

**Plant Biomass and Primary Production on
Bison and Elk Ranges in Yellowstone National Park -
Data Synthesis and Ecosystem Modeling**

**Part 1 - Final Report to
U.S. Geological Survey
Biological Resources Division
Bozeman, MT**

**Project:
Spatial-Dynamic Modeling of Bison Carrying Capacity
in the Greater Yellowstone Ecosystem:
A Synthesis of Bison Movements, Population
Dynamics, and Interactions with Vegetation**

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December 2005

INTRODUCTION

Understanding and predicting the spatial heterogeneity of primary production on complex landscapes remains a challenge, despite considerable amounts of plot and site level data that have been collected, and the more recent development of spatial information tools such as GIS and remote sensing. Spatial heterogeneity of primary production at the landscape scale is central to ecosystem functioning, it can have significant impacts on the dynamics of primary and secondary consumers, and it likely contributes to biodiversity and biocomplexity. It is well known that primary production is controlled by light, water, temperature, and nutrients, and countless studies have shown that spatial variations in vegetation types are the result of individual species responses to environmental gradients and mosaics. Spatial variations in climate and soils form the basis for spatial and temporal patterns of primary production across landscapes. Thus, scaling up plot level measurements of primary production involves combining understanding of plant responses to environmental factors with information about the distribution of those factors across the landscape.

Yellowstone National Park is located upon a physically diverse landscape with abundant large herbivores, particularly elk (*Cervus elaphus*) and bison (*Bison bison*). A considerable amount of research has been conducted on herbaceous (Barmore 2003, Houston 1982, Coughenour 1991, Frank and McNaughton 1992, Merrill et al. 1993, Singer 1995, Singer and Harter 1996, Wallace et al. 1995, Tracy 1996, Dawes 1998, Olnecki 2003) and shrubby (Barmore 2003, Houston 1982, Chadde and Kay 1991, Norland and Reardon 1996, Singer and Renkin 1995, Singer 1996) vegetation in various portions of Yellowstone Park. However, syntheses of this information to provide a comprehensive and complete picture of primary production over the entire landscape, have to date, been rudimentary. For example, a landscape carrying capacity model (LCCM) was developed using existing information on vegetation productivity in various habitats and modeled snow distributions as a basis for estimating elk carrying capacity (Coughenour 1994, Coughenour and Singer 1996, Wallace et al. 2004). Interannual production was modified by a simple equation relating annual or seasonal precipitation amounts to production. Turner et al. (1993) developed a landscape scale model of elk foraging in response to forage and snow distribution. Coughenour and Singer (1996) synthesized information from several early and more recent plant production studies. More recently, Hansen et al. (2002) sampled herbaceous, shrub, and tree production in a number of habitats outside the western boundary of the park, and scaled up the results to the landscape based upon the distributions of elevation and vegetation types.

There is a need to estimate landscape scale primary production in order to estimate forage-based carrying capacity for Yellowstone's bison. In 1980's and 1990's bison populations grew, and they expanded their ranges (Meagher 1989, Taper et al. 2000, Meagher et al. 2003). They then began to move outside of park boundaries in significant numbers. Since they carry

brucellosis, they have had to either be hazed back into the park, or slaughtered. In order to reduce the risk of brucellosis transmission, the current bison management plan calls for the removal of all out-migrating bison when the total population size is above 3,000. “This is the number above which an NAS (1998) report indicated bison are most likely to respond to heavy snow or ice by attempting to migrate to the lower elevation lands outside the park in the western and northern boundary areas” (NPS 2000). Importantly, it is not based upon an estimate of food-limited carrying capacity despite the likelihood that out-migrations are a combined outcome of increased competition for forage and the negative effects of snow on forage availability (Cheville et al. 1998). Improved estimates of forage availability are required to determine the degree to which out-migrations are a result of food limitation inside the park.

The general objective of this study is to determine how spatial and temporal variations in climate and physical habitats explain distributions of herbaceous primary production and biomass across a spatially extensive and heterogeneous landscape. More specifically, the objective is to calculate and predict herbaceous and shrub layer primary productivities as a basis for estimating forage availability for bison and elk in Yellowstone National Park. Available data on plant biomass production are synthesized and used to develop a data-driven model of biomass distribution across the landscape. Spatial ecosystem modeling is then used to simulate the distribution of biomass and production over time and space. In contrast to statistical modeling, ecosystem modeling predicts primary production and plant-soil interactions in terms of first principles and underlying processes such as photosynthesis and carbon allocation in the plant, turnover of plant materials to soils, decomposition and nutrient recycling, plant-water relationships, and plant responses to herbivory. An earlier effort to apply a landscape scale ecosystem simulation model to Yellowstone was promising, but limited (Coughenour and Singer 1996, Wallace et al. 2004). The results of this study are intended to be used in assessments of forage-limited and combined forage and predator-limited bison and elk carrying capacities.

STUDY AREA

The study area includes much of Yellowstone National Park, as well as significant areas outside of the park to the north and west (Figure 1). The study area boundary was drawn to include the combined winter and summer ranges of bison and elk. The ranges are further discussed in Part 3 of this report (Coughenour 2005b). Most of the outermost boundary of the study areas is defined by the approximate summer range of the northern elk herd (Houston 1982). The extrusion outside the boundary on the west side includes the western portion of the bison winter range.

The landscape can be characterized as a high plateau in the central and southwestern portions of the park, surrounded by rugged mountainous topography to the north and west (Figure 2). Heterogeneity in the Yellowstone landscape is an outcome of varied geological processes. Volcanic activity during the Eocene produced mountains in the northern and eastern portions of the park. This volcanic activity produced andesitic substrates. Volcanic activity

during the Quaternary led to the formation of a very large caldera in the central portion of the park. Ash and lava flows from this period were rhyolitic.

Elevations of higher peaks within the park range up to approximately 3000 m, with higher peaks outside the park to the northeast (Figure 2). Much of the central portion of the park lies at 2400-2700 m elevation. Lower elevation areas occur in the northern valley complex containing the upper Yellowstone and Lamar Rivers. This large valley begins in the northeast at elevations of 2000-2400m, but elevations gradually decline to 1500-1800 m in the northwest. Another low elevation area straddles the western boundary. During the last ice age, a large glacier filled the Lamar and upper Yellowstone river valleys, filling them with deep layers of till and large granitic boulders.

Hydrologically, a major divide runs through the central portion of the park. Northern and eastern portions drain into the Yellowstone River watershed. Yellowstone Lake occupies a low basin in the southeast (Figure 2), and is fed by the Yellowstone River coming in from higher elevations to the south and east. The Yellowstone then flows north out of Lake Yellowstone, after receiving added water from the central and southeastern portions of the park. The western side of the park drains into the Madison River, which then flows out through the low-lying area on the western boundary. Southern portions of the park drain southwards into two smaller lakes (Shoshone and Lewis), and out of the park via the Lewis River and the Snake River.

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 altitudinal gradient in snowfall and snowpack.

Precipitation is greatest in the southwest portion of the park (Figure 3), and at high elevations elsewhere. Precipitation generally increases with elevation. Prevailing winds are from the west. The most important source of moisture during winter originates in the Pacific. As the Pacific air masses move from west to east, successive mountain ranges experience orographic precipitation. This results in increased moisture on the western slopes, while the east slopes remain drier. As a result of these differences in precipitation and seasonal differences in the importance of Pacific air masses, the east and west slopes also have different seasonal precipitation patterns (Despain 1987, 1990). The study area is primarily located on the eastern side of the divide, however.

At Mammoth (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 Lake Yellowstone (elevation 2657 m), maximum and minimum 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 Canyon (elevation 2,526 m), maximum and minimum 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 West Entrance (elevation 3,150 m) maximum and minimum temperatures range from -8.8 and -3.1° C in January to 19.7 and 1.0° C in July.

