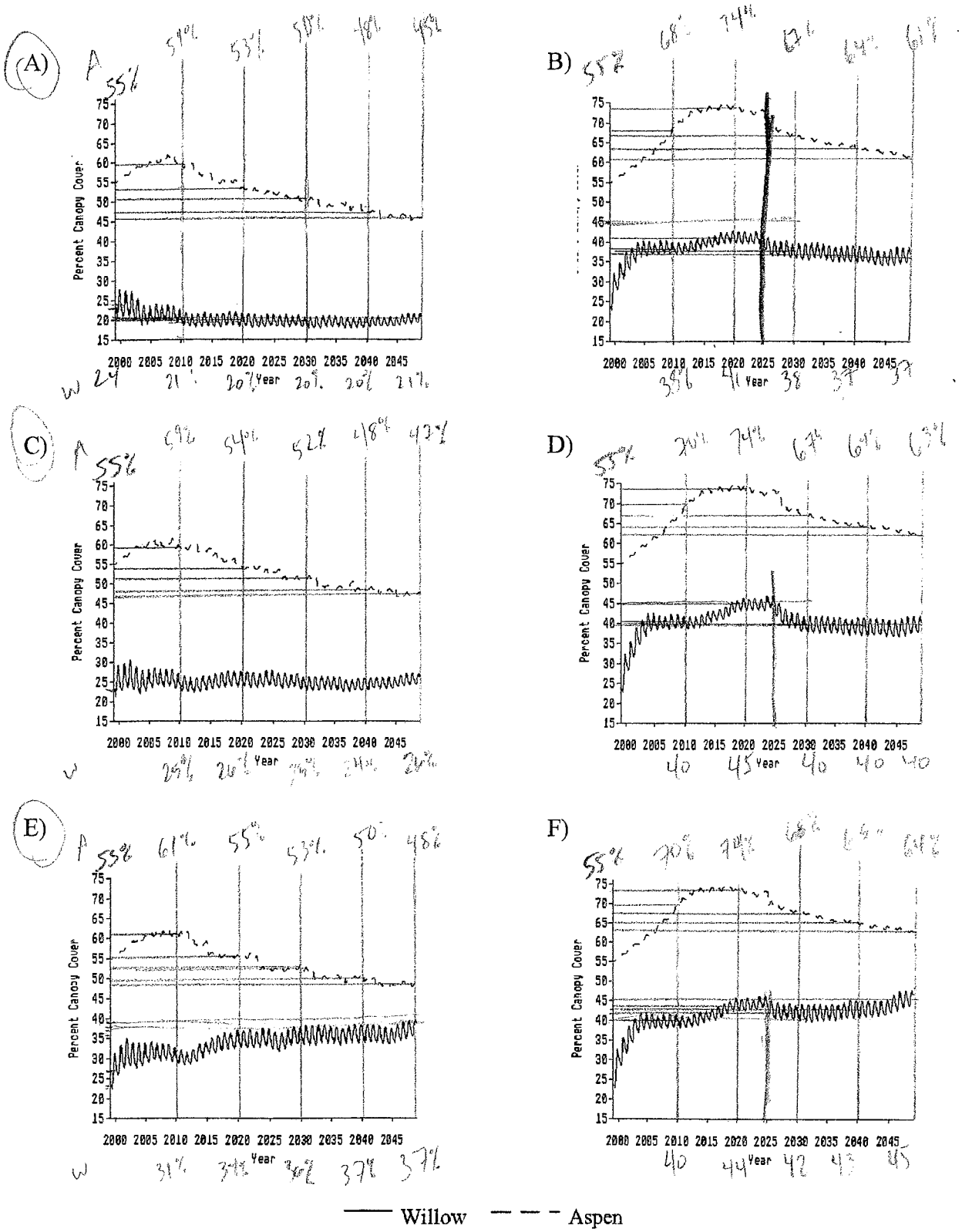


Figure 101. Responses of willow and aspen to management scenarios, using randomly selected weather from 1949-1998, for 50 years as mean canopy cover within grid-cells of that vegetation type. A) No elk removals. B) No elk removals, but fence all willow and aspen for first 25 years. C) Reduce elk to 600-800. D) Reduce elk to 600-800, and fence all willow and aspen for first 25 years. E) Reduce elk to 200-400. F) Reduce elk to 200-400 and fence willow and aspen.

Increasing water table heights had little positive benefit when elk were not reduced and willow were unprotected by fencing (Figure 102a). With fencing, the added water supported higher willow cover during the fenced period, which was sustained after the fences were removed, even with no elk reductions (Figure 102b). With no fencing, higher water tables led to small increases in willow cover when elk were reduced to 600-800, and larger increases in willow cover when elk were reduced to 200-400 (Figures 102c,e). With fencing, high water tables led to further increases in willow cover when fences were removed, and elk were reduced (Figures 102d,f).

Without elk reductions, willow in all but two grid-cells declined (Figure 103). Reducing elk to 600-800 resulted in continued suppression at most locations, but willow escaped suppression at three locations. Reducing elk to 200-400 released willow at four locations. Fencing released willow at eight locations, irrespective of elk reductions. Cover continued to decline at two locations, even with fencing. When fences were taken down, willow held constant at some locations, but at others, a decline occurred, particularly when elk were not reduced, or when they were reduced to 600-800. When elk were reduced to 200-400, cover continued to increase at all but three locations after the fences were removed. Elevating the water tables did not prevent willow declines when elk were not reduced (Figure 104a). With elevated water tables, willow at certain locations continued to be suppressed, even when elk were reduced to 200-400 (Figure 104e). Under fenced conditions, the elevation of water tables led to markedly increased in cover at some locations, which were likely locations where the water tables were otherwise lowest (Figures 104b,d,f). Interestingly, willow in the cell beginning with least cover responded to different elk densities even when protected from elk by fencing (Figures 103b,d,f, 104b,d,f). This is a stand consisting of young willow, and the effect was due to beaver (which were not excluded by the fence), and the effects of elk competing with beaver for forage outside the fences. As elk density increased, beavers foraged more heavily on the young willow inside the fences.

The effects of beaver can be ascertained by contrasting a simulation of reducing elk to 200-400, elevating water tables, and fencing (as in Figure 104f), with a similar run lacking beaver (Figure 105). Cover continued to climb throughout the simulation at all locations, even after fences were removed. Excluding beaver and elk, and raising water tables is the only set of conditions under which willow cover increased to maximal levels at all locations.

The spatial distribution of herbivory was heterogeneous. With no elk reductions, 3-15% of the upland herbaceous landscape was grazed at 50-80% (Figure 106a). In some years, 2-3% was grazed at >80%. Reducing elk to 600-800 reduced the percentage grazed >50% (Figure 106c), and reducing elk to 200-400 reduced the percentage of upland herbaceous grazed 50-80% to 1-4% (Figure 104e). With no reductions, fencing initially increased the fraction of the upland landscape grazed at 50-80%, but after 10 years grazing pressure was less in the fenced treatment (Figure 106b vs. 106a). The reason for this is that there were 30-40% fewer elk in the fenced simulation, as a result of the fencing off of a significant forage source (Figures 97a,b). When elk were reduced to 600-800, fencing increased the fraction of the upland landscape grazed to 50-80% as compared to no fencing (Figure 106d vs. c). Fencing clearly increased pressure on uplands while the willow communities were unavailable. After the fence was removed, the grazing pressure was similar in fenced and unfenced

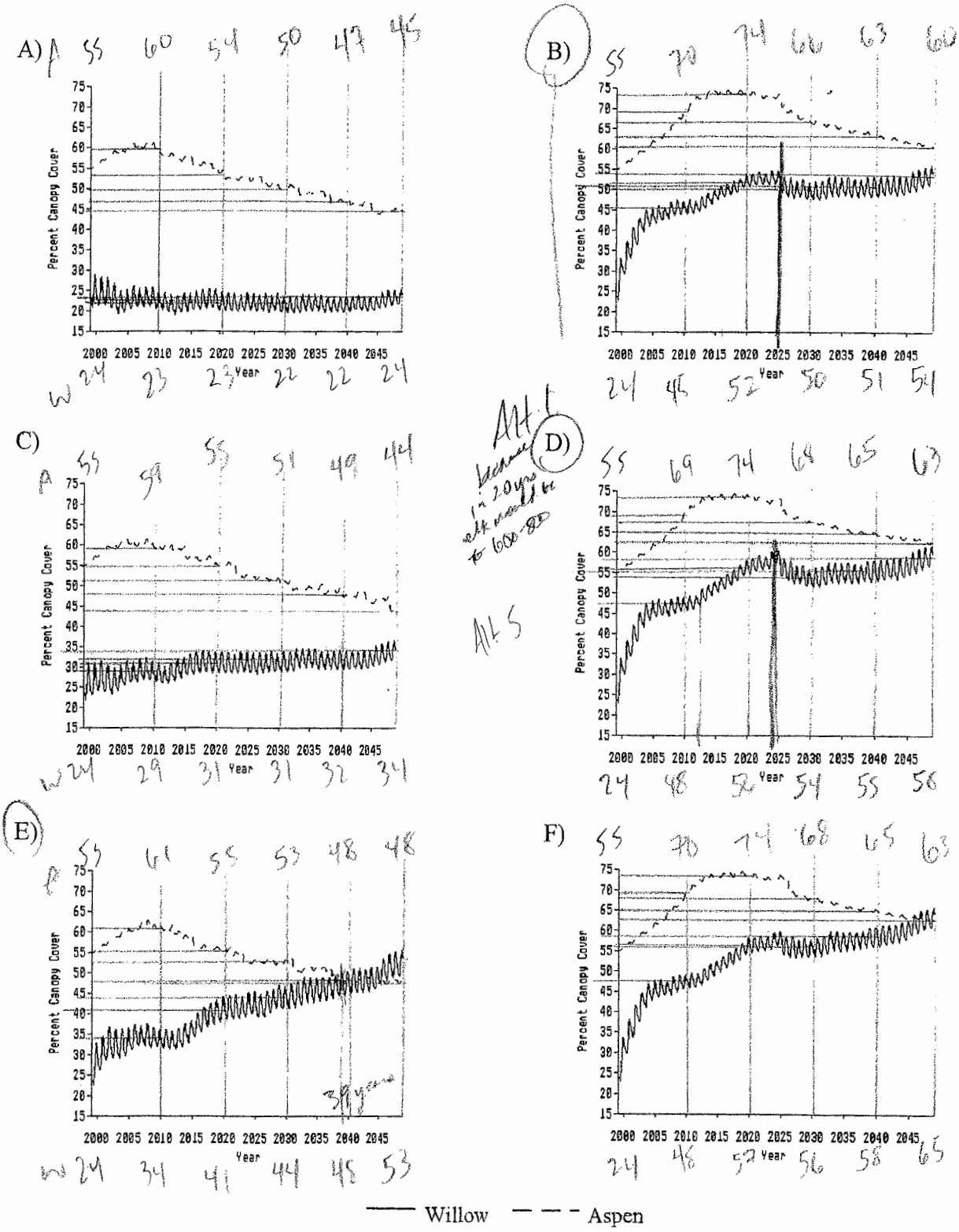
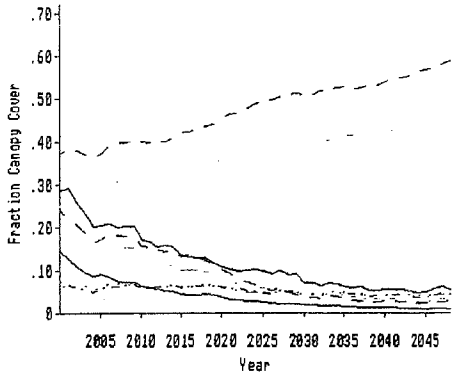
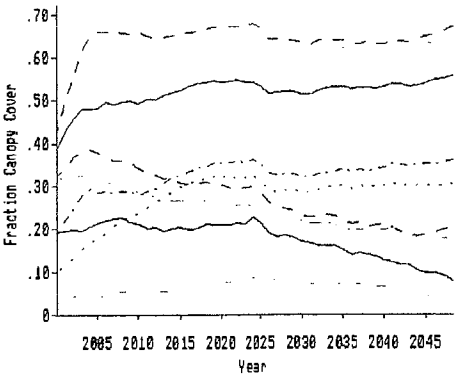


Figure 102. Responses of willow and aspen to alternative management scenarios, with higher water tables reported as mean canopy cover within the grid-cells having that vegetation type. A) No elk removals. B) No elk removals, but fence all willow and aspen for first 25 years. C) Reduce elk to 600-800. D) Reduce elk to 600-800, and fence all willow and aspen for first 25 years. E) Reduce elk to 200-400. F) Reduce elk to 200-400 and fence willow and aspen.

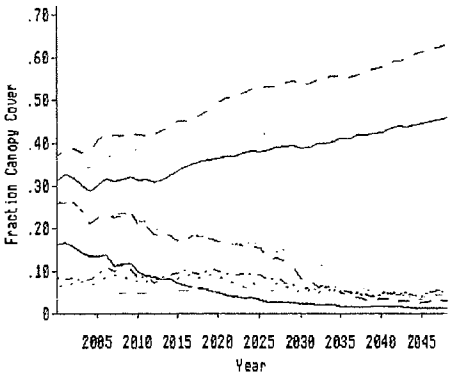
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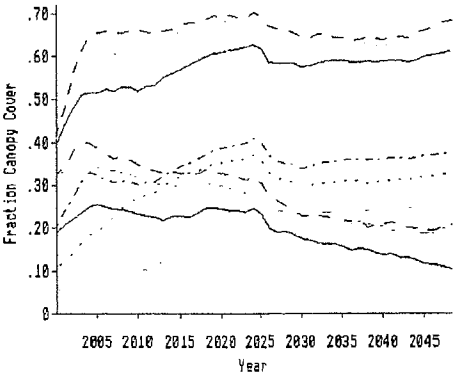
B)



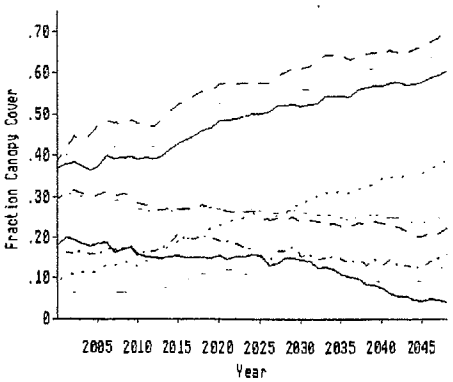
C)



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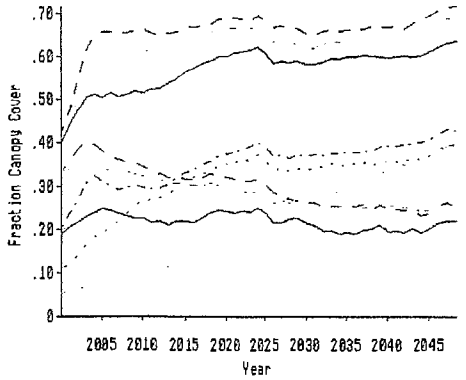
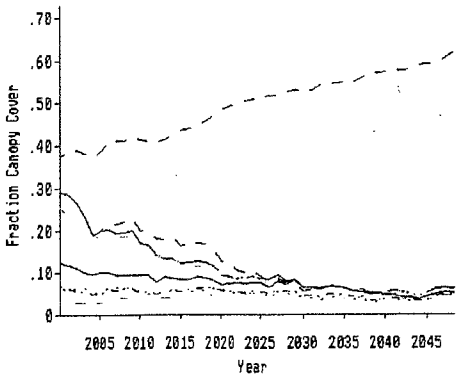


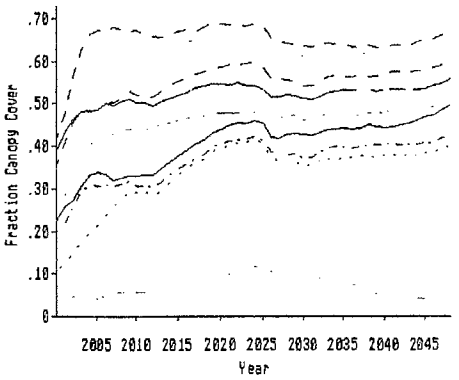
Figure 103. Responses of willow cover in individual grid-cells to alternative management scenarios, using randomly selected weather from 1949-1998, for 50 years. A) No elk removals. B) No elk removals, but fence all willow and aspen for first 25 years. C) Reduce elk to 600-800. D) Reduce elk to 600-800, and fence all willow and aspen for first 25 years. E) Reduce elk to 200-400. F) Reduce elk to 200-400 and fence willow and aspen.

existing water tables

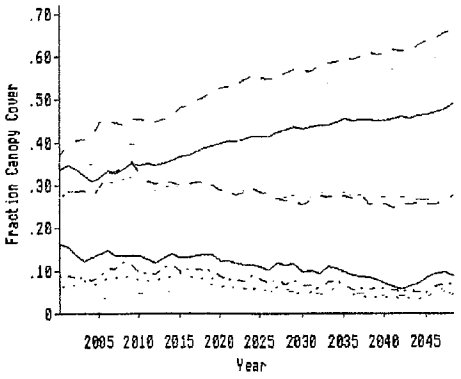
A)



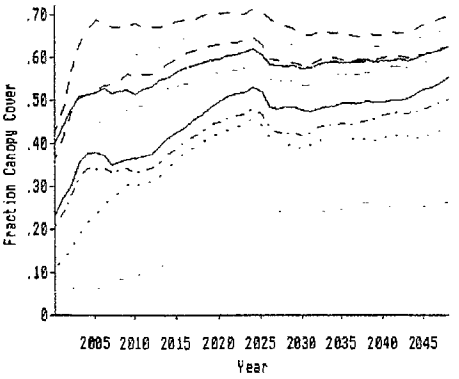
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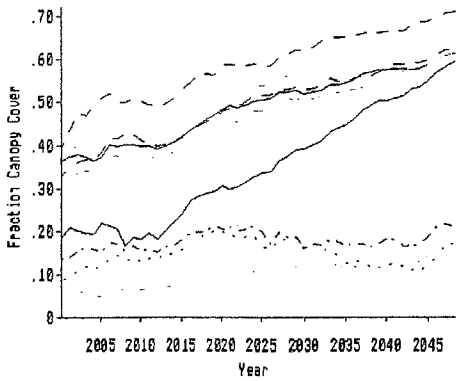
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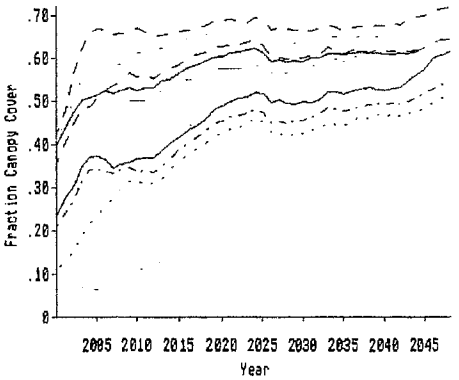
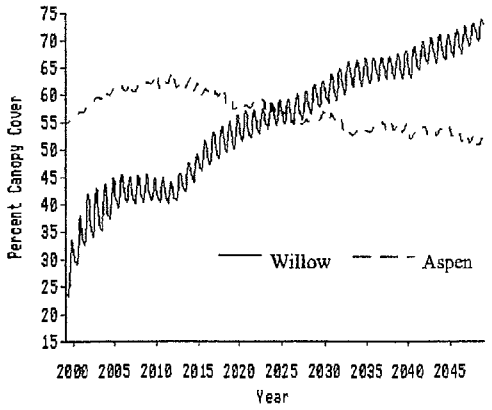


Figure 104. Responses of willow cover in individual grid-cells to alternative management scenarios, with elevated water tables. A) No elk removals. B) No elk removals, but fence all willow and aspen for first 25 years. C) Reduce elk to 600-800. D) Reduce elk to 600-800, and fence all willow and aspen for first 25 years. E) Reduce elk to 200-400. F) Reduce elk to 200-400 and fence willow and aspen.