Annual variability in precipitation is relatively low at Mammoth, with a standard deviation that is 22% of the mean. At Lake Yellowstone and Canyon the ratios of standard deviations to means are only slightly less, at 19% and 20% respectively. The difference between wettest and driest years at Mammoth is 85% of the mean, while at Lake Yellowstone it is 87 - 88% of the mean.

MODEL DESCRIPTION

Overall Model Structure

SAVANNA is a spatially explicit, process-oriented model of grassland, shrubland, savanna, and forested ecosystems. 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 developed and used for the Pryor Mountain Wild Horse Range (Coughenour 2000), northern Colorado (Weisberg et al. 2002), northern Australia (Ludwig et al. 2002, Leidloff et al. 2001), South Africa (Kiker 1998), Tanzania (Boone et al. 2001), and Inner Mongolia (Christensen 2001). A more developed Version 4 (f) was used for Rocky Mountain National Park (Coughenour 2000, Pienetti 1999, Weisberg and Coughenour 2003). Here, version 5a is used. SAVANNA is normally used to simulate ecosystems at landscape through regional spatial scales over 5-100 year periods. The model is comprised 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, predation, and predator population dynamics submodels (Figure 4A). The time-step of the model is one week.

SAVANNA has a hierarchical spatial structure (Figure 4B). 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.

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

covers are simulated variables, facet cover is a dynamic outcome of woody plant 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 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, linear regressions are performed between precipitation and elevation using data from all weather stations in each spatial precipitation domain. A study area may contain more than one precipitation domain if it is likely that precipitation responds differently to elevation in each domain. 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 grid-cell. Temperature for each grid-cell 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 randomly sampling from the weather files. Each simulated 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 and Longwave Radiation

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) and Spitters et al. (1986). Cloud cover is estimated from monthly precipitation and water vapor content (Nikolov and Zeller 1992). The total and mean daily global radiation on a horizontal surface is computed by dividing the day into two-hour periods. For each period, the fraction of direct and diffuse radiation is computed based upon cloud cover and the methods described by Spitters et al. (1986).

Incident solar radiation is corrected for slope and aspect using the tilt factor method described by Nikolov and Zeller (1992). Total radiation is broken into direct beam and diffuse. The daylight hours are divided into five periods. For each period, the solar declination and hour angle are computed and used to calculate the incident angle of direct beam solar radiation on the slope. The tilt factor for diffuse only depends upon slope. The mean tilt factor for the day is applied to the daily radiation calculated for a flat surface.

Longwave radiation is computed by considering clear sky and cloudy sky conditions. An effective sky temperature is calculated for clear sky and cloudy sky. Net longwave radiation is then computed by subtracting surface emissivity. Net radiation is computed as absorbed shortwave plus net longwave radiation. Absorbed shortwave depends upon surface albedo.

Snow Submodel

The snow submodel adds precipitation water to the snowpack when air temperature is below freezing. Melting during night and day are modeled separately. The rate of snowmelt is proportional to the positive difference between air temperature and 0° C at night and -1° C in the day. The fraction of melt due to short vs. longwave radiation is calculated based upon incoming short and longwave radiation and emissivities of the surface. The fraction is used to correct snow melt rate for differences in incoming shortwave radiation due to slope and aspect. Water is also lost from the snowpack through sublimation, based upon potential evapotranspiration and the ratio of latent heat of vaporization to that of sublimation.

A map of geothermally warmed ground is used to accelerate snow melt in such areas. The map may contain different classes of warming, and for each, a soil temperature is specified. Warming may due to an influx of geothermally warmed groundwater or surficial (river) water is also considered. Thus, the geothermal map also includes reaches of thermally warmed streams. Snow melt is then driven by the maximum of soil surface temperature or air temperature.

The weekly time step of the model and weather input data, do not permit process-based predictions of snow crusting events, which result from daily and diurnal patterns of precipitation and temperature. Instead, snow crusting events are prescribed to occur on certain dates based upon historical information. In stochastic weather runs, snow crusting occurs based upon a monthly probability. The probability may be modified by temperature - for example it may be unlikely for a crust to form if weekly temperature is quite high. Between 4 °C and 16°C it is assumed that the probability of crusting declines to 0. Once a crust forms, it is assumed to remain on or in the snow pack until the snow pack completely melts.

Water Budget

The water budget at each site is calculated from precipitation, interception, runoff, runoff, infiltration, deep drainage, bare soil evaporation, and transpiration. Incoming precipitation is partitioned between snow and rain depending upon air temperature. Rain interception amounts (mm) are calculated based upon litter biomass, herbaceous biomass of each herbaceous plant type, and leaf area indices (LAI) of each woody plant type. Fraction of snow intercepted by woody plants increases in direct proportion to LAI. Snowmelt water is treated the same as liquid precipitation with regards to infiltration and runoff. Bare soil evaporation is simulated using the Ritchie (1972) model (Wight and Skiles 1987). Evaporation also increases under low plant and litter cover. The curve number method of the USDA Soil Conservation Service (now the Natural Resource 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. A higher runoff curve number is specified for fair range condition.

Infiltrated 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 amount draining out of the lowest layer is considered to be deep drainage. Baseflow 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 stream flow patterns. Surface runoff, computed as described above, also flows into the stream. If the landscape redistribution function is being used, only runoff from the lowest elevation band flows into the stream. The output is total streamflow volume for that watershed over time. A physically-based approach to modeling ground water distribution and water tables is beyond the scope of this model. Instead, water table depth is empirically specified by month for each soil type or vegetation/habitat type where the ground water is shallow enough for plant water utilization.

Microclimate and Light Penetration

The microclimate submodel simulates wind speed profiles and aerodynamic resistances to water vapor diffusion. These depend upon canopy height, and reference height wind speed.

Potential evapotranspiration (PET) and transpiration are calculated using the Penman-Monteith formula (Monteith 1973). PET is derived using Penman-Monteith with zero stomatal resistance. Transpiration is calculated from canopy-scale stomatal conductance. PET and transpiration are affected by radiation, temperature, humidity, and wind speed.

The light penetration 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 depends upon leaf area index and a light extinction coefficient. The model tracks the relative heights of woody plants in different age classes, such that small shrubs and trees are more shaded than large shrubs and trees.

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.

Potential net photosynthesis is calculated as

$$P_{sl} = PAR / \sqrt{1 + (\alpha \times PAR / P_{smx})^2}$$

$$P_s = P_{sl} \times E_{fwp}(SWC) \times E_{ftp}(T_{day}) \times E_{fnp}(P_{nb})$$

where P_{smx} is maximum net photosynthesis rate, PAR is photosynthetically active radiation, α is the initial slope of the light response curve, and P_{sl} 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 E_{fnp} describes how P_s decreases as plant nitrogen concentration (P_{nb}) decreases. The 0-1 function E_{fwp} reduces P_s due to water stress. SWC is volumetric soil water content, weighted by root distribution in the three layers. E_{ftp} 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 (P_s) and humidity (H) increase, and as atmospheric CO_2 (C) decreases.

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

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 among layers. 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 thus depends upon transpiration rate, and the proportions of roots and water in that layer.

Photosynthate is allocated between roots and shoots to preserve a functional balance in herbaceous plants, and allometric relationships in woody plants. Phenology affects shoot:root partitioning, with an increased fraction being diverted to roots in later phenophases. Allocation to roots is influenced by nutrient and water availability, with slightly more allocation to roots when soil resources are limiting. In woody plants, allocation varies with plant size to preserve the proper allometric relationships. Herbaceous biomass is allocated to leaves, stems and roots. Woody plants allocate to leaves, fine branch, coarse branch, fine root, and coarse root. The allocation to various tissues in woody plants allometrically depends upon plant size..

Plants maintain a pool of labile carbon, largely consisting of carbohydrate carbon, but also including the carbon in metabolic proteins, amino acids, and other labile compounds. Early regrowth in the spring or following grazing is supported by this pool until growth demands can be met by photosynthesis. The labile carbon pool is regulated in relationship to phenology. The pool is replenished towards the end of the growing season to ensure plants have a reserve to draw upon when they break dormancy the following spring. Conversely, during early regrowth, the labile pool can be drawn down to minimal levels.

Respiration is separated into growth and maintenance components. Maintenance respiration is proportional to nitrogen concentration (Ryan 1991), and it increases with temperature with a Q10 of 2 (every 10 degrees it doubles). Maintenance respiration cannot exceed current photosynthate in herbaceous plants, and 50% of current photosynthate in woody plants. Growth respiration is assumed to be 25% of the biomass carbon that is synthesized

Plant tissues senesce at rates affected by water stress, temperature, and phenology. Tissues turn over at a nominal rate that reflects maximum longevity. 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".

Woody Plant Population Dynamics

The woody plant population model represents six age, size, or age/size classes of plants. The recommended approach, and the one taken here, is to simulate age classes, and allow plant

size to vary within each age class. Alternatively, size classes may be simulated where plants are promoted irrespective of age, or plants may be promoted to subsequent age/size classes if they reach a certain age, and they are also of a certain size.

Establishment rate is affected by water, 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 only occurs in gaps or openings resulting from tree death.

Plant mortality occurs at age or size-specific nominal rates related to characteristic plant life spans and survivorship curves. Water stress mortality is added to the nominal mortality. Sapling mortality (age/size class 1) can be caused by cold temperatures. Slow growth, expressed as mm of diameter increment per unit time, is a general indicator of stress that can be used to calculate a mortality rate. Self-thinning can be simulated using slow growth mortality, since as trees become larger they increasingly compete for limited resources (water, nitrogen, light) thus reducing individual tree growth rate.

Browsing and fire both result in losses of stem and branch biomass, thus reducing plant size, or reducing the rate of increase in plant size. Fire or heavy browsing can kill large branches, as well as the entire aboveground structure, while leaving the plant alive belowground. Heavy browsing of plant tissues, particularly stems and current annual growth, may contribute to plant mortality due to associated stresses of loss of meristems, branch breaking, and debarking. This source of plant mortality is expressed as a function of the fraction of the shoot biomass or current annual growth that is eaten. Separate rates are given for saplings (first age class) and for mature (subsequent age class) plants. Seedlings of woody plants are usually assumed to be more susceptible to browsing than older plants.

Herbaceous Plant Population Dynamics

A dynamic index of basal cover is simulated, measured in units of g m^{-2} of maximum shoot biomass. The logic of this is that as basal cover increases so does the maximum shoot biomass because shoots reach a maximum size, and basal cover is determined by the number of shoots. Maximum shoot biomass is a measurement that is readily understandable. Vegetative (asexual) reproduction is simulated by adding to maximum shoot biomass. Maximum shoot biomass increases when root biomass becomes large relative to potential shoot biomass. The maximum shoot biomass decreases when root biomass is low relative to maximum shoot biomass. Shoot biomass production in a given year cannot exceed the maximum shoot biomass. In this way, stress due to climate or overgrazing may reduce root biomass relative to potential shoot biomass. This causes a decrease in maximum shoot biomass, and thus productive potential. Under good growing conditions roots increase, and the maximum biomass and thus productive potential recovers. This simulates time-lags of vegetation recovery due to constraints on the rate

of vegetative reproduction.

An exogenous seed rain is assumed to replenish 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 basis is expressed in the units of grams of shoot biomass per m^2 . These basis values of g m^{-2} shoot biomass are then multiplied by the exogenous seed-based reproduction rates (grams of new potential shoot biomass produced per gram of basis shoot biomass, $\text{g g}^{-1} \text{yr}^{-1}$) to derive a rate in $\text{g m}^{-2} \text{yr}^{-1}$ of new potential shoot biomass. Similarly, an endogenous seed-based reproduction rate is modeled by multiplying an endogenous reproduction rate ($\text{g g}^{-1} \text{yr}^{-1}$) by the current potential shoot biomass (g m^{-2}) to give $\text{g m}^{-2} \text{yr}^{-1}$ of new potential shoot biomass.

Litter Decomposition, Nitrogen Cycling, and Soil Organic Matter Dynamics

A decomposition and nitrogen cycling submodel simulates the breakdown of dead plant materials and animal feces and urine, microbial respiration, nitrogen mineralization, 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 components, 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. A small fraction of N mineralization is assumed to be denitrified and lost to the atmosphere. 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 and nitrate).

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 volatilization is assumed to be 20% of urine N. 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 is necessary to support observed levels of plant growth and organic matter accumulation in such habitats. This N likely is transported into the system as N dissolved in ground or stream water. The N would be assumed to originate from precipitation, and leachate from upstream soils.

Soil carbon and nitrogen are initialized by providing values for %C and %N (weight) for the top 20cm. These are converted to gC/m² and gN m⁻² using soil bulk density. The data may be tied to habitat types on the vegetation input map, or to a map of soil fertility classes, which may or may not be identical to the soils map. Soil C is initially split among active, intermediate and slow pools in a 2:59:39 split. The C:N ratios of the 3 pools are initialized, for each vegetation type, to values that have been predicted in long runs of the CENTURY model with similar vegetation (eg. herbaceous, deciduous shrub, deciduous forest, coniferous forest).

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, 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 to roots when leaf tissues die.

Fire Responses

Plants respond to fire by being combusted, by being killed, and by either germination or resprouting of new plants. Fire severity maps are read in for each fire, at the simulated time that they occurred. These maps contain fire severity codes for each grid-cell. For herbaceous plants, a fraction of aboveground tissues lost to combustion, and a fraction of plants dying are specified for each fire severity class. For woody plants, the effects of fire are specified as fractions of pre-fire cover or number that will be present post-fire, for each fire severity class.

To represent the 1988 fires, the burned area map (Despain et al. 1989) was used, with codes for canopy burn, mixed burn, non-forested burn, and unknown burn type outside the park.

Higher elevation areas burned in August of 1988 while low elevation areas (the northern range) burned in September.

To represent herbaceous responses it was assumed that 80% of herbaceous roots are in the top 20 cm and 100% of meristems are in the top 10 cm. Consequently, for canopy burn, with a mean char depth of 2.5 cm, 10% of the roots might be charred and 20% of the meristems. Similarly for non-forested burn, if the mean char depth is 0.5 cm, then 2% of root and 4% of meristems would be charred. For mixed burn, the mean char rates of canopy, surface and unburned was applied. For unknown burn type, it was assumed half was canopy burn and half was mixed burn. It was assumed that post fire canopy cover was 5% of prefire cover for trees and *Vaccinium* shrubs, due to germination of new plants. For sagebrush and deciduous it was assumed that post fire plant numbers were 75% of prefire numbers due entirely to germination of new plants from seed. For willows it was assumed postfire cover was 5% of prefire cover, and 10% was due to germination and 90% was due to resprouting.

Carbon and nitrogen in combusted tissues were assumed to be 98% volatilized, with the rest being returned to the soil in ash.

Herbivory

The model simulates herbivory by large mammals by calculating a forage intake rate that asymptotically increases with forage biomass to a maximum rate. Maximum forage intake rate is expressed in terms of kg of forage per kg of body weight per day. Forage intake rate is reduced by increasing snow depths, and by snow crusting (Coughenour 2005a). Forage intake is distributed amongst forage items using a dietary selection model (Ellis et al. 1976, Coughenour 2005a). The herbivory portion of the model is described in more detail elsewhere (Coughenour 2005a).

PARAMETERS AND DATA INPUTS

Spatial Resolution

For most simulations the model was configured to simulate 1 km x 1 km grid-cells. Some simulations were conducted with 500 m x 500 m grid-cells. The 1 km resolution represents the primary features of the landscape while enabling simulations to be conducted in a reasonable amount of time on the current generation of computers. While vegetation patches smaller than 1 km x 1 km may not individually be represented, the GIS spatial aggregation procedure ensures that the total area of 1 km or 500 m patches will be approximately equal to the total area covered by such patches in the original finer scale, unaggregated data.