A)



B)

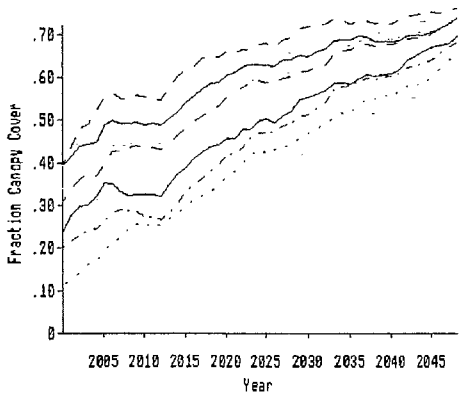
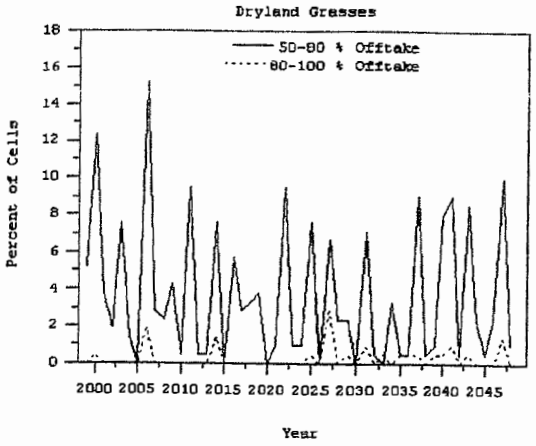
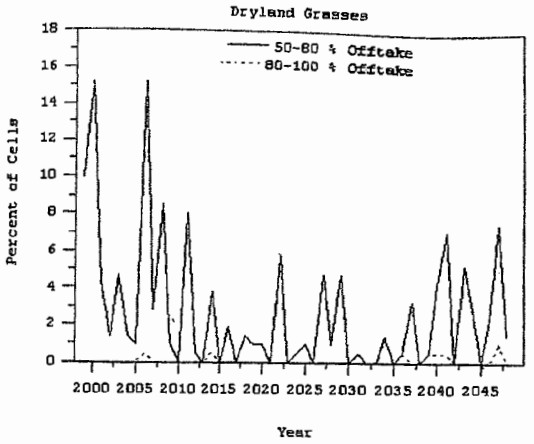


Figure 105. A) Willow and aspen cover and B) willow cover in individual grid-cells, with removals of elk to 200, ~~400~~ fencing willow and aspen for the first 25 years, elevated water tables, and no beaver. (Compare to Fig. 104f, 105f).

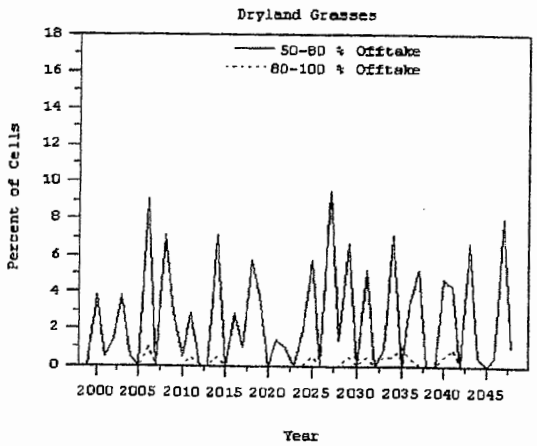
A)



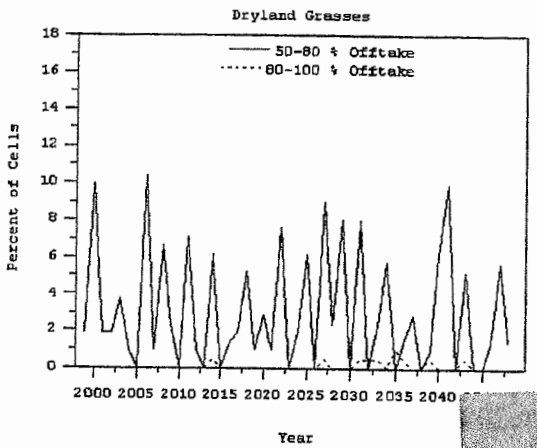
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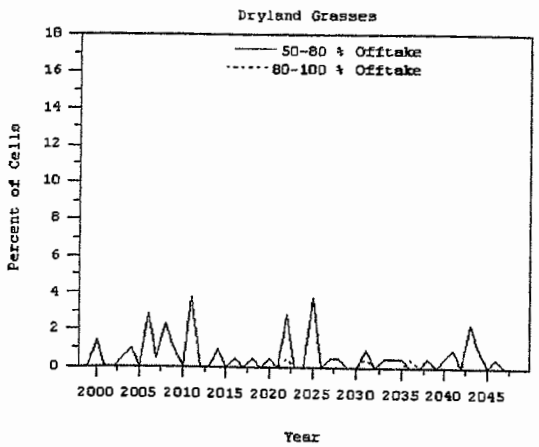
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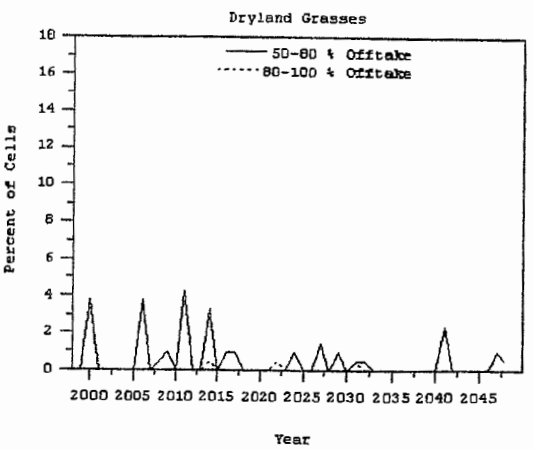


Figure 106. Percentages of grid-cells on the winter range with upland grass offtake >50% in A) no cull, B) no-cull, fence willow and aspen in yrs 1-25, C) cull to 600-800, D) cull to 600-800 and fence years 1-25. E) Cull to 200-400. F) Cull to 200-400 and fence years 1-25.

Off take - upland grass

treatments. Fencing had little effect on the upland grazing pressure when elk were reduced to 200-400 (Figure 106f vs. e).

With no elk reductions 25-55% of the willow was browsed at 50-80% and 5-20% were browsed at >80% (107a). When elk were reduced to 600-800, browsing pressure on willow was decreased in the first 25 years, but was comparable to browsing under no elk reductions in the second 25 years (Figure 107c). The fraction browsed >80% was reduced however. When elk were reduced to 200-400, only 10-15% of the willow was browsed to 50-80% in the first 25 years, but the fraction increased to 15-25% in the second 25 years (Figure 107e). The fraction browsed >80% was negligible in years 1-25, but increased to 5-10% in years 26-50. Fencing willow, of course, reduced browsing pressure in all cases. The browsing was due to beaver. When the fence was removed, there was slightly less browsing intensity in the no-reduction and 600-800 reduction treatments, due to fewer elk and more willow due to fencing. There was markedly less browsing pressure after the fence was removed in the 200-400 reduction treatment as compared to the no fence treatment (Figure 107f vs. e).

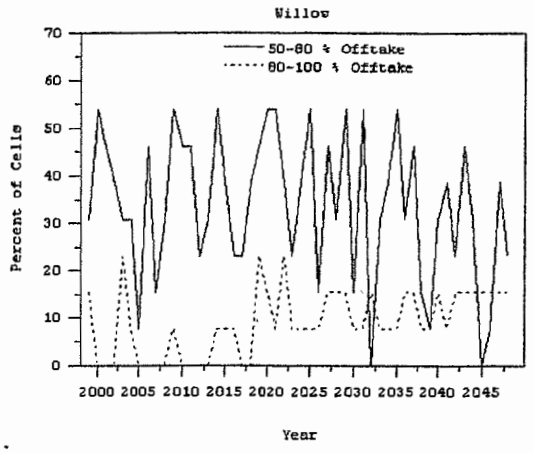
A hypothetical wolf reintroduction markedly reduced the fraction of upland herbaceous vegetation that was grazed 50-80% (Figure 108a), reducing it to essentially zero. Willow were also more lightly browsed than under no-reductions or reductions to 600-800 elk (Figure 108b). In the hypothetical undisturbed run, the fraction of upland grazed at 50-80% was held to 1-4% throughout (Figure 108c) and a very small fraction of willow were browsed in excess of 50% (Figure 108d).

The ranges of variation in upland herbaceous root biomass over the landscape are shown in Figure 109. Average root biomass was held constant with no reductions, but the range of variation between minimum and maximum values increased relative to initial conditions (Figure 109a). When elk were reduced to 600-800, root biomass increased at a slow rate (Figure 109c). With reductions to 200-400, root biomass increased at a relatively rapid rate over the whole simulation (Figure 109e). Fencing had very little effect on upland herbaceous root biomass (Figures 109b,d,f).

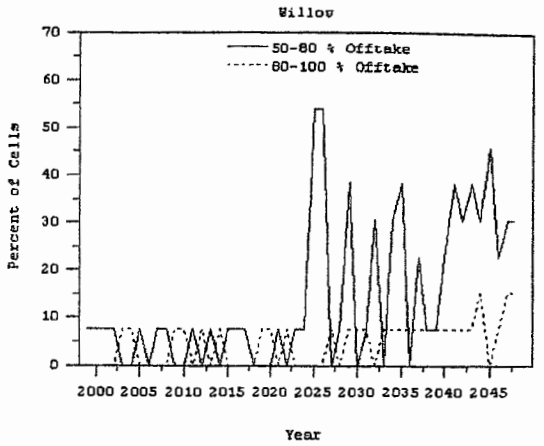
The spatial distribution of herbaceous root responses to elk grazing was as expected. The most heavily grazed areas were on the core winter ranges in Moraine Park and Beaver Meadows, and a small area in Horseshoe Park (Figure 110a). In those areas, root biomass was reduced 20-40% without elk reductions, relative to root biomass when elk were reduced to 200-400. When elk were reduced to 600-800, those same areas had root biomass reductions of 10-25% relative to that under elk reductions to 200-400 (Figure 110b).

The assessment of alternative management scenarios showed that a marked elk reduction to levels which may be lower than those present in pre-settlement times, or fencing, would achieve a recovery of willow, but only in locations where water tables are still elevated. Reintroduction of beaver or other manipulations to raise water tables would be required to achieve complete recovery. Aspen cover could be increased by fencing or severe elk reductions, however, elk numbers would have to be maintained very low, or once fences are taken down, aspen cover on the core winter range would again decline.

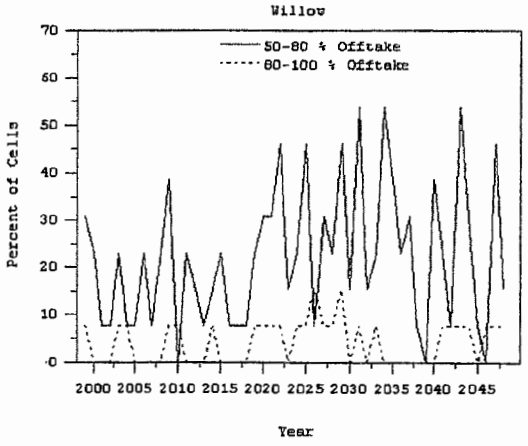
A)



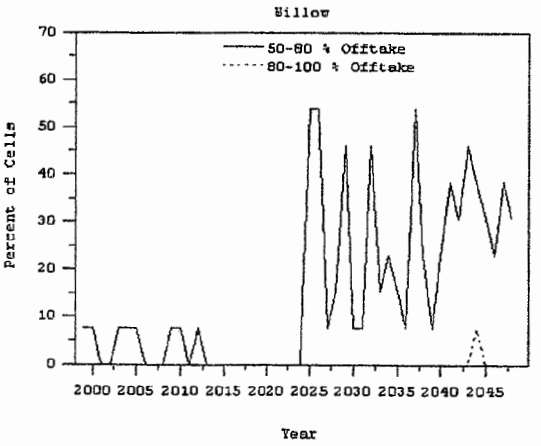
B)



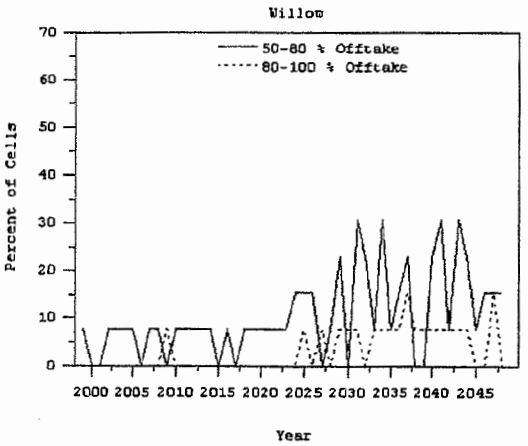
C)



D)



E)



F)

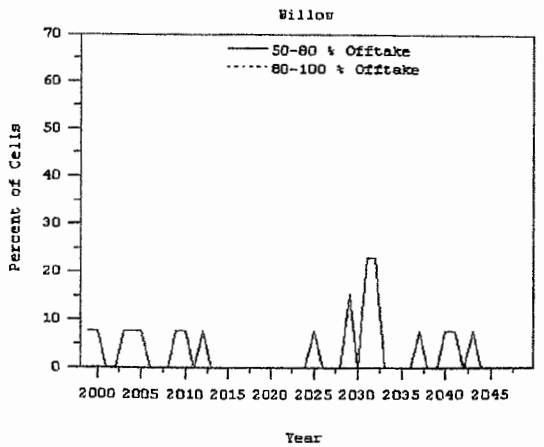
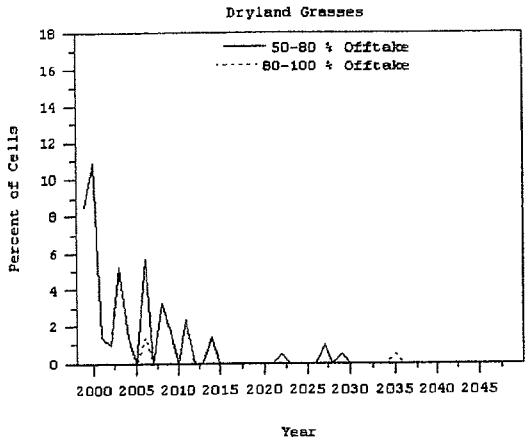


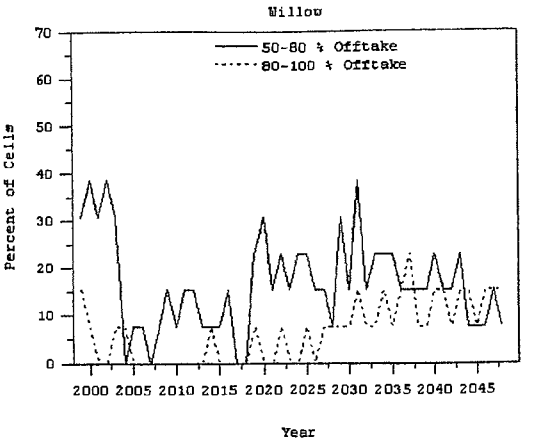
Figure 107. Percentages of grid-cells on the winter range with willow offtake >50% in A) no cull, B) no-cull, fence willow and aspen in yrs 1-25, C) cull to 600-800, D) cull to 600-800 and fence years 1-25. E) Cull to 200-400. F) Cull to 200-400 and fence years 1-25.

Willow Offtake

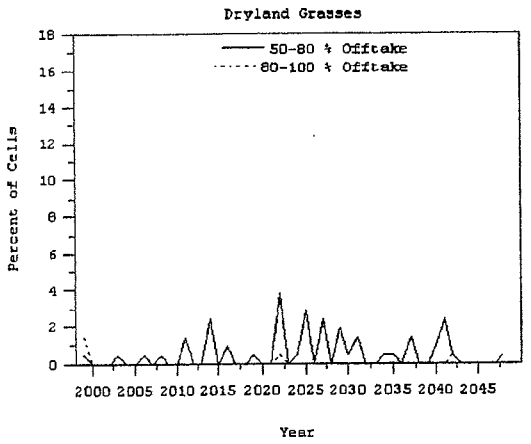
A) Offtake w/ wolves



B) Offtake w/ wolves



C)



D)

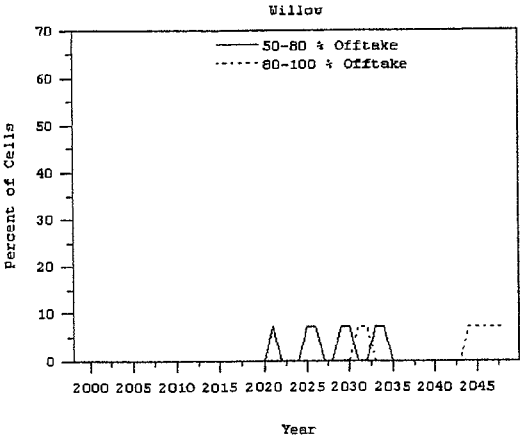
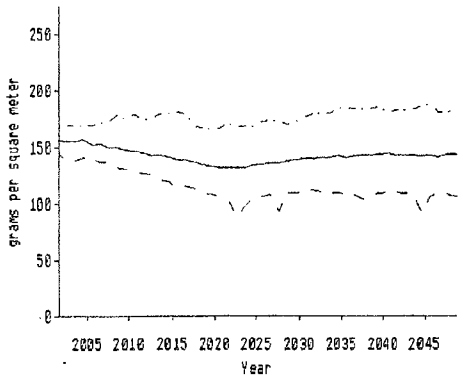
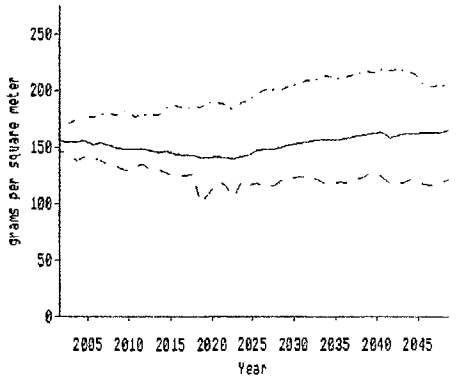


Figure 108. Percentages of grid-cells where dryland grasses and willow offtake is > 50% A) and B) in simulations with current vegetation and ungulates and with a hypothesized wolf reintroduction, and C) and D) in simulations with undisturbed vegetation and initial ungulate numbers as in the undisturbed 1912-1948 run.