Climate

Monthly weather data from 10/1/1949 to 09/30/1999 were derived from the daily weather set developed by Phil Farnes (Farnes et al. 1999). Farnes' data set combines data from SNOTEL and climate stations in the region (Figure 5), with additional levels of data quality checking. SNOTEL stations are remote recording devices that record precipitation and snow water equivalents. Temperature data have been recorded by SNOTEL stations since the 1980's. SNOTEL data after 9/30/1999 were obtained from USDA NRCS (National Resource Conservation Service) via their internet site. Weather station data after 9/30/1999 were obtained from NOAA's "Summary of the Day" database. Two spatial precipitation domains were identified for developing regressions of precipitation on elevation. Southwest and northeast domains were separated by the continental divide, based upon the climate analyses of Despain (1987) showing different precipitation regimes and relationships between precipitation and elevation.

Soils

Soils in the study area are very diverse, due to the wide assortment of geological substrates, topographic positions, climate, and vegetation (Figure 6A). Soils surveys have been conducted, and maps have been developed for the park itself (Rodman et al. 1996), for the Gallatin National Forest area outside the park to the north (Davis and Shovic 1984). A few small areas were not included in either of these surveys. The first was a small area of private land not in the National Forest in the extreme northwest tip of the study area, and the others were those slivers of land lying outside the park boundary on the west. For these areas, soil types were taken from Greater Yellowstone Landscape and Soils (Shovic and Urie 2001).

Soil water holding capacity affects plant growth, especially in water limited environments. This variable can be derived as the difference between relative soil water content at field capacity and at wilting point (mm water per mm soil depth), multiplied times rooting depth or soil depth (mm), whichever is less. Textural classes and soil depths were noted for each of the soil types in the surveys. Values for field capacity and wilting point were typical values for soil textural classes. A complete list of soil types soil depths, field capacities and wilting points can be found in the Appendix 1. The resulting map (Figure 6B) shows a prevalence of low water holding capacity soils in the central and southwestern portions of the study area, and in high elevation mountainous terrain in the north. Soils in the east and most of the north have considerably higher water holding capacities.

Soil fertility is the other main factor affecting plant growth. Soils derived from andesitic substrates are known to have higher soil nutrient levels than soils derived from rhyolite (Trettin 1986, Despain 1990). In the Yellowstone Park soil survey (Rodham et al. 1996), soil parent material types were noted, enabling the creation of a map of soil substrates (Figure 6C). The broad distribution of substrates shows the prevalence of andesitic soils in the east and north, and rhyolitic soils in the center, west, and southwest. Sedimentary soils are also generally higher in nutrients than rhyolites, and these soils are found in the northwest, with a few pockets elsewhere, notably Hayden Valley and Pelican Valleys in the central region.

Soil carbon and nitrogen contents are the primary variables of interest in affecting and being affected by primary production. Generally, fertile soils are high in both C and N, and C and N contents are positively related. Although a great amount of detail was described in the Yellowstone soil survey (Rodham et al. 1996), soil C and N data were not available for each soil type. The most complete soil fertility data to date comes from Trettin's (1986) study. Data from this study were used as a basis for initializing soil C and N in the ecosystem model. Trettin recorded habitat types for each of his 67 plots. He covered 23 of the primary habitat types on the detailed map of Despain (1990). An additional set of soil C and N data from 12 soil pits in 5 forested and non-forested habitats was provided by Ann Rodham of the Yellowstone Center for Resources. The combined Trettin and Rodham data are summarized in Table 1.

Habitat maps were used as the basis for mapping soil fertility. Habitat types were originally mapped as part of a grizzly bear habitat mapping program in the 1980's (Mattson and Despain 1985). The grizzly bear study included all of the park, plus considerable land area surrounding the park. A refined version of the habitat map was developed by Don Despain for Yellowstone National Park (see Despain 1990), and this is stored in the park's GIS data base. The YNP habitat map was used inside the park and the grizzly bear habitat map was used for areas outside the park. A small piece of private land outside the park in the northwest of the study area (primarily the Paradise Valley) was not included in the grizzly bear habitat map. To fill in this area, the USGS National Landcover Data (NLCD) were used (USGS, EROS Data Center, Sioux Falls, S.D.). These data were obtained via the CD of Nesser et al. (2001). The habitat map is not shown due to the fact that there are too many types to develop a readable legend. Habitat types and codes are listed in Appendix 2. The grizzly bear, Despain, and NLCD habitat types were aggregated. Then the aggregated map was reclassified to correspond to the 23 habitat types included in Trettin's study (Figure 7A). Trettin's soil data were then combined with the aggregated habitat map to create maps of soil C and N contents (Figure 7B,C).

The soil C and N distribution patterns correspond with one another, as would be expected. Additionally, there is correspondence between the soil fertility maps and the soil substrate map (Figure 6C), with higher soil C and N contents being observed on the andesitic soils. The rhyolytic soils have markedly lower C and N. Areas outside the park to the west, and to the north have exceptionally low fertility either due to substrate or thin soils.

The thermal areas map, used to affect snow melt, is shown in Appendix 3. A temperature of 13°C was used for all types of thermal areas except thermal ground and thermally warmed streams for which 12°C was assumed.

Atmospheric Nitrogen Inputs_____

Rates of N deposition from the atmosphere were based upon data from the National Atmospheric Deposition Program (NADP) from their Yellowstone National Park site (data obtained from NADP web site). There are 0.21 g N m⁻² yr⁻¹ input irrespective of precipitation, and an added 0.0033 g N per mm precipitation. An additional N input amount of 0.5 g N m⁻² yr⁻¹ was

necessary for willow and heavily subirrigated vegetation, $0.35 \text{ g N m}^{-2} \text{ yr}^{-1}$ was needed for aspen, and $0.25 \text{ g N m}^{-2} \text{ yr}^{-1}$ was needed for partly subirrigated sites. . The additional N requirement is consistent with findings of Menezes (1999) who showed N inputs from stream water to willow based upon ^{15}N stable isotope concentrations in plants, soil, and stream water.

Tree Cover

A tree cover type map was available for the park (Despain 1990). This map was a refined version of the original grizzly bear tree cover type map (Mattson and Despain 1985) which covered nearly all of the areas outside of the park in the current study area, except for one section of private lands north of the park. The original grizzly bear tree cover map was used for areas outside the park. For the area north of the park not covered, data from the NLCD (National Land Cover Data Base) were used (mentioned above) Cover types on the grizzly bear cover map differentiated dominant species (lodgepole pine, spruce-fir, Douglas fir, whitebark pine) and stand successional stages (eg. lp0, lp1,lp2,lp3). There were no data for percent canopy cover. The tree cover type map is not shown here because there are too many cover types to create a visually meaningful legend.

A wide variety of lodgepole pine stands have been characterized in terms of density and size class distributions (Kashian 2002). However, no maps of tree canopy cover or size existed for YNP when this modeling was carried out. In lieu of such information, a model and remote-sensing based estimation approach was employed to develop a map of tree canopy cover.

Canopy cover was estimated by taking advantage of the fact that nearly all of the trees in YNP are coniferous, remaining green in winter, and the fact that tree canopies project above the background snow cover in winter. Two hundred twenty-four biweekly normalized difference vegetation index (NDVI) scenes based upon 1 km AVHRR satellite data 1990-1999 (USGS EROS Data Center, Sioux Falls, S.D.) were processed, and visually examined. The scenes were classified by season (winter, peak biomass, green-up, dry-down), and winter scenes were visually classified into “open” and “closed” snow cover conditions, where “open” meant there was considerable area of non-forested cover types that were not covered with snow and where “closed” meant that most or all non-forested cover types were covered with snow. A single map was computed as the average of all closed-winter NDVI scenes.

The NDVI of snow is near 0, while NDVI increases with increasing green leaf area. For purposes here, it was assumed that the spectral mixing between background snow and green leaf in a 1 km pixel provided a good index of projected green leaf area and thus canopy cover. It is well known that relationship between NDVI and leaf area is non-linear, becoming asymptotic at higher leaf areas. However, the aim here was to index cover, rather than total leaf area.

A GIS procedure was performed to extract the mean value of the closed winter NDVI for each cover type on the YNP cover map, which provided relative measures of canopy cover among different cover types. Cover types reflected stand age and dominant species (Despain

1990). Tree canopy cover was visually estimated for each cover type from photographs, field reconnaissance, and descriptions in Despain (1990). The tree cover estimates were then regressed against mean NDVI values for each cover type. Several outliers were identified and eliminated, and the regression was performed again (Figure 8). This 2-step iteration ensured that estimates were consistent with each other and with the NDVI data. Then, the mean NDVI values for each cover type were converted to cover values using the regression. This yielded a mean value of percent cover for each cover type. The mean values were then applied to the cover type maps pre- and post-fire to produce pre- and post-fire woody cover maps (Figure 9). The cover maps at 1 km resolution for the study area are shown in Figure 10.

Tree Sizes

A vegetation cover type map was produced for the grizzly bear habitat mapping program in the 1980s (Mattson and Despain 1985). The park portions were subsequently refined and included in the park GIS data base (Despain 1990). After the 1988 fires, Despain and colleagues produced an updated tree cover type map. Essentially, the tree cover type maps indicate the dominant tree species and the successional stage of regrowth since the previous fire. Using the cover type maps and typical tree sizes in mm stem diameter for each cover type (Table 2), maps of tree size were generated. The tree diameter maps at 100 m and 1 km resolution for the study area are shown in Figures 9 and 10.

Herbaceous Biomass

Data from herbaceous biomass studies in and adjacent to Yellowstone National Park were organized by habitat type (Table 3). Data from non-forested habitats mainly come from studies on the northern elk winter range (eg. Merrill and Boyce 1993, Coughenour 1991, Frank and McNaughton 1992, Singer 1995). However, studies were also conducted in Hayden Valley (Tracy 1996, Olnecki 2003) and geothermally warmed grasslands and riparian areas in the western and south western portions of the park (Dawes 1998). Data for forested habitats were scarcer (Table 4). Hansen et al. (2000) measured biomass in several locations outside the park western boundary.

At low elevations plant growth could be moisture limited because of low precipitation, warmer temperatures, and longer growing seasons (Coughenour 1991). Since precipitation increases with elevation (Despain 1990), there should consequently be a positive relationship between herbaceous biomass and elevation. A significant positive relationship was found between observed values and elevation in dry habitat types below 2800 m (Figure 11).

However, at higher elevations, plant growth could be more limited by low temperatures and short growing seasons than by moisture. A map of normalized difference vegetation index (NDVI) derived from 30 m Landsat Thematic Mapper images is shown in Figure 12. The NDVI has been widely used as an index of total green biomass (Prince and Tucker 1986, Hunt and Miyake 2006). Much of the area is covered by coniferous trees, thus confounding the use of

NDVI for assessing herbaceous biomass. However, the cover map can be used to mask out forested areas (Figure 13A). NDVI in non-forest areas clearly increases with elevation in the Yellowstone and Lamar Valleys (the lower northern range near and outside the north entrance) However, the map also shows that NDVI declines at higher elevations, especially east and north of the park (Figure 13A). A plot of peak NDVI vs. elevation of non-forested cover types on a pixel by pixel basis (Figure 14) showed that the optimal elevation range for NDVI was between 2000-2400 m, declining at lower and higher elevations.

An interesting feature of the NDVI map (Figure 12) is the region of lower NDVI in much of the western part of the park (the brown colors). Part, but not all of this area burned in 1988 (Figure 13B). This area corresponds to the low fertility rhyolitic soil substrates, and soils with lower water holding capacity (Figure 6). The lower NDVI values likely reflect both reduced tree cover and reduced herbaceous cover.

Based upon the preceding observations, the following rules were developed as a “data model” to estimate herbaceous biomass across the Yellowstone landscape. A computer program was written to apply the rules to GIS data inputs (elevation, habitat type, cover type maps) to compute an herbaceous biomass map.

1. In all dryland non-forested habitats below 2400 m elevation, biomass is calculated from elevation using a regression (Figure 11) developed from a synthesis of data in Table 3.

$$\text{Biomass (g m}^{-2}\text{)} = -38 + 0.053 \cdot \text{Elevation (m)}.$$

2. In all dryland non-forest habitats above 2400 m elevation, biomass is equal to that predicted based upon the regression of biomass versus elevation at 2400 m, multiplied by a 0-1 scalar that decreases biomass with increasing elevation following the NDVI trend. The function linearly interpolates between the following three pairs of X (m),Y (scalar) points:

$$X1 = 2400 \text{ m, } Y1 = 1.0; \quad X2 = 3000 \text{ m, } Y2 = 0.65; \quad X3 = 3300 \text{ m, } Y3 = 0.$$

The equations for the scalar are then:

$$\begin{array}{ll} Y = 2.39 - 0.00058 \cdot \text{Elevation(m)} & \text{Elevation} < 3000 \text{ m} \\ Y = 7.25 - 0.0022 \cdot \text{Elevation(m)} & \text{Elevation} > 3000 \text{ m} \end{array}$$

3. Some habitat types in YNP below 2400 m are water-subsidized through runoff or ground water seepage, thus making productivity somewhat independent of the precipitation/elevation gradient. Mean values from these habitats are summarized in Table 5. These means are applied to all areas occupied by those types.

4. Results from the study of Hansen et al. (2000) were used to calculate understory biomass in forested lodgepole pine, spruce-fir, and whitebark pine habitats. Their data suggested a decrease

in forest understory biomass with increasing elevation. The following regression was fit through their data for mature lodgepole pine stands.

$$\text{Biomass (g m}^{-2}\text{)} = 98 - 0.032 * \text{Elevation (m)}.$$

5. Data of Hansen et al. (2000), J. Norland and F. Singer (unpublished), and J. Reardon (unpublished) all indicated that biomass was higher than predicted by the equation above by a factor of 1.75 in Douglas fir stands. A 1.75 scalar was accordingly applied to Douglas fir stands.

6. Herbaceous biomass in wet forests was set to 100 g m⁻² in clearings and 91 g m⁻² in understories, based upon data collected by Tracy (1996) and J. Reardon (unpublished).

The data model predicted a very heterogeneous distribution of herbaceous biomass across the region (Figure 15). When scaled to show differences at the low end of the spectrum (Figure 15A), lowest biomass areas were seen to occur primarily at higher elevations as a result of the effect of lower temperatures and shorter growing seasons. An apparent exception to this were the high meadows north of the park boundary. Biomass in these areas was consistent with the effect of elevation on upland herbaceous productivity. Productive high meadows can also be seen scattered in patches on the Mirror Plateau (between the road and east boundary), and in the southwest.

Herbaceous biomass in forested grid-cells was generally lower than in non-forested grid-cells (browns, yellows and light greens as opposed to dark greens in Figure 15A). Important exceptions were the wet forests west and south of Lake Yellowstone, and the woodlands around the western boundary north of the road to the west entrance, which have intermediate levels of biomass. The forests west and southwest of Lake Yellowstone and along east eastern shore were predicted to have higher biomass than other forests due to the fact that this habitat type (21l/2do) is a fine-grained mosaic of *Vaccinium* and wet forest understories. The largest block of pure wet forests located south of Lake Yellowstone was predicted to have the highest biomass values. The increase in biomass in the west-central region was due to the fact that this area is at the optimal elevation for biomass (Figures 4,14).