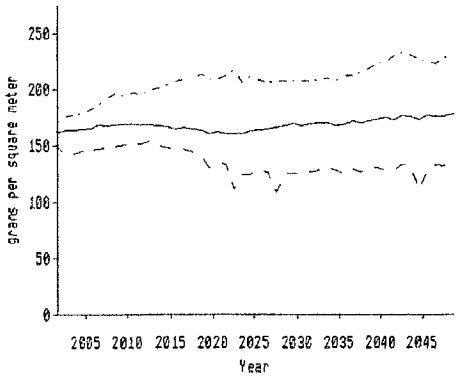
A)



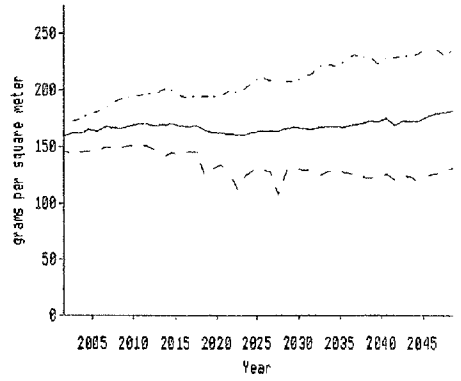
B)



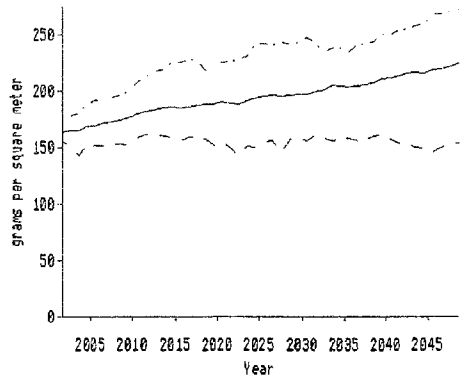
C)



D)



E)



F)

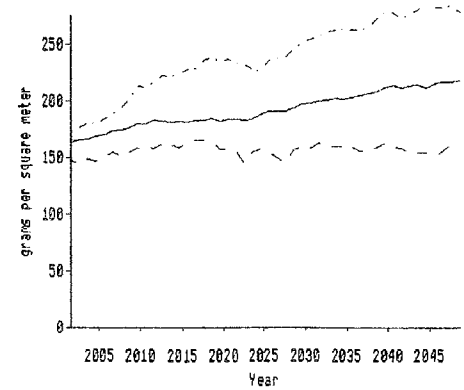
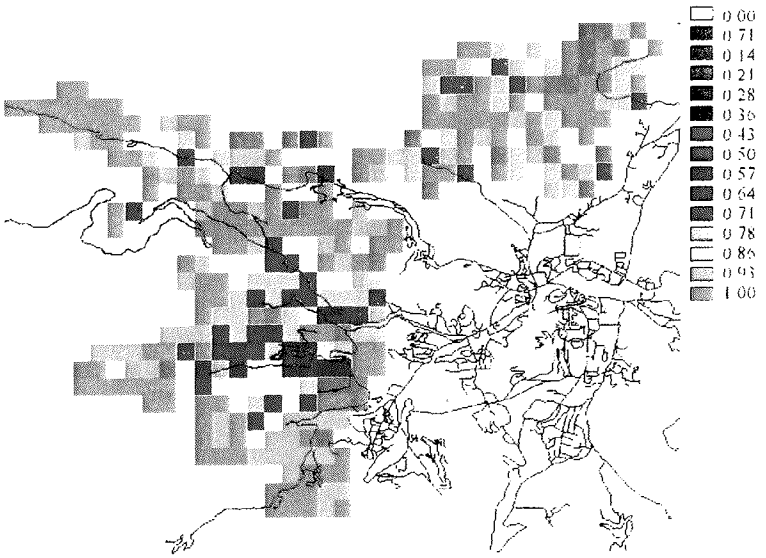


Figure 109. Herbaceous root biomass on grassland vegetation types in the park range in July. A) No elk culling. B) No elk culling, but fence all willow and aspen for first 25 years. C) Cull elk to 600. D) Cull elk to 600, and fence all willow and aspen for first 25 years. E) Cull elk to 300. F) Cull elk to 300 and fence willow and aspen for 25 years.. Minimum, maximum, and average values among grid-cells illustrate the range of spatial variation.

A)



B)

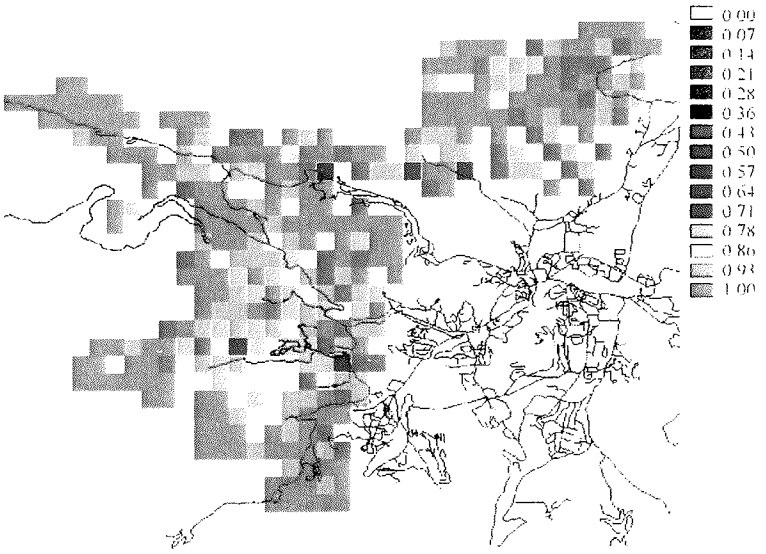


Figure 110. A) Ratio of dryland herbaceous root biomass in the last 10 years of the no-cull simulation 1999-2048 to that with elk culled to 20-4000. B) Ratio of root biomass with elk culled to 400-600 to that with elk culled to 200-400.

Hypothetical Scenarios with Wolves

It would be instructive to know how the system might respond if wolves could be reintroduced, how it would have responded if wolves were present all along but vegetation had been altered by human land use, and how it would have responded if wolves were present all along and vegetation had not been altered. An experiment was conducted with conditions as in Table 25. Wolves were initialized at the level simulated at the end of the run for 1949-1998 under similar conditions. Beginning with current vegetation, water table conditions, and elk numbers, wolves quickly reduced elk numbers in both the town and park subherds (Figure 111a). Wolf numbers then declined as prey abundance declined. After 15 years, the system stabilized at 14 wolves, about 200 elk in the park population, and about 1,000 elk in the town population. Deer were held to 200. A similar final result was obtained when plants, elk and wolf populations were initialized to values modeled at the end of the 1949-1998 undisturbed run (Figures 111c,d), however more animals were supported in both populations in the middle portions of the run. This was likely due to more abundant forage at the beginning of the run. However, there was a gradual downward trend over the course of the simulation. Changing water tables and vegetation to pre-disturbance conditions supported more elk throughout the simulation, which in turn supported slightly more wolves (Figures 111e,f). The park population could support 500-600 animals when wolves were present, and the town population could support 1,000-1,600 elk.

Elk condition was initially low when starting with current elk numbers (Figure 112b), but then increased as elk numbers were reduced. Condition generally remained high when starting with low elk numbers, or with undisturbed vegetation (Figures 112c,d).

Willow cover increased from current levels when wolves were present (Figures 113a,b). Willow cover decreased from the high levels at the end of the undisturbed run for 1949-1998, due to reduced water tables at some at some locations under current water tables and vegetation (Figures 113c,d). With undisturbed water table conditions, willow cover remained high (Figures 113e,f). Aspen cover decreased in all three simulations.

Sensitivity Analysis of Wolf Model Parameters

Given the importance of the simulated ecosystem responses to wolves, a set of simulations was performed to examine sensitivity of the model to the wolf submodel parameters. Nine different parameter permutations were examined (Table 26). All runs were continuations of the 1949-1998 undisturbed run, using the same stochastic weather sequence as that used in the analyses of future management scenarios. The control run, using the wolf model parameter values used in previous runs (Figure 114a), was identical to the run shown in Figure 106c,d. A comparable run without wolves is shown in Figure 114b.

The effect of the wolf density vs. prey density function was examined by running the model with the maximum and minimum density lines shown in Figure 23. Using the minimal wolf density per unit prey density function resulted in 12-14 wolves rather than 14-16 wolves, and higher elk

Table 25. Conditions for future management scenario model experiments with wolves. Run refers panel letters in Figures 111-114. Deer are present in all runs.

Run	Elk Herds	Elk Removals	Deer Removals	Wolves	Beaver	Vegetation and Water Table Conditions	Animal Initial Conditions
A/B	2	No	No	Yes	Prescribed	Current	Current
C/D	2	No	No	Yes	Prescribed	Current	As at end of 1949-1998 run with wolves.
E/F	2	No	No	Yes	Prescribed	Natural	As at end of 1949-1998 run with wolves.

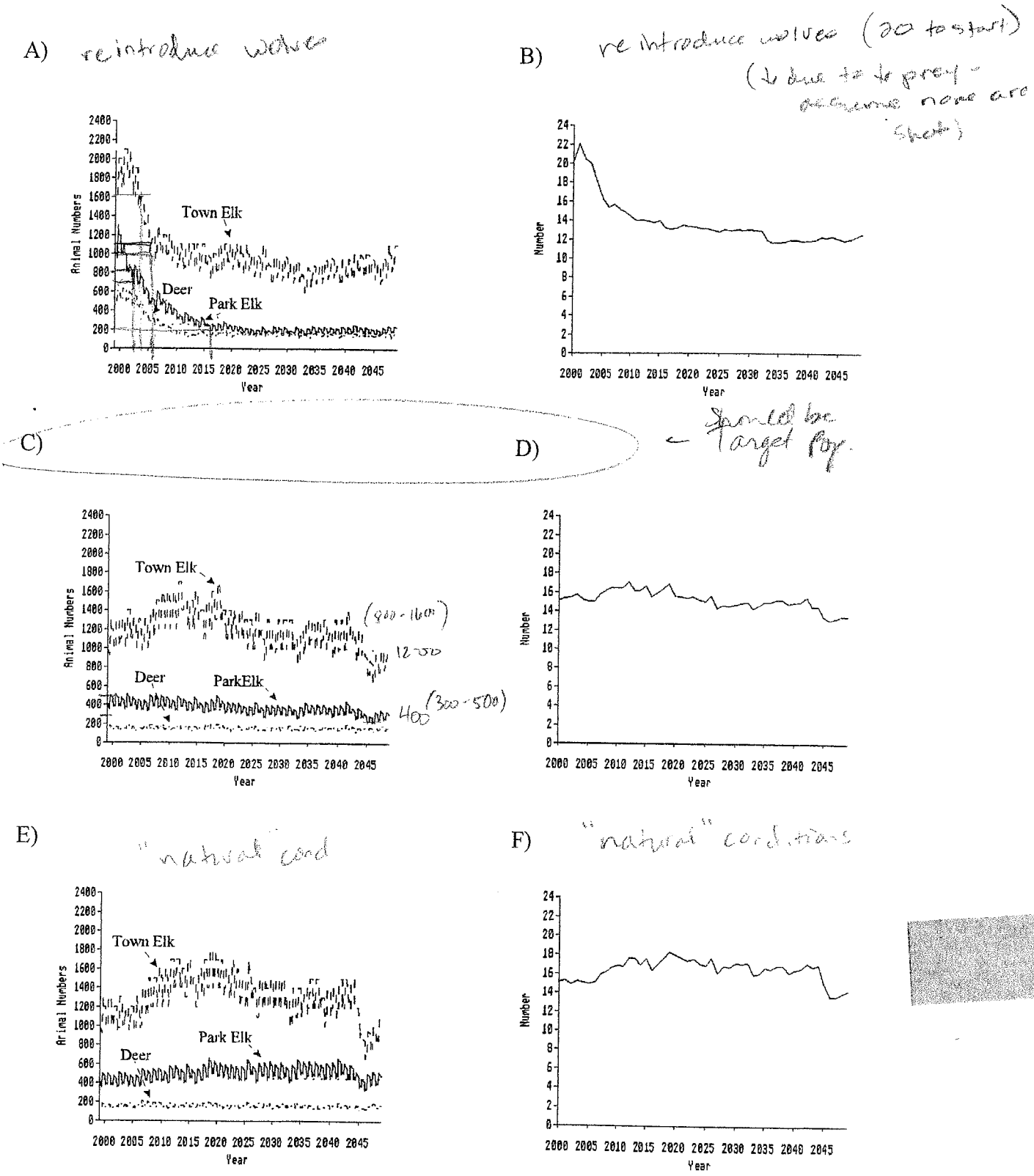
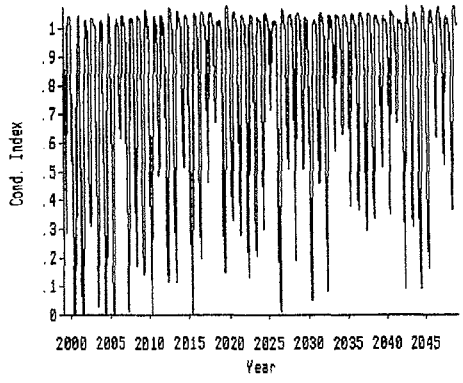
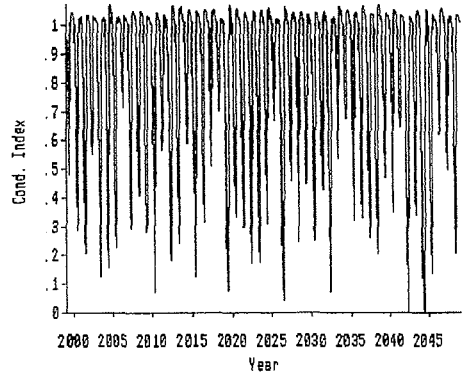


Figure 111. Herbivore and wolf populations in hypothetical scenarios with wolves. A) Herbivores and B) wolves with current vegetation and soil water tables, starting with current plant and animal abundances . C) Herbivores and D) wolves with current vegetation and soil water tables, starting with plants and ungulates at end of the 1949-1998 run with wolves. E) Herbivores and F) wolves with undisturbed vegetation and soil water tables, starting with undisturbed 1949-98 final results.

A)



B)



C)

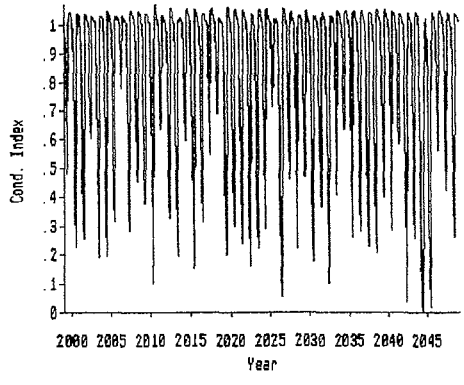


Figure 112. Elk condition in simulations with wolves. A) With current vegetation and soil water tables, starting with current plant and animal conditions. B) With current vegetation and soil water tables, starting with plants and ungulates at end of the 1949-1998 run with wolves. C) With pre-1900 soil water tables, starting with plants and ungulates at end of run 1949-1998 run with wolves.

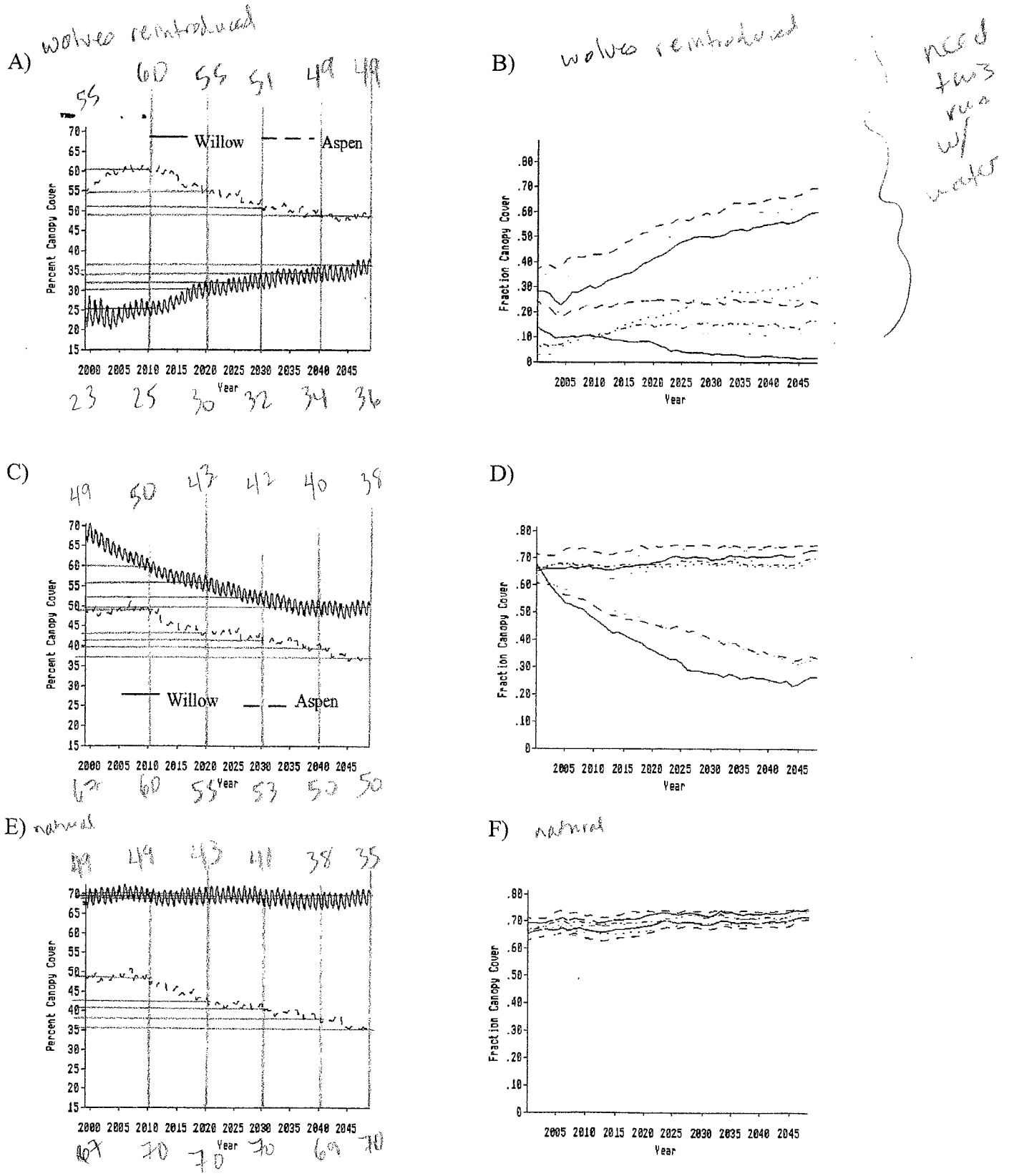
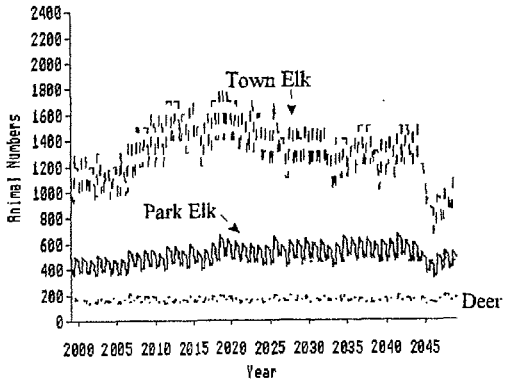


Figure 113. A,C,E) Willow and aspen cover in simulations with wolves. B,D,F) Aspen cover in 10 individual grid-cells. A,B) With current vegetation and soil water tables, starting with current plant and animal conditions. C,D) With current vegetation and soil water tables, starting with plants and ungulates at end of the 1949-1998 run with wolves. E,F) With pre-1900 soil water tables, starting with plants and ungulates at end of run 1949-1998 run with wolves.