Higher biomass densities generally occurred in non-forested areas. Intermediate levels of biomass were predicted to occur at lower elevations of the northern winter range, along the road exiting the northern boundary. The effect of low elevation, and thus low precipitation, can be seen further north along the road and outside the park. Although much of this land is irrigated, irrigation was not considered in the model. The highest herbaceous biomass densities were predicted to be found in the moist grasslands of the upper northern winter range, Gardners Hole (south of Mammoth), Hayden Valley (south of Canyon), Pelican Valley (northeast of Lake Yellowstone), in riparian areas southeast of Lake Yellowstone, and in a meadow area in the southwest corner of the park (Bechler Meadows). Productive patches were scattered in riparian areas and meadows throughout the central and south eastern portions of the park. On the northern winter range, biomass declines with decreasing elevation. This is consistent with the pattern

observed in the NDVI data (Figure 12).

Plant Functional Group Composition

The model was configured to simulate at most four types of plants on any single patch type (herbaceous, shrub, tree patch types or facets) in any single grid-cell. Four “bins” of computer memory were reserved for these 4 types. In the Yellowstone application, each bin corresponded to a major life-form (grass, forb, shrub, tree). In each “bin”, there was one functional group, which depended upon the species composition of the vegetation type, or habitat type. There were three functional groups of grasses that could be assigned to the grass bin, 2 types of forbs for the forb bin, 4 types of shrubs for the shrub bin, and 2 types of trees for the tree bin, depending on habitat. Model functional groups were often aggregations of several more detailed functional groups, and several species. The relationships among these classification systems are shown in Table 6. The final selection of modeled functional groups was based upon plant traits, but also upon data availability. For example, since there was insufficient data to differentiate palatable and unpalatable grass species composition in different vegetation types throughout the study area, so these groups were lumped. The distribution of graminoid functional types (i.e. the type of grass put into the grass “bin”) throughout the study area was then mapped based upon the distribution of YNP habitat types (Figure 16A).

Total herbaceous biomass was split among graminoids and forbs with a 70/30 split in most all habitats. There have been no systematic studies of grass vs. forb biomass composition across different habitat types in YNP. Herbaceous biomass studies on the northern range provide sufficient data to characterize mean forb percentage for those habitat types (Table 7), but there is nothing quantitative known about how forb percentage varies within habitat types on the northern range. No consistent patterns were apparent in relations between forb percentage and habitat type for most habitats. Without any basis for predicting forb percentage, the best that could be done was to use the mean value across all of these habitats. For certain habitats, there were data from other sources suggesting markedly different forb percentages. No species composition data from mesic habitats (hairgrass, sedge, willow) in YNP could be located. However data from riparian areas in Rocky Mountain National Park (Ziegenfuss et al. 2002) suggested a grass:forb split of 90/10.

Many habitat types on the YNP habitat map consisted of mosaics of 2-3 primary habitat types (Matson and Despain 1985, Despain 1990). For example, the habitat type “2do/2l” is a mosaic of “2do” (wet forests) and “2l” (subalpine fir/grouse whortleberry). If there were two types and both were forested, the herbaceous species composition was weighted 65/35 of the species compositions and abundances of the primary types. If there were three forested types, then the weighting was 50/30/20. When one of the phases was non-forested, the herbaceous composition of the non-forested phase was used to initialize the herbaceous patch type in the grid-cell.

Shrub Canopy Cover and Sizes

The spatial distribution of shrub functional types (Figure 16B) was derived from the YNP habitat map and descriptions of dominant species given by Despain (1990). Sagebrush was the dominant shrub species in most of the non-forested areas. Miscellaneous deciduous shrubs were prevalent in low to mid elevation forests and woodlands. *Vaccinium* species were noted as being prevalent in most of the remainder of the forest habitat types.

Willow/sedge habitat types were uncommon, and based upon personal observations, it seemed likely that these were underestimated in the habitat map. Notably, the YNP habitat map had no willow on the northern winter range. To correct this situation, a riparian willow habitat type was added to the habitat map. This was accomplished by creating a 100 m resolution grid-cell map of riparian zones from the hydrology map. Effectively this is a 100 m buffer zone about streams. From that map, 25% of the riparian cells were sampled at random. When the 100 m map was resampled to 1km, only a fraction (1/10th) of the 100 riparian cells were ascribed to become 1 km riparian cells, thus preserving the total areal extent. These willow habitats can thus be seen scattered about the study area in the 1 km shrub cover map (Figure 16B).

Shrub cover outside of upper winter range enclosures was estimated from plant size and density data (Norland and Reardon 1996) as 2.2% in 1957/61, 5.4 % in 1970, 14.2 % in 1987/89 (Table 8). Cover was estimated as 2% on the lower winter range based upon data outside enclosures near Gardiner, Montana. Sagebrush height was set at 30 cm. Willow cover was estimated from Chadde and Kay (1991) and Singer (1996) using data from plots located outside of grazing enclosures (Table 9). Willow height was set at 1500 mm.

Few shrub cover data could be located for the remainder of the habitat types. Jakubaskis (1996) measured 3-7% shrub cover in various lodgepole pine cover types, however, the data were not broken down by habitat type. Hansen (2000) reported shrub biomass, but not cover. Descriptions and photos presented by Despain (1990) of understory cover for each habitat type were used as a basis for assigning shrub canopy cover percentages. For example, he described grouse whortleberry understory as “cover nearly continuous”. Deciduous shrub heights were set at 70 cm. Grouse whortleberry (*Vaccinium* spp) height was set at 25 cm.

The final shrub cover assignments to each habitat type are given in Table 10.

Water Tables

Water table depths were empirically specified by month for those habitat types that are clearly water subsidized. These included all riparian, sedge, hairgrass, and willow habitat types. Water table depths were calibrated to achieve observed levels of herbaceous biomass production in those habitats (Table 11).

Plant Model Parameters

Parameters affecting photosynthesis and stomatal conductance are shown in Table 12. Some parameters were based upon previous modeling of N. American temperate grasses (Coughenour and Chen 1997). Other values were 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). Willow parameters were developed in Peinetti (2000) and Peinetti and Coughenour (2001) based upon ecophysiological data of Alstad et al. (1999), Peinetti (2000), and other sources.

Plant tissue senescence rates, and transfer rates from standing dead to litter were calibrated to match observed biomass dynamics, and ratios of live to dead shoot tissues. Root turnover rates were based upon previous modeling experience (Coughenour and Chen 1997, Parton et al. 1997, 1993), which was in turn based upon data from comparable species.

Allometric relationships between metrics of plant form and mass, for example between tree crown diameter and stem diameter, are usually described as equations. In the model, allometry was specified by providing values for all of the metrics for each of the six woody plant size classes (Table 13). 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 sagebrush and other upland shrubs were based upon sagebrush data reported by Sturges and Trlica (1978), Branson et al. (1976), and Fetcher (1981). Allometry data for willow were developed by Peinetti (2000), based on original data, and data of Zeigenfuss et al. (1999, 2002), and Cannell (1987).

Values for the seed-based reproduction rates, and vegetative reproduction and mortality function(vegetative growth rate vs. actual shoot : potential shoot ratio) are given in Table 14 . Parameters affecting woody plant population dynamics are shown in Table 15.

Herbivores

Bison and northern elk herd numbers were specified based upon data from aerial surveys (Meagher 1973, Houston 1982, Coughenour and Singer 1997, Taper et al. 2001, Taper et al. 2002, Hess et al. 2002). Another herd of elk winters in the Madison River drainage and summers at surrounding higher elevations (Singer and Mack 1993). Additional elk winter outside the park but utilize summer ranges inside the park (Singer and Mack 199).

Aerial survey counts underestimate actual numbers due to a variety of reasons including animals being out of sight due to tree cover and animals blending into the underlying vegetation and soil as opposed to being in contrast on snow covered ground. Sightability also decreases with

decreasing group size. Sightability has been estimated for some elk counts (Coughenour and Singer 1997) and for bison counts (Taper et al. 2001, Hess et al. 2002). Although sightabilities were not available for every count, mean sightabilities from counts where they were determined were applied to all of the remaining counts to estimate the actual numbers of animals present. It was important to use actual animal numbers rather than counted numbers in order to accurately consider the impacts of herbivory.