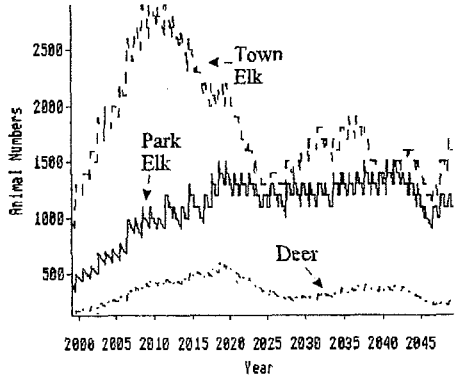
Table 26. Conditions for wolf model sensitivity analysis runs. Run number refers to panels in the indicated figure. In all runs there were 2 elk herds, deer were present, there were no elk or deer removals, vegatation and water table conditions were as at present, and beaver numbers were prescribed as in Figure 97a.

Run-Figure	Wolf Model Parameter
A-114	Standard parameters
B-114	No Wolves
C/D-114	Minimum wolf density on their territory
E/F-114	Maximum wolf density on their territory
A/B-115	Wprey = 5.5
C/D-115	Fmax = 18
E/F-115	Uniform prey vulnerability among sex/age classes
A/B-116	Year-long presence of wolves in elk ranges
C/D-116	Compensatory mortality of 0.8
E/F-116	Least effective predation parameters

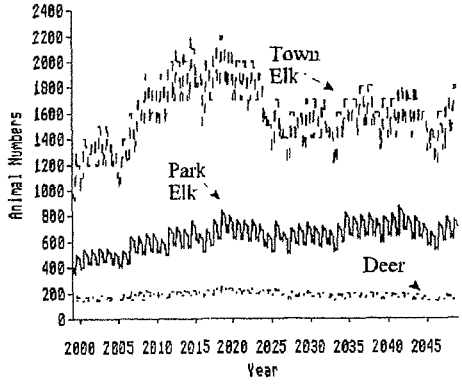
A)



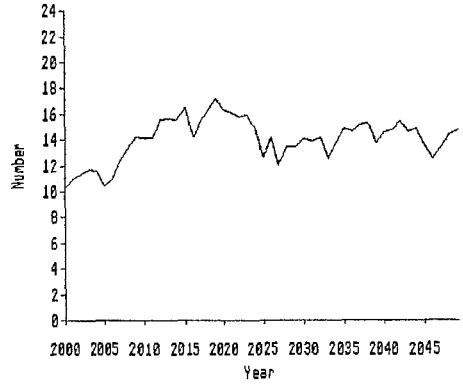
B)



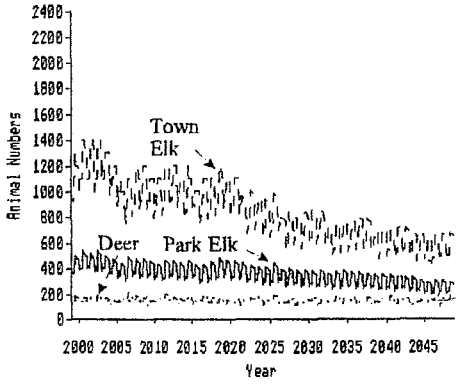
C)



D)



E)



F)

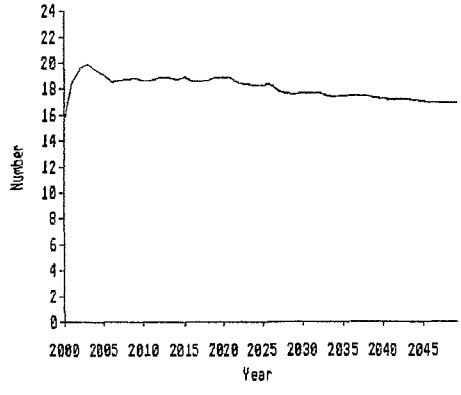


Figure 114. Sensitivity analysis of wolf model parameters. A) The control run (as Figure 106c), with wolf parameters in Table 9 and wolf numbers in Figure 106d. B) No wolves., C) and D) use wolf density vs. prey function giving minimal wolf densities at a given prey density. E) and F) use the wolf density vs. prey function giving maximal wolf densities. All runs are a continuation of the 1949-1998 undisturbed run.

densities (Figures 114b,c) than in the control run. The park elk herd reached a level of 600-800 instead of 400-600. The town herd reached 1,400-2,000 instead of 1,000-1,600. Using the maximum wolf density function resulted in 18-20 wolves, and marked reductions in the elk population compared to the standard run (Figures 114e,f). The park elk were reduced to 200-400 instead of 400-600, and the town herd was reduced to 600-800 instead of 1,000-1,600 in the same period of the control run.

The functional response curve (Figure 23) was altered to give a lower predation rate at a given prey density. The value for the w_0 parameter was changed to 5.5, as compared to 3.5 in the control run (see Figure 24c). This resulted in a slight reduction of wolf numbers, and a slight increase in elk density (Figures 115a,b) as compared to the control run. The park population varied in the 500-700 range instead of the 400-600 range. The town population varied in the 1,200-2,000 range instead of the 1,000-1,600 range.

Reducing the maximum predation rate (Fmax) to 18 from its standard value of 25 resulted in moderate increases in both wolf and elk numbers (Figures 115c,d). The park elk population varied between 600-800 instead of 400-600. The town population varied between 1,200-2,200 instead of 1,000-2,000. The increase in wolves was a numerical response to the increase in prey.

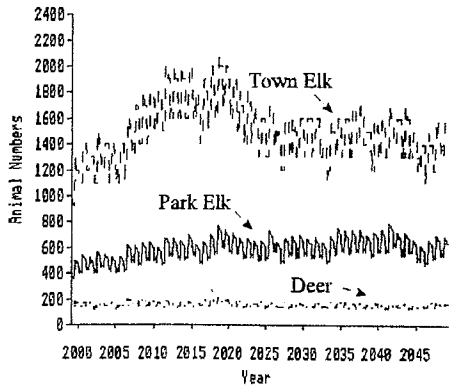
When wolves were assumed to prey equally on all age and sex classes, their impact on elk populations was markedly reduced (Figure 115e). The park elk herd was held at 800-1,000 instead of 400-600. The town population increased to 2,500, then varied in the 1,500-2,000 range.

Assuming all elk were in the wolves' range year around, instead of assuming that some were out of range of a western wolf pack in the winter, led to lower elk numbers (Figure 116a). The park population was held to 350-500, and the town population was reduced to 800-1,000.

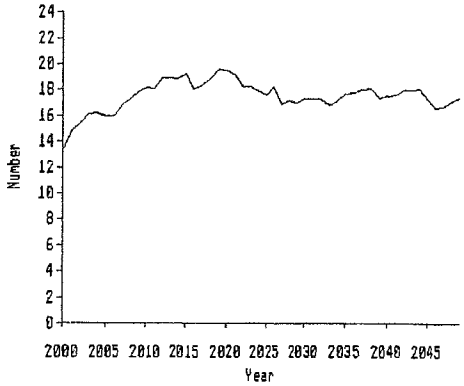
The assumption of a compensatory mortality fraction of 0.8 instead of 0.3 caused a large increase in the elk population (Figure 116b), as it was assumed that a larger fraction of the elk killed by wolves would have died due to other causes anyway. The park population increased to 800-1,000. The town population increased to 2,500, and then decreased to 1,500-2,000.

Finally, a set of least effective parameters was used. This included a w_0 of 5.5, an Fmax of 18, a compensatory mortality fraction of 0.8, and the minimum wolf density function. In this scenario, the park elk population varied in the 1,000-1,400 range while the town population increased to 2,700, then varied in the 1,500-2,000 range (Figure 116e). The park population was regulated to levels only slightly lower than the levels achieved without wolves (Figure 114b). The town population dynamics were essentially the same as without wolves after the initial irruption.

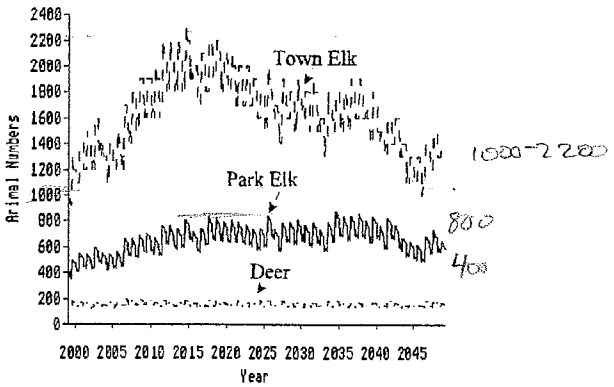
A)



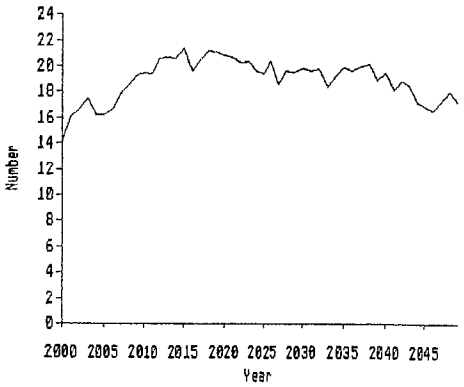
B)



C)

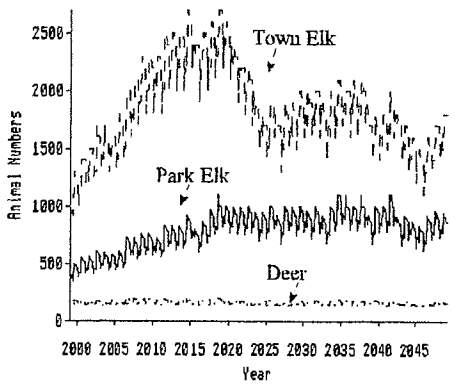


D)



E) Unrealistic, They will prey on calves more

F)



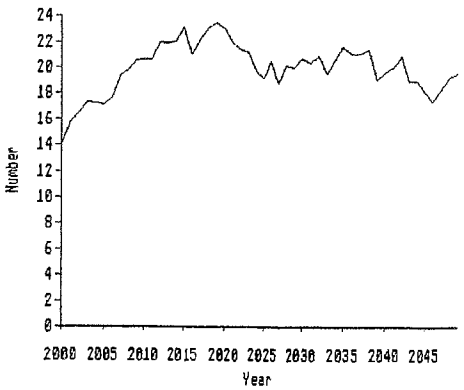
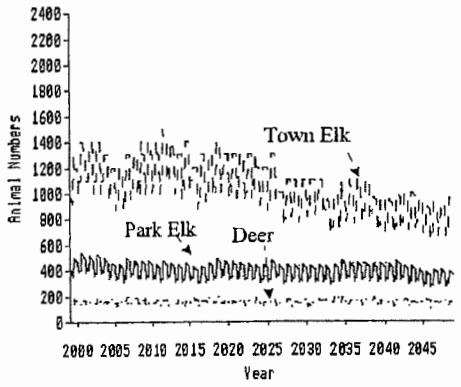
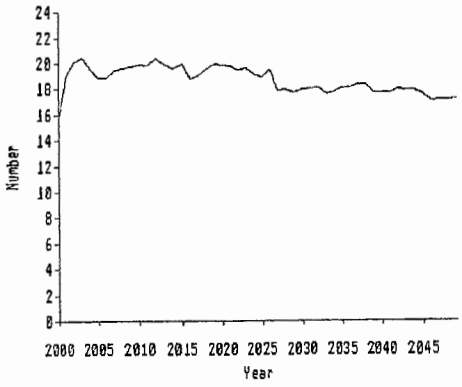


Figure 115. Sensitivity analysis of wolf model parameters. A) elk, and B) wolves, use a w0 value of 5.5 rather than 3.5, C) elk and D) wolves use an Fmax of 18.0 rather than 25.0, E) elk and F) wolves use a uniform vulnerability value among all sex and age classes, instead of making calves and older animals more vulnerable. All runs are a continuation of the 1949-1998 run using undisturbed vegetation.

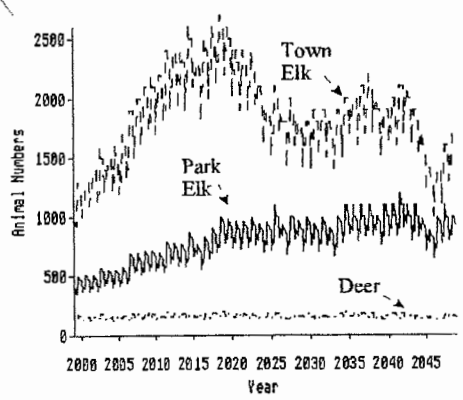
A)



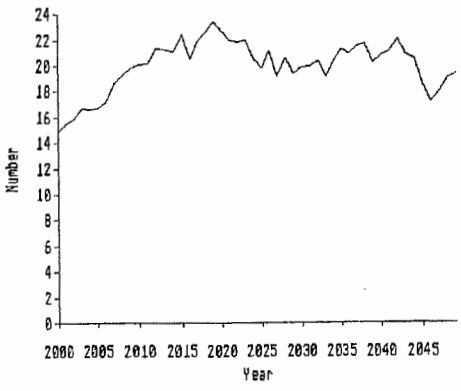
B)



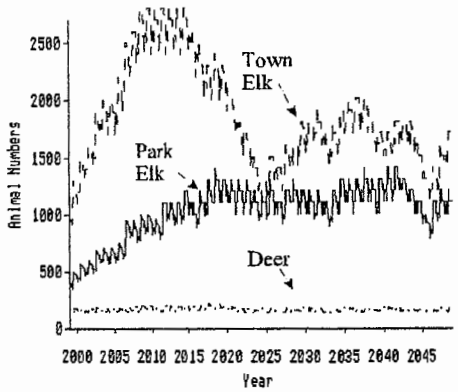
C) Unrealistic



D)



E) Unrealistic



F)

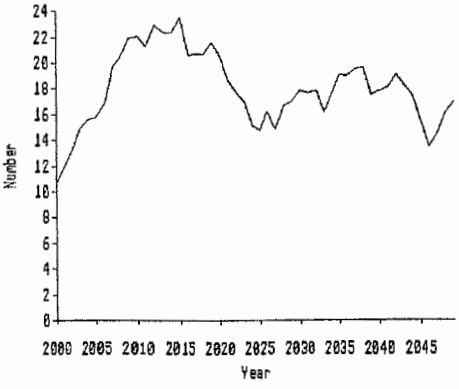


Figure 116. Sensitivity analysis of wolf model parameters. A) elk and B) wolves assume all prey are in the wolve's range year-around, instead of assuming some are out of range in winter. C) elk and D) wolves with compensatory elk mortality of 0.8 instead of 0.3. E) elk and F) wolves use a combination of parameters that are least effective for predator control of prey (see text).

DISCUSSION

1775-1911

Simulations of this period attempted to characterize the baseline condition prior to settlement, and the perturbations imposed on the system by the first settlers. Despite wolf presence, the system supported a significant number of elk, but the large majority were in the town range when two subherds were simulated. Wolves reduced the elk population, and prevented an elk irruption that would have resulted in reduced plant growth, low elk condition indices, and elk mortality due to starvation. Without wolves, upland herbaceous biomass was reduced. With wolves, there was little herbaceous offtake in excess of 50%. Willow cover was reduced severely at some locations when wolves were not present to control the elk population.

The heavy livestock grazing that occurred following elk extirpation was not simulated. Consequently, herbaceous biomass would probably not have increased after the extirpation as simulated. It is more likely that it decreased due to the livestock grazing. Herbaceous biomass densities may have been more like the densities that were simulated in the scenario with no wolves, since the higher number of elk would have had similar impacts as the livestock that were actually present. Livestock grazing would have reduced range condition and herbaceous productivity, thereby reducing the quantity of forage available to elk even after the livestock were removed. However, the residual effect of previous livestock grazing would have been captured by the initialization of herbaceous biomass to lower values in the subsequent simulations for 1912-1948.

The simulated increase in willow cover to high values despite elk presence was enabled by the improved water table conditions, which in turn were assumed to be due to beaver damming. The reduction of beaver by trapping in the 1830s-40s and subsequent reductions to a reported low point in 1890 was not considered. The beaver reduction could also have caused a reduction in willow habitats. Percent offtake of willow remained low despite significant numbers of elk. This was due to the large amount of willow cover and associated current annual growth. Willow stands also supported an increased prevalence of tall willow, which is beyond the reach of elk.

Aspen declined, even with wolves present. The decrease was due to elk, as shown by the fact that aspen increased when elk were not present, and stayed high when deer were also eliminated. The decline was a result of herbivory on stands in the core winter range, where elk are concentrated in winter. Empirical evidence also indicates that aspen regeneration is highly sensitive to elk, even at low elk densities. For example, bark scarring was occurring shortly after the elk reintroduction (McLaughlin 1931, Thompson 1933). The simulated decrease in aspen at low elk densities raises the question of whether the simulated decreases in stands in the core winter range could be a result of those stands not having existed there prior to elk extirpation. The model results suggest that few if any aspen stands would have existed on the core winter range prior to 1870.

The only evidence for aspen presence on the winter range prior to 1870 is the historic photographs from approximately 1910 that were studied by Baker et al. (1996). Their analysis of

photographs showed aspen which were large enough to have regenerated prior to 1870. Furthermore, these aspen had no bark scars, suggesting that elk were not present at these locations prior to 1870. The locations of those photographs were not provided, however, and no evidence was presented which showed that those stands were located in the core, lower elevation, portions of the elk winter range. The single photograph that was published was clearly not on the core winter range, but some distance up the Fall River above Horseshoe Park. There is a need to examine this evidence more carefully, with respect to exact spatial location before generalizing across the entire winter range, which experiences differential elk utilization and considerable environmental heterogeneity.

One mechanism by which aspen may have regenerated on the core winter range despite the presence of wintering elk, is through relatively fine-scale spatial alterations of elk distribution caused by wolves or humans. It has been argued that elk would avoid areas frequented by wolves, and in such areas aspen recruitment would be possible (Ripple and Larson 2000). This pattern has been observed in Jasper National Park in Canada (Dekker et al. 1996, White et al. 1998, White and Feller 2001). It is conceivable that wolves might have focused their activities and located their dens in areas of the core elk winter range which were suitable aspen habitat, thus allowing aspen to regenerate in those locations. Native Americans could similarly have located hunting camps with a similar result. Aspen could also have regenerated in areas where culling operations took place in the 1940s-1950s (Stevens 1980). These fine-scale spatial responses were not simulated in the model. Simulation of these patterns would require a spatial representation of wolf activity.

Importantly, the model simulated a dramatic increase in aspen when elk were extirpated. This suggests that when elk were absent, there could have been considerable regeneration and growth of aspen trees, even on the core winter range in areas of formerly high elk concentration. Older aspen stands with large trees would still have been present at slightly higher elevations on the winter range.

1912-1948

During 1912-1948, elk increased to a point where it was felt they had to be controlled to prevent or reverse range damage. It was also a time of transition between livestock grazing and increasing elk. Because of this transition, care must be taken to distinguish between the early range damage due to livestock, and the subsequent effects of elk. In 1925, ranges were perceived to be in a generally depleted condition due to years of heavy livestock grazing (Guse 1966). Livestock utilization of the core winter range reduced the amount of forage available to elk. Dixon (1931) observed that "the present winter range is entirely inadequate for the elk and deer now on hand." He recommended that the park purchase additional lands on the core winter range. Several holdings totaling 12,000 acres were purchased, including Beaver Meadows and Horseshoe Park. Thus, it would appear that the decision to purchase added winter range for elk was a result of competition with livestock, as well as an increasing elk population.

An often overlooked event during this time was the eruption of the mule deer population (Stevens 1980). The model likewise indicated that deer numbers would have increased due to lack of competition from elk. If deer had not been hunted and reduced, as they were, they would have

likely increased to upwards of 2,000. However as elk increased in number, they reduced the growth rate of the deer population, which must have contributed to the decrease in their number. The model showed deer numbers would have declined even if deer were not hunted or reduced. The park biologists at this time recognized the effects that deer were having, especially on shrubs such as bitterbrush and sagebrush, and also on aspen. The eruption while elk were present in low numbers raises the question as to why deer numbers did not erupt earlier when elk were absent. One possibility is that deer were over hunted, just as elk were, during that earlier time period.

It is unclear exactly when meadows were drained in Moraine Park and Beaver Meadows to create irrigated hayfields, but haying took place from the 1890s onwards. There could have been further hydrological manipulations throughout 1910-1949. Some time during this period, beaver numbers increased from the low that was reported for 1890. It is possible that there could have been an initial increase from 1890-1900, but the increase could have been limited by human activities on the winter range until the acquisition of lands and removal of livestock, and the absence of predators in the early 1930s (Packard 1947b). Historical photography from 1937 and 1946 showed 20% more willows than in 1998 (Peinetti 2000, Peinetti et al. 2002). So either the willow responded very quickly to beaver activities in the 1930s, or despite the negative effects of humans on willow habitats between 1890-1930, there were still more willow in 1937 and 1946 than there were in 1998. The latter seems more likely. The actual extent of the area impacted by draining and willow clearing has not been quantified. The early descriptions portray Moraine Park largely covered by willow swamp (Gysel 1960), while later willow were mostly restricted to river banks. Thus, despite the fact that there was more willow in 1937 than in 1998, there was likely even more before that. The increase in beaver during 1890-1930 could have improved some of the habitat for willow, and reduced the rate of willow decline, but observations in 1939 of dying willow (Dixon 1939, Gysel 1960) suggest that some of the willow were likely dying by 1937.

With the observed number of elk, and high water tables, the model did not simulate a decrease in willow during 1912-1948. In particular, the model could not explain willow declines under the number of elk present up until 1930. If water tables were high, the model could only simulate willow declines 1910-1930 if elk were assumed to be in the 500-1,000 range for the entire period, which was unrealistic. Willow declines were simulated during this period only when hydrology was altered. The presence of elk accelerated the decrease in those locations where water tables were lowered, but was not the original cause of the decreases. As beaver flourished in the 1930s, conditions for willow could have improved or stabilized in some areas, but heavy herbivory on willow was reported in 1939 (Dixon 1939), and in 1941 (Ratcliff 1941), and Gysel's (1959) limited exclosure data indicated continued declines at willow-grassland ecotones from 1939-1959.

The model results and historical data suggest that decreases in beaver and increases in human activities during 1880-1910 could have set in motion a chain of events that made the system more susceptible to elk herbivory from 1920-1940. The subsequent increase in beaver could have help raise water tables, but did not completely rectify the past impacts. Furthermore, it is possible that high beaver numbers, combined with increased elk and deer numbers, could have been unsustainable, even with positive impacts of beaver on hydrology. The beaver-elk factorial experiment with the model

indicated that willow is sustainable at moderate densities of elk and beaver, but if both increase together, willow decline. Although deer consume little willow, their competition with elk for other forage could have caused increased elk utilization of willow. With fewer willow, some willow in decline on dewatered sites, and burgeoning elk, deer, and beaver populations, the level of herbivory on willow could have increased to an unsustainable level.

Since there is not enough information available to represent the actual changes in hydrology and beaver that occurred, either in time, or in space, we can only infer that the actual scenario was something in between the two extremes that were simulated, i.e., high water tables at all willow sites for the whole period (1912-1948), and reduced water tables at some sites for the whole period. In actuality, if water tables were reduced at some sites, they probably were not reduced for the whole period.

During this period aspen was predicted to increase until about 1925, then begin to decline. The initial increase occurred in all scenarios except when elk were initialized to high numbers in 1910. The increase occurred while elk numbers were low - below 200 in the park herd. The decline was a result of combined elk and beaver browsing, as elk numbers rose from 200-1,000. The decline did not occur in simulations without elk and beaver. In the undisturbed run, aspen held steady but at a much lower value than in the other scenarios. The declines had already occurred in stands on the lowest elevation winter range, and there was no increase in response to elk absence during 1775-1911. What the disturbed scenarios showed therefore, were continued departures from the undisturbed state due to low elk numbers before 1925, followed by gradual returns of aspen cover to the value that would be expected in an undisturbed ecosystem with moderate numbers of elk.

The fact that aspen declined during a period of relatively low elk densities in 1925-1935 suggests that elk are highly selective of aspen and, on the core winter range, elk may suppress aspen even at low densities. The model results were consistent with the earliest observations of elk damage to aspen in the early 1930s (McLaughlin 1931, Thompson 1933), and Packard's (1942) observations of heavy damage and essentially no regeneration in Beaver Meadows. Olmsted (1980) noted that nearly all of the aspen stands in the elk concentration areas regenerated prior to 1925. Gysel (1960) stated that even after the big elk reductions aspen in many places were having difficulty in regenerating. Grater (1945, cited by Buttery 1955) noted that "the assumption that barking of aspen by elk is an indicator of food shortage is not true. It has been noted that elk eat bark regardless of food conditions, and that freshly barked trees have been found in the midst of fine grass stands." Olmsted (1980) made the important observation that the mule deer population may also have had a significant effect on aspen regeneration in the 1930s. The deer population grew to maximal numbers 1925-1935, and then declined as the elk herd increased.

Baker et al. (1997) inferred that aspen throughout the winter range only regenerated when elk numbers were low, as they found patches that regenerated every few years until the 1930s. However, they found a stand that regenerated in 1936, when it was estimated there were 555-675 elk, two stands that started in 1960-1962 when it was estimated there were 666-800 elk, and another stand that started in 1978 when 1,100 elk were present. Baker et al. (1997) noted long periods of

no apparent regeneration during the period when elk were absent (1875-1912). They sampled 18 stands out of 72 in a stratified random fashion. Thus, if half the winter range were considered to be in high density elk concentration areas, then half of the stands would fall within these concentration areas. The locations of the 18 stands were not paired to the reported years of aspen regeneration in the publication (Baker et al. 1997), so it was not possible to determine if the stands that regenerated when elk were present in low to moderate numbers were located in zones of high or low elk densities. If the regenerated patches were only located in areas of low elk density, then it could be argued that low to moderate elk numbers primarily inhibit regeneration in high density areas. If so, the stands that are currently present in the high density areas would have probably been established when elk were absent, and their current presence would have to be considered to be an artifact of elk absence, rather than a feature of the pre-settlement ecosystem, since elk were evidently present in pre-settlement times. However, Baker et al. (1997) did provide evidence of decreased regeneration throughout the elk winter range since 1968 as did Stevens (1980) and Olmsted (1979, 1997), suggesting there was also a lack of regeneration in stands located on lower elk density areas since 1968. It is quite possible that as the elk population has grown, elk have increasingly used more marginal habitats at higher elevations, and that densities have increased in what formerly were low-density areas.

1949-1998

Responses during elk reductions

A large number of elk were removed in 1949-1950, setting the stage for a period of regular controls that kept the elk population in the 500-700 range through 1972. The period through 1972 provided an opportunity to examine ecosystem responses to active management of the elk population.

During the period of elk reductions 1949-1968, the model predicted that range condition would have improved, as shown by increases in herbaceous root biomass and increases in willow cover on well-watered sites. However on sites with reduced water tables willow decreased, and on the core winter range aspen also decreased, despite the elk reductions. Conditions would have improved only slightly faster in areas where elk were excluded, with the exception of aspen, which would have markedly increased if elk were excluded. The increases could be attributed to the simulated elk reductions because in the no-reduction scenario, herbaceous cover did not increase, and willow decreased at more locations. These results are consistent with Buttery's (1955) observations of modest increases in range conditions in some areas. For example he stated that sagebrush areas were in fair condition with a slight upward trend, with similar grass biomass inside and outside exclosures. He found little difference in herbaceous cover in bitterbrush areas, but a significant species shift. Although the model did not represent different grass species, it would have represented such a shift if elk selected for certain species (e.g., *Muhlenbergia*) and avoided others (e.g., *Stipa*). Buttery also noted that willow were showing signs of recovery in the meadow areas, but aspen was still being suppressed outside the exclosures. Gysel (1960) found willow were declining in transition zones, but tall willow were doing well along stream banks. Grass was higher inside exclosures due to shrub decline, but there were more species of forbs outside exclosures. Aspen were very suppressed, and at Horseshoe and Moraine Parks, there was no recruitment outside the exclosures while the opposite

was true inside the exclosures. Baker et al. (1996) found six stands that regenerated during the early 1950s and early 1960s, but it is unclear where the new stands were located with respect to elk concentration areas.

It seems likely, therefore, that the elk reductions brought about modest range improvement, and protected some, but not all willows and aspen. The reductions did not appear to have led to a restoration of willow to its former range, primarily because elk reductions do not address the problem of lowered water tables. While the elk reductions would have created opportunities for aspen recruitment in some areas, it seems unlikely that they would have promoted aspen regeneration on the primary elk concentration areas. Since most of the earlier range damage in Moraine Park, and Deer Ridge was due to heavy livestock grazing rather than elk (McLaughlin 1931), some of the increase in condition could be more fairly attributed to the removal of livestock in 1933 rather than the reduction of elk numbers. Because of the spatial heterogeneity of elk herbivory and residual effects of localized past disturbances to willows and meadows, it is dangerous to make sweeping generalizations about how elk reductions affected the overall condition of the range. In some areas conditions could have improved, but in others condition could have remained unchanged or continued to decrease.

Upland responses after the cessation of reductions

Ecosystem responses following the cessation of elk reductions followed a different pattern. In order to assess the effect of halting the reductions, or conversely the effect of not halting them, it is necessary to make comparisons between the control run and a run where the reductions were not terminated. The simulation with continuous elk reductions to 400-600 through 1998 showed that if the reductions had continued, the increases in herbaceous cover would also have continued but would not have been as great as the increases with no elk at all. Continued reductions would have returned root biomass to 85-95% of what would be present in the undisturbed scenario with wolves (Figures 87,88). The implications are that reducing the elk population to 400-600 would bring the herbaceous vegetation to a state that is more similar to that of an undisturbed ecosystem, but would not bring about complete restoration.

Although simulated herbaceous biomass did not continue to increase following the cessation of elk reductions in 1968, it appeared not to decline either. Instead, it appears to have stabilized. This is consistent with findings of Stevens (1980) and Zeigenfuss et al. (1999). Stevens found no significant changes in bare ground or species composition on eight transects in bitterbrush and four transects in sagebrush from 1968-1978. He found an increase in bare ground in the grassland type, rising from 14% to 20%, but he concluded the grassland was stable. Zeigenfuss et al.'s analysis of the longer data set for 1968-1988 showed similar results. They concluded that the data showed little or no declining range conditions since 1968. The increase in bare ground in grassland was minor (4%) and there was no evidence of a reduction in plant cover. They documented an increase in Timothy (*Phleum pratense*), an exotic grass which is resistant to grazing. Singer et al. (2002) and Schoenecker et al. (2002) reported results from sampling in three 34-year old exclosures. They found no significant differences in bare ground, herbaceous biomass, or fine root biomass. They found more sagebrush

cover inside exclosures. Binkley et al. (2002) and Schoenecker et al. (2002) also found no differences in soil organic carbon or nitrogen. However, as Zeigenfuss et al. (2002) point out, these exclosures are poorly replicated and since all three exclosures are located in Beaver Meadows, they represent a small portion of the winter range. Sample sizes for root biomass were also very limited (two of the exclosures, 15 cores inside and 15 outside each exclosure).

Thus, while upland herbaceous range condition may not have improved, it probably has not retrogressed significantly further during the last 30 years. Stevens (1980) pointed out that this might be considered to be a grazing induced disclimax. The lack of movement of grasslands to climax conditions has been cited as evidence of overabundant elk (Hess 1993), but that assumes vegetation should be in an ungrazed climax. The stabilization of the elk-grassland subsystem is consistent with the theory that when elk reach food-limited carrying capacity, they reach a dynamic equilibrium with vegetation, at which vegetation will be in a stable, although different state than an ungrazed climax (Caughley 1979, Cole 1971, Cayot et al. 1979).

Altered, but stable vegetation structures due to herbivory occur in the Serengeti (McNaughton 1983a,b) and in Yellowstone (Houston 1982, Frank and McNaughton 1992, Coughenour 1991b, Singer et al. 2002). In the Serengeti, the most abundant herbivores are migratory while predators are sedentary. Thus, predator populations are consequently limited by prey availability during a portion of the year, which keeps predator populations below the level necessary to control herbivore population sizes (Fryxell et al. 1988). As a result, herbivores exist at their food-limited carrying-capacities. In Yellowstone, elk also reached food-limited carrying capacity (Houston 1982, Coughenour and Singer 1996); however, it has been argued that this is not a condition which would have existed in pre-settlement times due to the effects of wolves and humans (Kay 1990,1994, Wagner et al. 1995, White et al. 1998, Ripple and Larson 2000, White and Feller 2001).

Aspen

The aspen decline that was simulated in the control run for 1949-1998 was consistent with observations. Stevens (1980) noted that historical photographs showed aspen occupied more area in 1930 than in 1978. He also examined two small exclosures constructed in 1933-1934. One site was successional to lodgepole pine so aspen were declining inside as well as outside the exclosure. The other site was concluded to be marginal for aspen because tree sizes were small inside the exclosure. Consequently, a small amount of browsing was apparently sufficient to eliminate aspen outside. At two large exclosures constructed in 1963, Heifner (1969) found one third as many trees outside as inside the exclosures and the difference continued to increase through 1979 (Stevens 1980). Stevens (1980) found reductions of young and mature tree numbers in three of four transects between 1968-1998. However, Zeigenfuss et al. (1999) found the sample size was too small to statistically conclude anything. Stevens (1980) concluded that most of the aspen stands on the core elk winter range would continue to decline, except for stands on optimum habitat. Olmsted (1979) found no stands that had regenerated during 1925-1980 except those which regenerated in 1950s following a reduction of the elk herd to 700. He also noted that the stands that regenerated in the 1950s were stands that received light browsing pressure, even in 1975-1976. Stevens (1980) commented that the stands which

regenerated in the 1950's were near roads where the maximum direct reduction efforts on elk took place, and therefore, received little elk use. Olmsted (1997) later found that woody twig volume had decreased by 66% over the 20-year period 1978-1997. He found no evidence of regeneration in any of the sampled stands, and very low survival of browsed leaders.

Aspen also declined in all the other model experiments from 1949-1998, except those in which elk were absent. Declines also occurred in the undisturbed run with wolves. The declines were brought about by elk browsing on stands on the core winter range. This result reinforces the results from runs in 1775-1911 and 1910-1924, which suggested that aspen stands on the core elk winter range may be vulnerable even to low numbers of elk. It also raises the question of whether most or all of the aspen patches on the core elk winter range emerged during elk absence and low elk densities 1875-1920. The fact that Olmstead (1979) found patches of aspen that regenerated in the 1950s must be carefully examined for reasons cited above, that elk densities could have been lower near roads where elk reductions took place during that time. Stevens (1980) noted that one of the two stands that regenerated in the 1950's was located in lower Beaver Meadows. This stand is right next to the road and in one of highest elk use areas. Baker et al (1996) found patches of aspen that regenerated in 1961, 1963, 1964, 1970, and 1978. Stevens (1980) pointed out that the single stand that regenerated in 1978 was located close to the upper elevation margin of the elk winter range and outside the elk winter range as described by Larkins (1997) and used in the model here. Nearby (300 m), Stevens found a stand that had declined markedly during the period 1975-1985. The locations of the stands that regenerated in 1961-1970 could not be discerned from Baker et al.'s paper, but the locations are very important to the interpretation. These results highlight the importance of the spatial location of regeneration in interpreting relationships between elk densities and regeneration. Both Olmsted (1979) and Baker et al. (1996) refer to the regeneration patches as "cohorts." However, they are actually only individual stands or one to three isolated stands. Since aspen very rarely reproduce from seed, the regeneration events are most likely independent vegetative reproduction events in different stands, not reproductive outcomes the entire population. Referring to these events as population-level cohorts ignores the importance the functional independence of the stands, and the significance of their individual spatial locations relative to elk browsing pressure. There is insufficient evidence to show when the stands on the lower elk winter range first became established. These authors infer that the stands regenerate, based on the lack of seed-based reproduction in aspen. Seed-based reproduction has been shown to occur following fires (Romme et al. 1995). However there were no significant fires during this time period in those areas. The clones could have first been established during sporadic periods of low elk numbers due to severe winters, predation, or aboriginal hunting. Clones can persist for long periods as primarily belowground organisms with short-lived, small aboveground shoots. Thus, the fact that there are clones there does not rule out high elk densities, but it does indicate that elk herbivory may have been reduced for undetermined lengths of time. This would be consistent with the prevailing views that most ecosystems are subject to periodic disturbances, and that they are either non-equilibrial, or are in dynamic rather than steady-state equilibria.