Animals were distributed spatially and seasonally based upon observed distributions (Meagher 1987, Houston 1982, Taper et al 2002, Coughenour and Singer 1997). The seasonal ranges for bison and elk and the modeled spatial distributions within ranges are discussed in Part 3 of this report (Coughenour 2005b).

Simulated herbivores consumed plants at rates affected by body size, forage biomass, snow cover (Coughenour 2005b).

Initializing Runs

An initializing simulation of 60 years was carried out. The model was initialized using the soil and vegetation maps described above. Herbaceous biomass was initialized based upon the data model outputs. Weather data were randomly sampled from the monthly weather data for 1949-2001. Herbivore numbers were held constant at 2,000 bison, 12,000 elk in the northern herd, 800 elk in the Madison herd, and 7,600 elk immigrating into the study area during the summer months. At the end of the run, all of the model state variables were saved to a file. Soil state variables, but not plant state variables, were used as initial conditions for a simulation of 1949-1968 that used observed weather data and observed numbers of bison and elk. Soil and plant state variables at the end of the 1949-1968 run were saved to a file and used as initial conditions for the simulation of 1969-2001.

RESULTS

Snow Model

The snow submodel was verified by comparisons between observed and predicted data at snow course, SNOTEL, and climate stations. The snow model performed satisfactorily at most of the sites (Appendix 4). Variations among years and among sites were adequately captured. The range of simulated snow conditions was quite large, varying from less than 100 mm in dry years at lower sites, to over 1200 mm in moist years at higher sites. Monthly outputs for a dry year (1981) and a heavy snow year (1997) are shown in Appendix 5. Mean maximum snow water content over the entire study area varied from 200 mm to 600 mm (Figure 17A). As expected, snow depths increased with elevation (Figure 17B). Mean snow depth at the end of February varied from approximately 10 cm to over 220 cm (Figure 17B). Reduced snow depths were predicted in thermal areas, including thermally warmed riparian zones

Simulated Ecosystem Processes

Simulated ecosystem processes are illustrated by examining temporal outputs for a ten-year period for a typical sagebrush steppe site on the upper northern winter range. Simulated daily photosynthetic rate for fine-leaved grasses (Figure 18A) increased with the onset of growth. There was a decrease as the soil dries in mid-summer, followed by an increase in fall. The summer depression in 1988 was especially large. Stomatal conductance (Figure 18B), and thus plant water use, mirrored photosynthesis according to the Ball and Berry equation. Photosynthetic rate was affected by moisture, temperature, nitrogen, and light. The temperature limitation (Figure 19A) was particularly strong, basically defining the growing season. During the time when temperature was non-limiting, soil moisture exerted an limiting effect (Figure 19A). Soil moisture was especially limiting at this site in 1987 and 1988. Nitrogen limitation existed, but the limitations were not as strong as temperature and moisture (Figure 19B), amounting to at most a 12% reduction. Light was essentially non-limiting during the growing season.

Leaf N concentration began high during first green-up, then declined as the season progressed (Figure 20A). Plant N concentration was drawn down during the active growth phase each spring, but was replenished between summer and fall. Soil moisture in the herbaceous rooting zone was drawn down each summer (Figure 20B). Topsoil (0-20 cm) moisture was usually replenished in the fall and early winter. Subsoil moisture was replenished in the spring during snowmelt. Topsoil was dry in winter of 1987. After the spring moisture, early drying of the topsoil occurred in summers of 1987, 1988, and 1989. Topsoil was moist by early winter in 1990-1992, but not in 1993-1994.

Decomposition and nitrogen mineralization from dead plant material and soil organic matter were controlled by temperature and soil moisture. As with plant growth, microbial activity was highly temperature limited in this ecosystem (Figure 21A). Peak decomposition rates occurred in mid summer, and even then, the rates only reached 50-60% of maximum potential. As temperature became less limiting, moisture became more limiting. Moisture limitations reduced decomposition by another 50% during the driest part of summer.

Annual cumulative nitrogen mineralization (Figure 21B) was set to 0 each January 1st, and then accumulated throughout the year. At this site, 4-6 gN m⁻² were mineralized each year beginning rather early in each season. Dead plant litter on the surface (Figure 22A) and in the soil (Figure 22B) fluctuated on an annual basis. Litter was decomposed during spring and summer, and it built up again in late fall through winter as dying plant tissues were transferred to the soil and as decomposer activities were increasingly limited by cool temperatures. Structural litter fluctuated less than metabolic litter..

Northern Range Non-Forested Areas

Precipitation on the northern range varied from a low of 500 in 1987 to a high of 850 in

1972 (Figure 23C). Snow cover varied markedly among years (Figure 23D).

Fine-leaved grasses in dry and moist habitats reached on average 50 g m^{-2} each year while coarse graminoids growing in hairgrass and sedge habitats averaged 220 g m^{-2} . Forbs averaged 25 g m^{-2} , across all habitats. Offtake by herbivores reached approximately 30% of fine grasses and 55% of coarse graminoids in the mid 1980's but declined in the 1990's. Offtake of forbs was very low, reflecting selectivity for graminoids by both elk and bison, and the greater rate of transfer of dead leaf tissues to litter.

Live herbaceous root biomass fluctuated seasonally, as it was drawn down by the end of winter and replenished by the end of the growing season. Peak root biomass of fine grasses increased slightly through 1988 (Figure 24B). In summer of 1988, root biomass did not increase as much as in prior years, and in winter 1988/89, root biomass fell to its lowest level. The decrease in 1988 was due to low soil moisture late in the growing season and was not due to the 1988 fires. Root biomass did not recover to pre-1988 values by 2002. Coarse (mesic) graminoid root biomass did not decrease in 1988, due to the lower degree of water stress in those habitats (Figure 24D). There was a declining trend in coarse graminoid roots on the northern range since the late 1970's due to increased numbers of bison grazing these habitats during the summer. Forb roots increased until 1988, decreased in 1988/89, and then slowly recovered (Figure 24F).

In an extended 50-year run with 750 northern bison, 2500 central bison and 15000 northern elk, fine grass biomass fluctuated between $45\text{-}50 \text{ g m}^{-2}$ and fine grass root biomass increased during the first 20 years then decreased slightly in the following 30 years (Figure 25A,B). Coarse grass biomass fluctuated between $200\text{-}220 \text{ g m}^{-2}$, while coarse grass root biomass increased then decreased (Figure 25C,D). Forb biomass leveled off at about 26 g m^{-2} while roots leveled off at 55 g m^{-2} (Figure 25E,F).

Sagebrush cover on the northern range gradually increased through 1969-1988 (Figure 26A). Some of the sagebrush cover was lost in the 1988 fires, but the model simulated a recovery between 1988-2002. Leaf dynamics varied seasonally, but sagebrush maintains some of its leaves over winter (Figure 26C). There was very little herbivory on sagebrush. While there is herbivory on sagebrush on the lower northern winter range by mule deer and pronghorn antelope, those species were not simulated here. In the 50-year extended run, sagebrush cover increased to about 7% (Figure 26E)

Willow cover fluctuated little (Figure 26B). A small amount of cover was lost in the 1988 fires, but recovery was very rapid.. There was a slight increase in willow cover between 1996 and 2002. Leaf dynamics were remarkably regular (Figure 26D). Offtake increased from about 14% in the early 1970's to 20% in the mid 1980's, averaged over the entire winter range. Offtake dropped slightly in the late 1990's, probably due to the decrease in elk numbers. Offtake tended to be higher in winters with deeper snowpack, such as in winter of 1996/97. Cover remained at 60% in willow habitats in the extended 50-year run (Figure 26F).

Soil moisture was recharged every year during snowmelt (Figure 27A). However there was variation among years in the rate and amount of drying during summer. Minimum subsoil water levels varied markedly among years. The surface soil layer dried rapidly and more completely in 1987 and 1988 than in most other years. Differences among years were more clearly reflected in soil water potential (Figure 27B), which was non-linearly related to total soil moisture. Here, higher soil water potential indicated drier conditions. The high degree of drying in 1987 and 1988 was evident. There were several other dry summers, but none as dry as 1987. It appeared that on average, soil was drier between 1990-2002 than between 1969-1986.