The "Town" Elk

The model simulated an increase in the number of elk wintering in the "town" subherd range. The fraction of this range which is actually within the city limits of the town of Estes Park was not assessed here. The emergence of the town segment during this period has important management and ecological implications. As Lubow et al. (2001) suggested, the growth of the town herd can be explained by a low rate of emigration from the park herd, coupled with the high potential growth rate of the herd under conditions of underutilized forage. Although the area of the town range is actually smaller than the park range (69 km^2 vs. 96 km^2), it can support more elk due to a higher proportion of grassland vs. coniferous forest, reduced snow cover, and possibly increases in forage quantity and quality by irrigation and fertilization. By 1998, the town population was simulated to have in excess of 1,800 elk, while the simulated park population had about 1,000. The growth rate of the herd was initially very high, because elk body condition was high, thus reducing mortality and increased calf survival. A question with important implications is whether the current land use in the town range is supporting an artificially high elk population compared to pre-settlement.

The undisturbed simulation with wolves featured a town elk population of 1,000-1,800 during this time, but the mean level was approximately 1,200 (Figure 76c). The question arises as to whether forage supplies have been elevated by current land use. In the simulation with current land cover and wolves, the simulated town elk herd numbered 800-1,600, slightly lower than with pre-settlement land cover, suggesting that there is less forage now than in pre-settlement times. Although grasslands have been irrigated and fertilized under current land use, there has also been a significant loss of forage to urban development and disturbance. In particular, the central feature of the valley in pre-settlement times was the Fall River - Big Thompson River alluvial floodplain and terraces, which supported mesic meadow and willow. This has been largely covered by a reservoir, and filled in to support development including an irrigated golf course. It can be argued that the irrigation and fertilization of lawns today, and removal of nitrogen in clippings, do not compensate for the water and nitrogen that was going into and cycling within the former alluvial floodplain.

The model does not address the issue of habituation, but assumes that elk will tolerate humans as much as humans will tolerate them, which seems consistent with the current situation. The combination of an ample forage base and habituation to humans has apparently created a refuge for the elk from sport hunters. Despite the increases in the town elk herd, sport hunting offtake has remained steady or has declined slightly. This means that sport hunting has not and is not controlling the growth of either the park or the town herd segments. The model corroborates that fact. One of the original premises of the joint management plan of 1962 between NPS, Colorado Division of Wildlife, and USFS (which also justified no further direct reductions within the park) was that elk would move in sufficient numbers outside of the park to allow hunters to keep the elk population in check. Instead, what has happened is that the park subherd has developed a fidelity for wintering within the park (Lubow et al. 2000) at their food limited carrying capacity, which has then caused an outmigration into the safe haven of the town range. The town herd segment has subsequently grown as much as the food base will allow. Again, the model supports this theory. Similarly then, when the town range fills to capacity, there will be an increased likelihood of outmigration from the town range

Park as a sink

into the domains of the sport hunters. However, it seems likely that the town elk will resist such an outmigration, imposing even higher demands on forage resources in town (i.e., lawns, golf courses, ranches, undeveloped yards, etc.). Furthermore, when the town population approaches its food-limited carrying capacity, a state will be reached where the surplus elk will be forced to either move west into the park, or east into the domain of hunters and other conflicts. At that point, if the park herd segment were reduced through management, a vacuum would be created which would likely draw the surplus town elk into the park. The NPS would then be managing elk which originated in town. Although the model runs did not address this scenario, the model runs and assumptions of outmigration from source areas to sink areas are consistent with this possibility. It would seem, therefore, that a coordinated management action would be required to reduce the park and town segments simultaneously, if it is decided that fewer elk are desirable within the park.

Willow, Beaver and Hydrology

A potentially serious consequence of overabundant elk, or human impacts, could be a runaway effect involving a positive feedback cycle of willow reduction, beavers decline due to loss of the willow, loss of beaver-induced hydrologically suitable habitat for willow, increased susceptibility of stressed willow to elk herbivory, willow declines, increased competition between elk and beaver, leading to further beaver declines and so on. This is a complex chain of events that could be set off by several individual factors, or different factors acting in combination. Because of the circularity of the process, once it is set in motion, it could be difficult to separate cause from effect. Packard (1947b) felt that elk were competing with beaver for willow and aspen in many places, and though he did not state it explicitly, the implication was that overabundant elk would lead to a beaver decline. This would seem to place the blame entirely on elk (e.g.., Hess 1993), which may not be quite true. There is no conclusive evidence that elk were solely responsible for the willow decline. The interaction between beaver and elk herbivory on willow and aspen cannot be discounted. The factorial model experiment using weather and other conditions for 1949-1998 showed that willow can readily tolerate beaver up to relatively high densities, but not in the presence of elk. Conversely, willow can tolerate elk herbivory, but not if the beaver population is exploding, as it could do in the absence of predators. Model experiments also demonstrated that willow could tolerate the levels of herbivory imposed by elk 1949-1998, but if water tables were lowered, willow would decline in some areas even without elk herbivory, but the declines would be much larger when elk herbivory is imposed. It could be argued that the hydrological declines were due to declining beaver, or due to human impacts, or both. The cause of the beaver decline could be partly or solely due to elk, but that has not been established. There is evidence that a decline had already occurred in Moraine Park between 1940 and 1964 (Hickman 1964, Stevens and Christianson 1980) when elk were actively managed. There was a perception of a sudden decline in 1976, and subsequent surveys showed less beaver in 1980 than in 1964 (Stevens and Christianson 1980), and further still in 1998 than in 1980 (Gense 2000, Zeigenfuss et.al. 2002).

An alternative hypothesis is that the beaver declined due to the combined effects of increased numbers of elk, high numbers of beaver, livestock competition with elk, and direct human impacts on willow. Beaver could have been artificially high due to lack of predators and lack of competing

elk. Maximal beaver numbers were observed following and during a period of intense land use in areas like Moraine Park. The loss of significant amounts of willow cover due to human impacts could have played a role, and a large number of beaver may have been compressed into a reduced area of suitable habitat. In addition, livestock grazing may have caused increased elk herbivory on willow, due to lack of grass. Packard (1947b) clearly referred to an overabundance of beaver relative to willow. He commented that in Moraine Park - "There is no indication that the supply of willow will soon be exhausted, but it is already insufficient to maintain the large number of beavers inhabiting the marsh, and it is suffering from competitive use by elk and deer while livestock grazing further reduces the amount of grass available. – In many places the carrying capacity (for beaver) has been overreached – ." The ratio of willow to elk was also reduced, heightening herbivory pressure. As elk increased, competition for the remaining willow could have intensified, subsequently reducing the supply of current willow leaders available to beaver. Furthermore, livestock grazing probably stimulated increased utilization of willow by elk (Packard 1947b). Subsequent willow declines and probable conversions from tall to short willow between the late 1930s and the 1990s (Peinetti 2000, Peinetti et al. 2002), could have been due to a protracted process of elk herbivory superimposed upon a background of beaver herbivory and residual effects of earlier hydrological change and livestock grazing. It was later observed that "a few areas, however, like lower Horseshoe Park and lower Moraine Park, because of the severe competition with elk and an apparent drop in the water table as the result of earlier beaver dams collapsing, may never develop a sufficient forage supply for the reestablishment of beaver" (Stevens and Christianson 1980).

The mechanisms of conversion from tall to short willow by elk herbivory can be difficult to understand given that once willow reach a certain height, they can largely escape herbivory. This escape mechanism must at least partially account for the persistence of current tall willow stands in the upper portions of the Moraine Park and Horseshoe Park valleys. In the model, as willow plants die, they must be replaced by new recruitment. Plant mortality could be simply due to finite longevity, but tall willow mortality can also be accelerated by dewatering and its effects on reduced replacement growth. When elk were abundant, the replacement recruits could have been suppressed in a short growth form by elk herbivory. This would require nearly complete offtake of new leaders by elk each year. Although mean herbivory levels on willow are in the 30-60% range (Zeigenfuss et.al. 2002), a disproportionate share of the herbivory could occur on shorter plants.

The predominance of tall willow in the upper portions of the valleys, with short willow predominance in lower portions of the valleys could either be a response to differential levels of herbivory or different amounts of water and nutrients in different portions of the valley. Elk census data indicate that there are indeed fewer elk in the upper valleys, probably because of deeper snow cover. The elevation difference is small, but significant in that regard. This hypothesis is supported by model predictions of lower elk densities in the upper valleys due to deeper snow.

It has been argued that tall willows are indicative of higher water tables (Zeigenfuss et.al. 2002, Singer et al. 2002). Tall willow could also be less negatively affected by herbivory when they have a more ample water supply. There is no doubt that willows obtain a substantial fraction of their water supply from subsurface sources. Certainly, an ample water supply is necessary to support the

transpiration of the dense leaf area in a tall willow stand. Alstad et al. (1999) showed that 80% was derived from subsurface stream water, as opposed to precipitation on-site. Willows likely also derive a significant fraction of their nitrogen from ground water (Menezes 1999). Willow on upper landscape positions obtained less N from ground water than willow nearer to stream channels (Menezes 1999). It is logical that the narrower upper portions of the valleys would be wetter, since the stream is more confined at that. These valleys subsequently widen downstream. As the stream widens, meanders, and becomes more braided in the more open portion of the valley, the water might be more dispersed, thus resulting in less water on a given surface area, and shorter-lasting water tables with deeper average depths.

The simplifying assumption was made that the initial willow size class distributions were similar to what is found in tall willow stands today and with 40% cover. The presence of some individuals in the smaller size classes, and new recruitment provided the opportunity for willow stands to increase in cover through increases in plant size and recruitment of new plants, as long as conditions would allow. Reductions in cover due to herbivory were simulated by the suppression of height growth in the short willow size classes, as observed (Peinetti 2000). Cover was also gradually diminished on sites with lowered or shorter lasting water tables, due to plant mortality, and the reduced ability of the site to support high leaf area.

Based on first ecophysiological principles, a smaller amount of leaf area can be supported on drier sites, because transpiration is directly proportional to leaf area (e.g., Woodward 1987). The simulation model includes mechanisms which would yield this result, since the model represents transpiration explicitly. In the model, transpiration demand is allocated among soil layers based on water and rooting distributions. Thus, if a portion of the profile is dry (e.g., without a water table), then a portion of the demand will not be met, especially if the demand is high as would occur with high leaf area indices. Furthermore, stomates must be opened and transpiring to support photosynthesis and plant growth. If transpiration is reduced due to less water, then growth will be reduced correspondingly. In this way, the extra growth afforded by shallower and longer lasting water tables would confer an advantage with respect to herbivory tolerance. If a willow plant accumulates more and longer leaders during the summer, then the proportion of current growth taken off by a given amount of herbivory is reduced, with fewer negative consequences for growth in the subsequent growing season.

The model demonstrated that it is possible for beaver, elk, and willow to coexist. They did so in the undisturbed simulations with wolves present, and often with abundant elk. In those scenarios willow were assumed to have been occupying sites with high water tables, presumably due to beaver. Ample water supplies increased willow tolerance of herbivory. Willow were more abundant, so relative browsing pressure was less. The importance of water was underscored by the simulation in which water tables were raised, but otherwise elk were managed as they were in the control run for 1949-1998 (Figure 83a). Even with elk present in the 800-1,000 range, the willow were able to persist. However, the initially low elk numbers before 1930 also allowed willow to develop into larger plants which could the escape herbivory. Low elk numbers also increased the ratio of willow to elk thus decreasing proportional offtake. In a comparable run without any elk reductions or wolves,

willow were suppressed despite elevated water tables (Figure 83e). Wolf predation was thus equally important to the coexistence of willow and elk. Predation held elk numbers to a sufficiently low level to enable well-watered willow to tolerate herbivory. However, predation alone could not prevent willow declines. Willow declined on sites with lowered water tables, despite the fact that wolf predation reduced elk numbers (Figure 83d).

If beavers are responsible for current willow habitats, then it would be logical to assume that beaver increased willow abundance. A possible scenario is that beaver initiated a gradual process of habitat expansion, starting with limited amounts of willow growing along stream banks which provided material for the construction of dams, which then created new ponds and meanders and new willow habitat, and so on. Hydrological events could also have periodically formed new channels and laid down new substrate for willow colonization. Occasional stream channel shifts in such an environment would not be unusual. Even if hydrological events contributed to initial willow colonization, it seems likely that beaver would have played a critical role in stabilizing the entire system. If so, then beavers were the "glue" that held the system together, enabling coexistence of abundant willow and elk.

With the gradual loss of beaver, portions of the system could have unraveled. The unraveling probably started earlier than the decline of 1940-present. The initial disruptions could have been beaver trappers who reduced beaver to low numbers by 1890, which could have resulted in the deterioration of some of the original dams. This was followed by human activities which disrupted some of the willow stands and their hydrology. Despite these disruptions, the beaver rebounded to high numbers in 1940, possibly due to lack of predators, reduced competition from the low numbers of elk, and a still sizeable remaining stock of willow. (This is not a prediction of the model here, but these dynamics were assumed to have occurred based upon the available evidence.) The loss of some of the willow and willow habitats earlier due to human activities, combined with the subsequent increase in beaver would have resulted in heavier utilization of remaining willow. Though elk were present in low numbers in the 1920s, they were likely compressed into a smaller range due to competition with livestock. Despite the removal of livestock in the early 1930s, increasing elk populations imposed heavy herbivory on willows by 1939 (Dixon 1939, Ratcliff 1941, Gysel 1960). Lack of predators and resultant increases in beaver (Packard 1947b) combined with the increasing elk herbivory in the 1930s, would have led to further willow declines. The loss of willow habitat and increasing competition with elk may have then contributed to a sustained beaver decline from 1940-1964, resulting in further loss of willow habitat, further loss of willow and beaver, and so on in a positive feedback cycle that has continued through the present.

Soil Organic Matter, Nitrogen Cycling, and N Limitation of Ungulates

In the RMNP modeling experiments, the sizes of the soil C and N pools remained relatively stable under a wide range of grazing intensities and elk abundances. There was a very slow, nearly imperceptible decline over long time periods (50-100 years). This was an average result for the winter range, and there could have been increases or decreases in different spatial locations. The sizes of the soil organic matter C and N pools were also very large relative to annual plant uptake and grazing

offtake, which provided a large buffering capacity. Given the large size of the pools, and the low impact of grazing, impacts on total soil C and N may be present, but not measurable after only 30 years of grazing protection.

This study did not include a detailed analysis of grazing impacts on soil fertility under different grazing conditions or spatial locations, but such a model assessment would be very useful, and the SAVANNA model could be used in such a study. For the purposes of this study, nutrient cycling and soil organic matter dynamics were mainly simulated to ensure that predictions of plant growth and animal responses were consistent with observed levels of soil nitrogen availability and realistic rates of nitrogen recycling. Plant growth was dependent on nitrogen derived from soil mineralization-immobilization processes, as in the Century Model (Parton et al. 1987, 1993). Nitrogen was recycled to soil in dead shoots and roots, and herbivore urine and feces. The long-term nitrogen budget of a site is determined by nitrogen inputs and outputs. Nitrogen fluxes between the surface atmosphere were consistent with best available data. These included N deposition in precipitation, N inputs through groundwater in riparian communities, denitrification losses associated with N mineralization, and volatilisation of ammonia from urine. Soil fertility was affected by the formation and turnover of soil organic matter (SOM) (Parton et al. 1987,1993). Thus, the sustainability of plant production over the simulated time frames (50-135 years) was the closely linked to the sustainability of nitrogen cycling and soil organic matter dynamics.

The model prediction of no impact of grazing on soil C and N is consistent with the findings of Binkley et al. (2002) and Schoenecker et al. (2002) who found no differences in soil C or N inside vs. outside of long-term grazing exclosures. It is also consistent with other findings, that grazing does not necessarily reduce soil C or N. The effects of grazing on soil C and N are variable, and no consistent pattern has been detected (Milchunas and Lauenroth 1993, Burke et al. 1997). Grazing can decrease, have no impact, or increase soil C and N depending on conditions. It is often expected that grazing will decrease soil C and N, inasmuch as it decreases plant growth and C inputs to the soil (Holland and Detling 1990, Archer and Smeins 1991, Holland et al. 1992). When grazing is heavy enough to significantly reduce plant cover, plant production, and thus carbon inputs into the soil relative to carbon lost in microbial respiration, soil carbon must decline (Parton et al. 1987). However, plant production is not necessarily impaired by moderate grazing (Briske 1991).

Schoenecker et al. (2002) and Binkley et al. (2002) both found no differences in N mineralization rates or absorption of inorganic N on buried resin bags between the inside and outside of long-term (35-year) grazing exclosures. In willow communities, however, Schoenecker et al. found markedly (5x) lower N mineralization outside of the seven short-term exclosures located in portions of the winter range judged to have high elk densities. All of the sites were in browsing-suppressed short willow communities. However, changes in N mineralization measured by closed-top soil cores preclude N mineralized from dung and recycled from urine. The large discrepancy in grazed vs. ungrazed N mineralization is also inconsistent with herbaceous plant growth measurements which showed no reduction due to grazing in the first 3 years, and only a 10-15% reduction in the last year (Zeigenfuss et.al. 2002, and unpublished data from movable grazing cages).

A number of mechanisms may ameliorate any negative effects of moderate grazing on the sizes of soil C and N pools. In two recent studies, grazing had no impact on soil C, possibly as a result in a shift of species composition to blue grama grass (*Bouteloua dactyloides*), which has a higher root:shoot ratio than the species it replaced (Frank et al. 1995, Schuman et al. 1999). Blue grama is highly resistant to herbivory, and has a long evolutionary grazing history (Milchunas et al. 1988). Although aboveground biomass was reduced by heavy grazing, root biomass was not, thus maintaining C inputs belowground. Plants can respond in a compensatory mode to grazing, and under some conditions plant growth is little affected, or stimulated by grazing (McNaughton 1983c, Briske 1991, Mazancourt et al. 1998). A variety of counterbalancing processes led to no effects of grazing on net CO_2 exchange rate of the soil-plant system (LeCain et al. 2000). An increase in nitrogen cycling and increased root turnover could offset gaseous N losses. Plant N uptake may be unaffected or stimulated by grazing (Ruess 1984, Coughenour et al. 1990, Seagle et al. 1992), which would help retain N in plant organic matter, rather than as inorganic N which is subject to leaching or other losses. The outcome of a complex interplay of plant and soil processes was demonstrated by recent studies in Yellowstone. Ungulates stimulated nitrogen retention by reducing the ratio of gaseous N losses to N mineralization, despite stimulating N mineralization. N retention was promoted by increased microbial productivity, probably due to an increased fraction of labile C (Frank et al. 2000). Earlier it was shown that grazing increased N mineralization and improved the organic matter quality of the soil by increasing labile and decreasing recalcitrant fractions (Frank and Groffman 1998). Similarly, moderate grazing promoted root decomposition and N mineralization compared to ungrazed or heavily grazed conditions (Biondini et al. 1998, Shariff et al. 1994).

In willow communities, Schoenecker et al. (2002) calculated 2.22 g N m^{-2} total return in dung and urine (per year). They estimated 0.83 and 0.42 g N m^{-2} in litterfall of ungrazed and grazed plots respectively. From this they estimated total N returns of 2.2 g N m^{-2} in grazed vs. 0.83 in ungrazed plots. They explained the greater input in grazed plots as possibly being due to import of N from summer to winter range. They also calculated that 2.64 g N m^{-2} was being removed in offtake, resulting in a possible net loss of 0.42 g N m^{-2}. However, the litterfall estimates of both Schoenecker et al. (2002) and Menezes (1999) may be very low, because the effectiveness of the litterfall traps is questionable. A very small fraction of herbaceous litter entered the traps (3-14 g m^{-2}) compared to aboveground herbaceous biomass (300-500 g m^{-2}, Zeigenfuss et.al. 2002), even inside grazing exclosures. Aboveground standing crop was only reduced 30% by grazing (Zeigenfuss et.al. 2002). Menezes et al. (2001) pointed out that the use of trays for collecting litterfall may have underestimated grass litter, since most of the senescent tillers still remain attached to the plant and are not collected by the traps.

It is important to recognize that nitrogen mineralization is both a cause and a response to plant growth. While plant growth depends on N mineralization, N mineralization depends on the size of the substrate pool. When plants produce more biomass, and return more biomass to the soil, the substrate pool is enhanced, and so is N mineralization. Thus, I would expect that where plant growth is reduced by grazing, N mineralization will also be reduced. Unfortunately, N mineralization was not a standard output of the model runs conducted here, however closer examination of SAVANNA outputs would likely support this hypothesis. It is also important to recognize that a difference in N

mineralization rate does not necessarily imply a difference in total soil N over the long-term. It is possible for grazing to enhance or decrease N mineralization and plant uptake, while having no impact on total soil N. Essentially, the N is still present, but it is turning over at a different rate. Instead, long-term soil N dynamics are primarily determined by the balance of inputs and outputs of N to the site, as gas fluxes or as groundwater inputs or outputs (Parton et al. 1987, 1993).

Nitrogen potentially affects forage-based carrying capacity for ungulates (Hobbs et al. 1982, Hobbs and Swift 1985). Ungulates could be limited by nitrogen as well as energy intake. A nitrogen deficit arising from a shortage of forage with sufficient nitrogen concentration could lead to reduced growth, and catabolism of lean body tissues, thus reducing body condition (Hobbs et al. 1982, Robbins 1983, Hobbs and Swift 1985). Ungulate populations could therefore be limited by the availability of forage items which have sufficient nitrogen concentration. The SAVANNA model did not consider this aspect of ungulate nutrition. However, the digestible energy content of forage is positively correlated to protein content, as are nitrogen-based and energy-based carrying capacities. Hobbs et al. (1982) calculated energy and nitrogen-based carrying capacities for RMNP elk, and found that energy was slightly more limiting than nitrogen. Similar results were obtained for elk in Yellowstone (Coughenour 1994, Coughenour and Singer 1996). Since SAVANNA considers the digestible energy contents of various forage items and their effects on ungulate energy balance, it implicitly accounted for variations in forage nitrogen content, and nitrogen is likely to be less limiting than energy in the final analysis anyway.

It has been hypothesized that increased nitrogen inputs and elevated nitrogen contents of lawns and golf courses in the town of Estes Park could increase elk carrying capacity (Singer et al. 2002). They found that N concentration was 3.4 times higher and total N yield (g N m^{-2}) was 2.9 times higher on golf courses than native grassland. While they calculated a forage-based carrying capacity, they did not attempt to calculate an N-based carrying capacity. Although SAVANNA did not address the effects of increased N yield on elk carrying capacity in town, it did account for the increased supply of digestible energy on the golf courses and lawns. Since the model assumed N content and digestible energy were related,, and because digestible energy is usually more limiting than N (as described above), the model indirectly represented the effect of increased N.

Elk and Vegetation Management Scenarios

The model predicted that with no management reduction of elk, the park population would continue to fluctuate around approximately 1,000. The town population would climb to 2,400 initially and then decline to 1,800-2,000. These could be considered to be the food-limited carrying capacities, but they are also outcomes of population processes. At these densities, elk condition indices would continue to fall to minimal values at the end of each winter. The 1,000 value for K is consistent with the level at which the population has been fluctuating for the past decade. It is also similar to the estimates of food-limited carrying capacity made by Hobbs et al. (1982), however, for slightly different reasons. Here, no assumption was made about an appropriate use level of 50%. Instead a certain amount of forage was unavailable due to snow, transfer to litter, and reduced intake rates at low forage biomass.

The predicted maximum population size of 2,400, and the long-term dynamic equilibrium of 1,800-2,000 for the town elk population was lower than Lubow et al.'s (2002) population-based K of 2,869±415, and Singer et al's (2001b) forage-based carrying capacity estimate of 3,082. The predicted maximum is in agreement with Lubow et al's estimate, but the longer-term equilibrium is not. There is uncertainty in our estimate as well as Lubow et al's. The Lubow et al. estimate was based on running a parameterized population model forward to a dynamic equilibrium, but since the town population may have only recently reached K, if at all, the data for parameterizing the density-dependent term were limited. Furthermore, that approach does not account for possible vegetation responses to elk herbivory. Previous experience has shown that when an ungulate is introduced to a new environment, there is an initial eruption due to the unexploited food source (Caughley 1970, 1979). As the ungulate population reaches a maximal value, vegetation productivity starts to decline due to the effects of grazing, thus reducing the forage supply compared to initial conditions. As a result the ungulate population declines until it reaches an equilibrium with vegetation. This is what occurred in the SAVANNA model. A reduction of vegetation production due to grazing was not considered by either Singer et al. (2002) or Lubow et al. (2002). Significantly, the population model for the town herd here used the same parameters as the park herd. That is, the birth and death rates responded to condition, and thus forage intake and forage biomass and quality, in the same way that the park population did. The data set for the park population is much longer, and provides a good basis for estimating population responses to changes in density and forage supply. There is no reason to expect that the town elk are somehow biologically different from the park elk. Thus, the discrepancy must lie in differences in estimates of vegetation production, or in implicit or explicit estimates of vegetation production responses to increased herbivory. Thus, further research is needed to improve estimates of town vegetation production and responses to herbivory.

Berry et al. (1997) conducted a "science-based assessment" which examined whether vegetation on the elk winter range has deviated from pre-Columbian conditions due to elk overabundance. Their guiding principle was that a primary goal of national parks is to manage for natural conditions and processes. They recognized that "identifying what is outside the range of natural conditions is the key." Furthermore, they rightly pointed out that maintaining pre-Columbian conditions (i.e., natural conditions) may not be possible through pre-Columbian methods (because pre-Columbian conditions cannot be fully restored due to conflicts with human land use outside the park, e.g., wolves, elk movement patterns). They made three recommendations relevant to vegetation management. 1) Assuming that elk are the main agent responsible for aspen declines, aspen clones should be protected for 10-20 years by fencing, elk reductions, or both. An unstated assumption was that the aspen which have declined were present in pre-Columbian times. 2) Assuming that elk browsing is the primary agent causing willow declines, along with hydrological changes arising from low beaver numbers, willow density should be increased by 10% through protection from elk herbivory and beaver reintroductions. 3) Assuming elk herbivory has created a homogeneous vegetation structure on shrublands and grasslands, and that vegetation was more heterogeneous pre-settlement, grasslands and shrublands should be protected from elk by any means, including fencing, reductions, and harassment.

Simulation experiments addressing these alternative management actions showed that fencing,

elk reductions, and improved water table conditions would all be effective, and combinations of two or more of these actions would be more effective than any single action. The primary purpose of the elk reduction experiments was to assess ecosystem responses to different numbers of elk. While direct reduction or culling has been used in the past, alternative ways to reduce elk might include contraception or translocation. Hobbs (2000) used a population model to show that contraception would be highly effective, and within a reasonable cost range.

Upland herbaceous vegetation would remain in its current condition if elk were not reduced, but improvements would occur if elk were reduced to 600-800 or 200-400. The improvements would be gradual, taking at least 50 years even with 200-400 elk. Aspen were projected to decline under any scenario, even when elk were reduced to 200-400; however, aspen cover was stabilizing at the end of 50 years in all 3 scenarios and at slightly higher values with reductions than with no reductions. The declines would occur in the stands which are on the lowest portions of the core elk winter range, and tree aspen in some of these stands would likely die out. It is possible, however, that even if tree aspen die out, some of the clones could persist as shrub aspen, as has been observed in Yellowstone (e.g., Renkin and Despain 1996). Without elk reductions, willow cover would decline below current values and stabilize at a low value, but with elk reductions, willow cover would improve, much more so if elk were reduced to 200-400 than 600-800.

Fencing would have a large effect on willow and aspen cover. Within five years, currently suppressed willow would exhibit large increases in size and cover, as they did in the recent five-year exclosure experiments (Zeigenfuss et.al. 2002). Over the following 20 years of fencing, further increases would occur due to recruitment of new plants. If the fences are taken down after 25 years, willow cover would start to slowly decline with no elk reductions, would remain steady with reductions to 600-800, and would continue to increase with reductions to 200-400. Higher cover would be sustainable with fences because stands on the remaining well watered sites would achieve tall stature, and largely escape herbivory. Fencing would allow aspen cover to increase in all stands, due to the lack of herbivory on new sprouts, and on leaders of small trees. Some of these new trees would grow to a sufficient height to escape herbivory after the fences are removed. However, once the fences are removed, a slow decline would ensue, even if elk are reduced to 200-400. In stands on the core winter range, mature trees will gradually die due to limited longevity (100-125 years), and they will not be replaced by new recruitment due to elk and deer browsing. Stands which are not on the core winter range would continue to thrive, as shown by Suzuki et al. (1998), but overall mean cover on the winter range would decrease due to the loss of stands on the core winter range. Thus, although fencing of stands on the lowest portions of the winter range will achieve the objective of increasing aspen cover initially, it will not be a sustainable solution over the long-term, unless elk are also controlled to less than 200 animals.

Improving hydrological conditions would result in significant increases in willow cover if elk are reduced to 200-400 or 600-800 or willow are fenced. It would not improve willow cover if elk are not reduced, unless willow are fenced, because even with shallower water tables, the existing short willow would continue to be suppressed. Reducing elk to 600-800 or 200-400 would reduce herbivory to a sufficient degree to allow short willow on rewatered sites to withstand and eventually

escape herbivory. The rate of recovery would be exceedingly slow if elk are only reduced to 600-800 and willow are not fenced. If willow are fenced and sites are rewatered, willow cover would increase to high levels irrespective of whether there are elk reductions or not.

Hydrological conditions would presumably be improved by beaver introduction and management. Introducing beaver into a situation where there are no elk reductions would be unlikely to succeed, due to continued competition with elk for willow. Even if beaver survived, and if water conditions were improved, willow cover would not increase. Introducing beaver and reducing elk to <600 would appear to be a viable solution, but unless elk are reduced to about 200, the recovery would be very slow. Most of the simulations with fences assumed beaver would be able to get inside the fences. If beaver are excluded from the fenced areas, willow recovery rates would be faster (Figure 105). If beaver are allowed into fenced areas, the fenced areas will need to be large enough to at least support a single beaver colony over the long term. This could involve supporting a disturbance mosaic by beaver on willow within the fenced areas. If the fenced areas were large enough, beaver could probably be introduced at the outset of fencing. Smaller fenced areas may require a delay of beaver introduction for several years until existing willow escape into the tall form with new leaders and more edible bark. A final complication is the possibility that introduced beaver may increase above a predator-limited carrying capacity, due to the absence of wolves.

The simulations of hypothetical future scenarios with wolves present provide a basis for estimating elk numbers in a pre-settlement, fully restored ecosystem. With current hydrological conditions, the model indicated that wolves would reduce the park elk herd to 200-400. However, if hydrological conditions could be restored, perhaps by increasing beaver numbers, then wolves would maintain the park elk herd in a range of 400-600. The difference between projected elk numbers with and without improved hydrology is partly due to willow cover. Willow cover would increase, more so if hydrological conditions increase. The difference is also due to the increase in number of elk in the town herd with natural land cover, which then forms a larger alternate prey base for the wolves, reducing predation on the park herd. With wolves, aspen would still decline on the lowest portions of the winter range. The scenario which emerges of a fully restored ecosystem is one with beaver, increased willow cover, 400-600 elk wintering within the park, and reduced aspen cover on the lower, but not higher, elevation portions of the elk winter range.

Wolf Model Uncertainties

Sensitivity analyses of the wolf model parameters indicated that a broad range of predation effects are possible, from greater elk reductions than with the standard parameterization, to a "least effective" scenario where wolves have essentially no impact on elk population size. There are four principle variables that are uncertain, but have substantial effects on wolf predation. These are, the density of wolves, functional response, maximum predation rate, and degree of compensatory mortality. A parameter that had a large effect on the results was that which described the density of wolves in relationship to prey density. Wolf density reflects the territorial spacing of packs as well as pack size. Wide ranges of values have been observed for both components, however the standard values used here resulted in wolf densities that were comparable to those observed in Yellowstone

National Park and Idaho (USFWS 1999).

Five Yellowstone wolf packs have parts of their territories on the northern elk winter range, but the total size of the wolf pack territories is larger than the elk winter range. The combined territories total 2326 km^2 (USFWS 1999). Yet, the total winter range of the elk totals 1,400 km^2 (Coughenour and Singer 1996). There were 57 wolves in these packs in 1999, including 44 adults and 13 pups. A further question is how or whether to include pups in calculating. In 2000, there were 6 packs with 76 wolves, including 39 adults and 37 pups (USFWS 2000), a much higher ratio of pups to adults than in 1999. Using the 1999 numbers, and 2326 km^2, wolf density is 0.02 km^{-2}. However, calculated on the basis of 1,400 km^2, wolf density is 0.04 km^{-2}. In considering impacts on elk, it seems more logical to express wolf density in terms of number of wolves per area of elk range. In calculating wolf density for RMNP, I used the total area of the combined winter and summer elk ranges (388 km^2). The winter range includes 177 km^2, and the summer range 197 km^2. Fourteen wolves (a typical value in the RMNP simulations) on 388 km^2 is 0.04 km^{-2}. The assumption used in the model was that half of the wolves would be located on the winter range, so again the density is at about 0.04 km^{-2}.

The question of elk and wolf migratory behavior is also important because the effectiveness of predation depends on the extent of overlap of elk and wolf ranges. This was demonstrated by the sensitivity analysis to the assumption of what fraction of elk are in wolf ranges throughout the year. Wolves with territories on the winter range may or may not follow the elk onto their summer range. Possibly, wolf pack territories would span part of the winter and part of the summer range as was assumed here. In Yellowstone in 1999, there was one pack which spanned winter and summer ranges and two packs that were entirely on summer range of the northern elk herd. In 2000, there were two packs which spanned portions of winter and summer ranges and one pack located entirely on summer range. The Yellowstone system is considerably more expansive than the RMNP system. The distance between winter and summer ranges is larger, so it may be more difficult for a single pack territory to span portions of both ranges. In RMNP in contrast, the distance is small enough so that a single territory can span winter and summer ranges, perhaps making RMNP elk more vulnerable to wolves than in Yellowstone.

The parameter for maximum rate of predation (Fmax) had an expected impact on predator effectiveness. Fortunately, more is known about this value, and the parameterization used here was based on information from the wolves in Yellowstone. The model was relatively robust to the shape of the functional response (w_0), for which little information is known. Higher sensitivities were simulated for the age/sex composition of prey, and degree of compensatory mortality. The age/sex composition of prey was very important to predator effectiveness. With non-selective preference among age/sex classes, predation effectiveness was much reduced compared to the standard parameterization with preference for calves and old age classes. This is most likely due to an impact on recruitment through calf survival. With no prey selectivity, a much smaller fraction of calves will be preyed upon. Instead of 43% (USFWS 2000) to 54%(K. Murphy pers. comm.) of prey, calves would comprise only about 10-20% of prey with non-selective preference. Fortunately, the evidence for selectivity of calves in Yellowstone is straightforward. The uncertainty is higher for compensatory

mortality. As yet, there are no estimates of compensatory mortality in Yellowstone. However, half of the adult elk taken were older than nine years old (K. Murphy pers. comm.), and old cows do seem to be taken out of the population (USFWS 2001). These effects were taken into account in the age/sex preferences, however. Some fraction of predation may be compensatory, but it seems highly unlikely that it exceeds the 30% used as the standard value here.

Trophic Interactions

Wolves had significant effects on elk populations, and thus plants, soils and ecosystem dynamics. Using a set of parameters that was mid-range in terms of what is known about predation effectiveness, wolves reduced elk, which then altered vegetation structure and function. In the 1775-1911 simulations, wolves reduced elk 15-40%. Herbaceous cover and willow cover were higher than without wolves. During 1912-1948, wolves had a moderate effect on the elk population. Wolves reduced elk in the town subherd by approximately 10%. During 1912-1935, wolves reduced the park population by about 25-30%, but during 1940-1948, wolves reduced the park herd twofold. Wolves caused a 10-15% increase in upland grasses and a 20-25% increase in upland forbs; however, 5-10% of the upland grasslands were still grazed at 50-80% offtake. Willow cover at locations where water tables were not reduced was 20% higher with wolves than without wolves (Figure 69e vs. 74d). During 1949-1998, wolves could hold town elk to 1,000-1,700, and park elk to 300-500, and herbaceous cover increased. Wolf presence also led to an increase in willow cover (Figure 81c vs. 83e, 81b vs. 83d). Under the stochastic weather scenario, wolves held the park elk herd at 200 with current water tables and vegetation and at 500-600 with predisturbance water tables and vegetation, and willow cover increased. Additionally, in all simulations with wolves elk were in better nutritional condition than without wolves, and thus there were fewer starvation mortalities with wolves present. In general, wolves transformed the entire ecosystem from one with less plant cover and nutritionally stressed elk to one of more plant cover and a higher elk nutritional status.

The response of elk to wolf reintroduction in Yellowstone is highly relevant, since Yellowstone is the nearest analog to RMNP that we have. The effectiveness of wolves in controlling the elk population in Yellowstone is still unclear. The original modeling studies suggested wolves could reduce the elk population by anywhere from 15-25% (Boyce 1990), 10% with 75 wolves (Garcon et al 1990), 5-18% for 78 wolves and 11-30% with 100 wolves (Mack and Singer 1993), to 5-20% (Boyce and Gaillard 1992). A recent model assessment suggested a 20-30% reduction with 78 wolves (Singer et al. 2001b). Since reintroduction, Yellowstone elk counts were down markedly in 1997-1999. Elk were in the 18,000-19,000 range in the late 1980s through 1994 (Coughenour and Singer 1996, Yellowstone NP 1997). In 1995, 16,791 were counted, but following a severe winter (1996-1997) and high hunter harvest, elk declined to 11,000 in 1997. Wolves were introduced in 1995 and 1996, so could have played no role in that decline. In 2001, elk numbers were up again to over 14,000 (USFWS 2001). Thus, elk numbers are increasing despite wolves, and a substantial annual hunter harvest outside the park. Based on the similarity of current elk numbers to historical averages since 1976, it might appear that wolves are not having any noticeable effect on the elk population (USFWS 2001). However, because elk numbers are at 14,000 now with wolves, does not rule out the possibility that they would be significantly more abundant without wolves. There is really

no control treatment to compare with, i.e., no identical ecosystem without wolves.

Potential differences in the ratio of wolves to elk should be considered in comparing Yellowstone to RMNP. The Yellowstone elk herd is over 14,000, with 57-76 wolves, giving a ratio of 0.004-0.0054 wolves per elk. In RMNP, I simulated 14-20 wolves with approximately 2,000-3,000 elk, including the park and town subherds. This gives a higher range of ratios, of 0.0046-0.01 wolves per elk. Combined with the decreased spatial extensiveness of elk migration patterns RMNP relative to YNP discussed above, an greater impact of wolves on elk could be expected in RMNP than in YNP.

Other predators could have increased the total predation impact on elk in pre-settlement times. Grizzly bears are significant predators on elk calves (Singer et al. 1997), and were present in Colorado even in historical times. Mountain lions could also have been more abundant than they are today. Since grizzly bears and mountain lions were not included in the model scenarios, it could be argued that total predation was even higher than that simulated here. However, since bears are omnivorous, and are not active in winter, their effects on elk would be reduced accordingly. Little is known about the suitability of RMNP as grizzly bear habitat, or of competitive interactions among bears and wolves.

The model simulated an interesting feedback loop in which wolves reduced elk, which then allowed plants to increase, which then supported more elk as well as higher vegetation production. With no wolves, elk reduced their own carrying capacity by reducing herbaceous vegetation cover, so that by the end of the simulation, elk numbers were, ironically, as low as they would have been under wolf predation. A critical mechanism for this shift was that wolves affected the ratio of vegetation productivity to vegetation consumption so as to increase vegetation cover. With higher vegetation cover and productivity, the fractional offtake and thus grazing impact of a given number of elk is less than with lower vegetation cover and productivity. At this point of increased vegetation productivity, the elk population could increase further, but was prevented from doing so by wolf predation. Thus, at the tri-trophic equilibrium amongst plants, elk, and wolves, vegetation cover was greater than at the bi-trophic equilibrium between plants and elk. The higher plant cover would likely have cascading effects on other species in the ecosystem.

Simulations showed that the number of elk that can be supported in the presence of predators is dependent on forage availability. Forage availability is in turn affected by forage production and snow cover in the short-term, and by herbaceous vegetation development over the long-term. In the simulation of an undisturbed ecosystem, wolves reduced the park elk herd to 300-400 through 1949-1998. This was fewer elk than in comparable runs for 1775-1911 and 1910-1949. The lower number of elk was not due to differences in initial vegetation conditions, because the undisturbed water table and vegetation conditions were used in all cases. Willow cover increased to high values in all three simulations. Part of the explanation is that the 1775-1911 simulation was much longer, allowing herbaceous vegetation to increase to a higher level than could be achieved in the 1949-1998 run. During the first 50 years of the 1775-1911 run, wolves held elk to 300-400. It was only after 75 or more years of herbaceous expansion that an elk population of 600-800 could be supported. The

increase in elk to 800-1000 during the 1910-1949 scenarios was likely due to climate. There were a number of mild winters with little snowpack in the mid-late 1920's (Figure 64) which increased forage availability.

In addition to the numerical impact of predation, wolves could have affected elk spatial distributions, and local densities. There is increasing evidence that herbivores avoid areas frequented by predators (Mech 1977, Dekker et al. 1996, Schmitz et al. 1997, White et al. 1998, 2000, Ripple and Larson 2000, White and Feller 2001). There is evidence from Yellowstone that elk avoidance of wolf concentration areas may result in decreased elk herbivory and increased growth of aspen (Ripple and Larson 2000) and willow (F. Singer, pers. comm) at some locations on the northern winter range.

The model showed that the situation in RMNP is more complex than the simple plant-herbivore equilibrium predicted by natural regulation theory. While the elk-grassland subsystem may reach an equilibrium, that equilibrium would probably not have developed in the presence of wolves and other predators. Instead, a different dynamic equilibrium would be expected, involving interactions among three trophic levels. It would not be totally accurate to refer to this as a predator-limited number of elk, because the productivity of the forage base also has an influence. In a more productive system, there would be more herbivores and more predators alike, up until a limit on predator and possible herbivore numbers imposed by other factors aside from food, such as behavioral spacing. Because the tri-trophic equilibrium involves fewer elk than the bi-trophic equilibrium, there could be ramifications for plant species which are not necessarily limiting the elk population in a bi-trophic system, in particular aspen and willow.

Tri Trophic system

Aboriginal Hunting

Predation by humans prior to Euro-American settlement could have had significant additional impacts on elk (Kay 1990, 1994). This predation was not considered in the model experiments, primarily because there appeared to be an insufficient amount of quantitative information on human density and hunting behavior to construct and parameterize such a model. Furthermore, human densities and hunting practices have changed over the millennia, from spears, to adalades, to bows and arrows, to horseback-based bow and arrow, and finally to guns. Big game drive systems were used for over 4,000 years in RMNP (Benedict 1992). Native Americans also used domesticated dogs to hunt big game (Kay 1990). Thus, it would be difficult to make a general statement about the effects of aboriginal hunting on elk populations. Recently, a modeling study was conducted of the potential impact of aboriginal hunting on large mammals in North America (Alroy 2001). The model simulated a scenario of human population growth and dispersal and game consumption following their arrival in North America which was consistent with observed values. In this scenario, the model correctly predicted the extinction or survival of 32 out of 41 prey species. In fact, 30 out of 41 of the species went extinct within 1,200 years of the arrival of humans on the continent. The model assumed that humans would obtain as many calories from mammal hunting as possible, at a rate which would support observed human population growth rates. For a broad-scale analysis, such a simplifying assumption is reasonable. However, application at a finer scale would require estimates of local human population densities, for example, in the region of RMNP, along with their presumed hunting

success rates using different technologies.

Kay (1990) synthesized data from numerous archeological sites in the Great Basin and Northwestern U.S. Elk bone fragments comprised only 3% of the total ungulate remains, while mule deer and bighorn sheep fragments comprised 56% and 23% respectively. This and other evidence suggested that big game comprised a relatively small fraction of Native American diets in the intermountain region. Based on this information, Kay concluded that aboriginals reduced ungulate populations to low levels, and changed the composition of the ungulate community to few elk compared to deer and bighorn sheep (Kay 1990, 1994). However, there is actually no way to infer ungulate population sizes from the archeological indices that Kay used, due to a large number of uncertainties including sampling error and taphonomic problems (Canon 1992). A discussion about what can or cannot be inferred from the archeological record is beyond the scope of this report, but a conclusion that elk were rare in pre-settlement times seems inconsistent with a considerable amount of other evidence. Historical accounts of early explorers and settlers are filled with accounts of seeing herds, groups, and isolated elk, as well as large concentrations of cast antlers in Yellowstone and elsewhere in the northern Rockies (Houston 1982, Schullery and Whittlesley 1992). Large elk herds were seen by the first settlers in the Estes Valley (Sprague 1922, Estes 1939). Game drive systems used 4,000-220 years ago were most probably used to hunt elk rather than bighorn sheep, bison, or mule deer (Benedict 1992). These other types of evidence cannot be used to determine elk numbers, but they raise doubts about the hypothesis that elk were rare. Although elk may not have been rare, aboriginal hunters were nevertheless effective (Kay 1990, Cannon 1992, Alroy 2001), and they could certainly have contributed to the effects of other predators in reducing elk numbers and altering their spatial distributions.

Lack of Bison

Bison were not uncommon in the Rocky Mountains (Fryxell 1928, Meagher 1973, Canon 1992). Two elderly Native Americans stated in 1913 that the Arapahoe regarded Estes Park as their own game preserve (Fryxell 1928). The interviewer recounted that "sometimes they (Native American hunters) would come on little enclosed parks with so many buffalo that the whole bottom of the valley would be dark with them." The Arapahoe left the region to follow the buffalo north where white man drove them to, probably about 40 years before settlement. Many bison skulls were found in RMNP, and both bison and elk remains were found at an old hunting camp in Tuxedo Park (Fryxell 1928).

The presence of bison prior to settlement has important implications both for the number of elk, and their impacts on vegetation. Elk and bison have considerable dietary and habitat overlaps. Although elk are mixed feeders, herbaceous vegetation comprises a majority of their diets. Bison nearly exclusively feed on herbaceous plants. In one study, bison and elk overlapped in habitats extensively in winter but less so in summer, while food habits differed in winter but overlapped strongly in summer (Telfer and Cairns 1979). Therefore, if bison were common, they could have been significant competitors with elk. In particular, they could have reduced herbaceous biomass on elk winter ranges, particularly if the bison grazed the elk winter ranges in summer, as they are doing now

in Yellowstone (Taper and Meagher 2001). However, since elk were most likely held below food-limited carrying capacity by predators, the competitive effect of bison may have been reduced. To the extent that bison did displace elk, they would also have reduced elk browsing levels on woody vegetation. Conceivably, the aggregate dietary composition of the ungulate community would have consisted of less woody and more herbaceous vegetation. Bison were one of the dominant large herbivores in low elevation areas of Banff and Jasper National Parks in Alberta (White et al. 1998). Thus, both Kay et al. (1994) and White et al. (1998) recommended restoring bison to reduce elk numbers and elk impacts on woody vegetation.

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT AND POLICY

Management of ungulates in U.S. National Parks is directed by the enabling legislation which states that National Parks should preserve vignettes of pre-settlement, or "natural" ecosystems (Wagner et al. 1995). This goal is an ideal, and is clearly not attainable in every park. Many if not most parks are too small to support their pre-settlement complement of predators and other fauna, and are affected by the movements of animals, exotic plants, pollutants, and other materials across park boundaries. Simple preservation and protection may therefore be insufficient to preserve the desired natural vignettes. Some have interpreted the mandate to justify the use of active management, to substitute for missing ecological components, or to otherwise make the system function as close to its pre-settlement configuration as possible (Leopold et al. 1963, Wagner et al. 1995). Thus, if predators kept elk populations lower than food-limited carrying capacity in pre-settlement ecosystems, and predators are lacking, then there should be management intervention to emulate the impacts of the missing predators. In this view, managers must conserve the vegetation structure that was a product of pre-settlement climate, water table conditions, and ungulate herbivory. In Yellowstone and RMNP, this vegetation structure is thought to be characterized by greater abundances of aspen and willow than are present at the food limited carrying capacities of their elk populations. The model-based assessment here also supports the idea that in RMNP predators kept elk numbers lower than at food limited carrying capacity, which lessened browsing impacts on willow and aspen.

Another view places more emphasis on the conservation of natural processes, and recognizes that ecosystems are dynamic, not static entities (Houston 1981, McNaughton 1996, Boyce 1998, Sinclair 1998, Huff and Varley 1999). National Park Service Management Policies (NPS 1988,2001) state that park ecosystems should represent a natural environment that has been allowed to evolve through natural processes and they should rely upon natural processes to control native species to the greatest extent practicable, except when human activities result in unnatural herbivore concentrations (Huff and Varley 1999). Natural processes are general characteristics of ecosystems described in terms of processes. These are more fundamental than ecosystem characteristics described in terms of states, since processes give rise to states. That an ecosystem can function independently without human intervention while conserving the indigenous floral and faunal species, is thought to be more fundamental to its naturalness, than whether the vegetation does or does not look exactly like it did prior to settlement. Thus, there is a fundamental policy discord, between a strict reading of the NPS Organic Act, and what many believe is a more modern and scientifically informed view about ecosystem dynamics in nature.

Current ecological theory recognizes that ecosystems can exist in more than one stable-state, depending on external perturbations which force the system from one state to another (Holling 1973, Walker et al. 1981, Coughenour and Singer 1991). The RMNP winter range is not in the same stable-state as it was prior to settlement. It is in an alternate stable-state, or at least on a trajectory to an alternate stable-state, having been pushed there by numerous perturbations involving human activities and livestock since before the park was established. If left alone, it will likely continue on this trajectory. It is also recognized that these non-linear systems may exhibit hysteresis, i.e., the return

path to a stable-state may be different from the exact opposite of the path which led to an alternate stable-state. This means for example, that if the absence of predators or an abundance of elk has led to a new stable state, it may not be sufficient to simply reintroduce predators or reduce elk to their former abundance to restore the system to its original configuration. It may be necessary, instead, to reduce elk to much less than their former abundance in order to achieve vegetation restoration.

There is more than a single vegetation structure that might support a sustainable grazing ecosystem on the RMNP elk range. For example, range managers have agreed that from their point of view, the primary resource of concern to long-term ecosystem viability is the soil resource rather than the successional state of the vegetation (Task Group on Unity in Concepts and Terminology Committee Members 1995). The composition of an ungrazed climax plant community is no longer considered to be a realistic or ideal endpoint for a grazing ecosystem. The Task Group recognized that a Desired Plant Community (DPC) must be selected based primarily on soil conservation, and secondarily on other management objectives for that site. It is conceivable that the RMNP elk range could function as a sustainable grazing ecosystem, without any control of elk, and the vegetation would be different from that present prior to settlement. For example, since there is little evidence for decreased soil fertility (Binkley et al. 2002, Schoenecker et al. 2002), the RMNP grazing ecosystem might be judged to be functioning sustainably. The ecosystem model indicated that if elk were left to self-regulate at food limited carrying capacity, the vegetation would probably look different than it did prior to settlement, but it might still be a sustainable grazing system. There would be fewer willow and a higher proportion of the willow would be short-statured. There would likely be more regeneration of aspen on the upper, but not lower portions of the winter range. Basal cover would be higher in some grassland areas, and more standing dead shoots would accumulate. Although the effects of elk browsing on beaver was not addressed in the model, the predicted reduction in willow cover and current annual growth could have negative consequences to beaver, since willow appears to be their primary winter food supply in RMNP. Other studies have shown negative effects on ptarmigan on the elk summer range (Melcher 1992). Similarly, there could be fewer birds and other species which typically inhabit willow and aspen stands (e.g., Berger et al. 2001). If the aspen, willow, beaver, or other indigenous populations are driven to extinction within the park, or to a level that puts them at risk of extinction, then by the Organic Act and the 2001 NPS Policy, elk should be reduced. However, if aspen, willow, beaver, or other wildlife numbers are simply reduced to nonthreatening levels in a thriving, minimally intervened ecosystem, then perhaps RMNP could still be considered to be a naturally functioning ecosystem that harbors viable populations of all of its original species.

Ultimately the choice of elk management tactics reduces to a decision between trying to reconstruct and then maintain the vegetation structure which is believed to have been characteristic of the pre-settlement ecosystem, or allowing ecosystem processes to unfold with a minimal amount of human intervention so long as indigenous species are conserved. Would the reconstructed and intensively managed ecosystem be intrinsically organic, or more of an artifact? Which would be more natural? This question cannot be answered here. The model provided insight into how a pre-settlement ecosystem might have looked and functioned in comparison to the current ecosystem, and into what it might require to reconstruct and maintain a vegetation structure similar to that which

existed prior to settlement. But it did not consider whether or not such an ecosystem would be natural, most appropriate to NPS policies, or desirable to the public.

The model prediction of reduced elk numbers in pre-settlement times is based on the simulated effects of predation. The model experiments did indicate that there was some uncertainty in the effectiveness of predation, due to uncertainty in certain parameter values. Therefore, there is a risk that the model could be wrong. This aspect of the model deserves further attention, and continued input from what is being learned about the impacts of wolves on elk in Yellowstone and elsewhere.

Should it be decided that a pre-settlement vegetation structure is desirable, in contrast to a focus on preserving unimpeded but sustainable processes, then the model-based assessment suggested that a number of actions will be required. In order to reconstruct pre-settlement vegetation structure, the model predicts the park elk herd would need to be reduced to approximately 600-800, and the town herd would need to be reduced to 1,000-1,500 to emulate the effects of wolves if vegetation were also in the same state as in pre-settlement times. However, the vegetation is probably not as productive as it was in pre-settlement times, so even lower numbers of elk might be required. With current vegetation and wolves, the model suggested that there would only be 250-300 elk in the park population and 1,000-1,200 in the town population. Although the effects of wolves on elk spatial distributions were not simulated, these should be considered. Fences or hazing may or may not be judged to be acceptable practices in the park. However, the model indicated that fencing would greatly accelerate willow and aspen growth. The possibility should be considered that fences might artificially protect certain aspen stands on the core winter range which would not be present even with reduced elk numbers. Reducing elk or changing elk distributions are unlikely to completely restore willow unless it also elicits a positive response by beaver, and their effects on hydrology. The model did not predict how beaver numbers would respond to decreased elk numbers, but it did indicate that more areas will need to be flooded by beaver dams or their surrogates to support increased willow.

The modeling exercises, as well as data, have indicated that sport hunting outside the park, in the National Forest, have not controlled the elk population within the Estes Valley. The park and town components of the Estes Valley winter range have ample forage bases which have supported elk population growth towards food-limited carrying capacity. Although elk are free to move in and out of the park and town winter ranges into the National Forest, they show fidelity to these two refugia (Larkins 1997, Lubow et al. 2002). In order to decrease the size of the elk population in the park and town ranges, control actions would need to be taken in those areas, rather than in the National Forest. Whether or not such actions would be consistent with land management objectives that have presumably been developed through a democratic process, or with other societal values, is beyond the scope of this study.

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