Nitrogen mineralization varied significantly among years (Figure 27C), ranging from 3.5-8 gN m⁻² yr⁻¹. Lowest values occurred in drier years due to the moisture effect on decomposition rate. Soil organic carbon remained relatively unchanged over the entire period, except for a very slight increase in the intermediate turnover rate pool (Figure 27D). In the 50-yr extended run, N mineralization varied between 3.5-5.5 gN m² yr (Figure 27E). Soil organic carbon in the intermediate pool continued to increase slowly (Figure 27F).

Hayden Valley Non-Forested Areas

Precipitation was approximately 33% higher in Hayden Valley than on the northern range (Figure 23E). However, snow pack was approximately double that on the northern range (Figure 23F). The difference between driest and wettest years was greater in Hayden Valley than on the northern range.

Fine leaved grass biomass was nearly constant through 1987 (Figure 28A). However in 1988, peak biomass was lower. The effect of the drought was much more pronounced than on the northern range, probably due to the shorter growing season. However there was a substantial recovery in 1989 and biomass trended upwards through 2002. Aboveground net primary production increased from approximately 90 g m⁻²yr⁻¹ in 1970 to 110 g m⁻² in 1987 and fluctuated around 100 g m⁻² from 1989 onwards (not shown). As on the northern range, roots were at a minimum in winter of 1988/89. Offtake of fine grasses increased between 1970 and 1982 reflecting the growth of the central bison herd during this time. Offtake reached 50% or more between 1982 and 1995. Offtake decreased between 1996 and 1998 due to a decrease in the bison herd. Coarse graminoid peak biomass was at highest levels in the mid 1970's and mid 1990's (Figure 28C). Aboveground net primary production increased from 220 g m⁻²yr⁻¹ in 1970 to 300 g m⁻²yr⁻¹ in 1977, then declined in the mid 1980's and increased again in the mid 1990's. Offtake increased between 1970-1982. Between 1982 and 2002 there was no consistent trend, but there was high interannual variability in offtake between approximately 30% and 55% of peak biomass. Forb biomass increased over the period and suffered a smaller decline in 1988 than graminoids. Offtake increased steadily to the 10% level. Forb ANPP increased from 40 g m⁻²yr⁻¹ to 45 g m⁻²yr⁻¹.

Live root biomass of fine-leaved grasses increased slightly between 1969-1987 but declined in 1988/89 (Figure 28B), followed by recovery in 1989 and a slight increasing trend

through 2002. Roots of coarse graminoids showed the same long-term temporal pattern as aboveground biomass dynamics (Figure 28D). Similarly forb roots increased over time, with lower values in 1988.

In the extended run Hayden Valley fine grass biomass remained between 60-70 g m⁻² (Figure 29A). The offtake by 2500 central herd bison varied between 35-35 g m⁻². Root biomass increased initially, and then trended downwards in the latter 30 years (Figure 27B). Coarse (mesic) graminoid biomass fluctuated between 160-180 g/m² (Figure 29C). Root biomass varied between 450-700 g m⁻², with no apparent long-term trend (Figure 29D). Forb aboveground and root biomass increased slightly in the first 25 years (Figure 29E,F).

Sagebrush cover trended upwards slightly between 1969-2002 (Figure 30A). Similarly, peak leaf biomass also increased (Figure 30C). Willow cover declined slightly in the early 1970's then increased 1975-1990, then declined and increased again 1980-2002 (Figure 30B). Leaf biomass followed a similar pattern (Figure 30D). Willow offtake was low (8-15%). Sagebrush cover increased then level out at about 9% in the extended 50-year run (Figure 30E). Willow cover cycled between 50-62%, with no apparent trend (Figure 30F).

Soil moisture dynamics exhibited similar patterns to those on the northern range (Figure 31A). Subsoil moisture again showed marked interannual variation in minimum values. Surface soils dried at faster rates in 1987 and 1988. Soil water potential reached highest (driest) values in 1987 and 1988. However 1974, 1979, 1994 and 2002 were also comparatively dry.

Nitrogen mineralization rates were quite similar to those on the northern range (Figure 31C), varying between 4-8 gN m⁻² yr⁻¹, depending on moisture and temperature. There was a slight upward trend in the intermediate soil organic carbon pool (Figure 31D). N mineralization rates varied between 4-5.5 gN m⁻² yr⁻¹ in the extended simulation (Figure 31E). Intermediate soil organic matter continued to increase (Figure 31F).

Biomass and Cover Dynamics - Entire Study Area

Over the entire study area fine grass biomass increased between 1969-1988, dropped in 1988, and increased slightly 1989-2002 (Figure 32A). Offtake was approximately 25% in the mid 1980's and declined slightly in the 1990's. Coarse (mesic) graminoid remained nearly level through the period (Figure 32B). Offtake increased between 1970 and 1990 from 19% to 44%. Offtake decreased slightly to 30% after 1996. Coarse forest graminoid biomass increased throughout the simulation although they were reduced in 1988 (Figure 32C). The increasing trend indicates that the initial conditions were likely set at values below levels that would be in equilibrium with the site. Unlike the other plant groups, coarse forest grasses increased throughout the 60 yr and 1949-1969 initializing runs. Runs for an additional 50 yrs showed they eventually stabilized at roughly 60-65 g m⁻². Offtake of the coarse forest grasses was low, at only 2-5% of biomass. Forb biomass increased slightly through 1987, dropped in 1988, then remained level through 2002 (Figure 32D). ANPP of fine grasses increased from 32 g m⁻² yr⁻¹ to 36 g m⁻²

yr⁻¹, ANPP of mesic graminoids varied around 250 g m⁻² yr⁻¹, ANPP of coarse forest grasses increased from 80 g m⁻² yr⁻¹ to 90 g m⁻² yr⁻¹ and ANPP of forbs increased from 12 g m⁻² yr⁻¹ to 13 g m⁻² yr⁻¹.

In the extended 50-year simulation and over the entire study area, fine grass biomass increased to pre-fire levels within 20 years, then fluctuated between 25-30 g m⁻² (Figure 33A). Mesic coarse graminoids fluctuated between 170-180 g m⁻² (Figure 33B). Coarse forest graminoids continued to increase for another 20 years then leveled off at about 65-70 g m⁻² (Figure 33C). Forb biomass increased slightly and leveled off at 9-10 g m⁻² (Figure 33D).

Tree cover declined slightly 1969-1988, probably due to stand aging and self-thinning (Figure 34A). Total tree cover dropped from 40% to 30% as a result of the 1988 fires. Tree cover then began a slow recovery post-fire. In the extended simulation, tree cover remained essentially constant (Figure 34E).

Sagebrush cover over the whole area increased slightly over the period from 5-7% (Figure 34B). Willow cover first decreased, then increased between 1976-1985 to about 35%, then dropped in 1988, then increased 1989-2002 (Figure 34B). Deciduous forest understory shrubs declined slightly between 1970-1987, dropped further in 1988, then increased 1989-2002. *Vaccinium* understory shrubs declined slightly from 44% to 42% 1969-1987, dropped in 1988, then increased markedly 1988-2002 to 50%. The latter was due to reduced competition for light and soil resources from trees that burned off in the 1988 fires.

Vaccinium stem biomass was 275 g m⁻² pre-fire and 175 g m⁻² post-fire (Figure 34C). Leaf mass averaged 100-120 g m⁻² (Figure 34D). Willow stem mass dropped from 550 g m⁻² to 450 g m⁻² and willow leaf mass averaged 60 g m⁻². Deciduous shrub stem mass was approximately 220 g m⁻² pre-fire and 180 g m⁻² post-fire and leaf mass was 22-25 g m⁻². Sagebrush stem mass was 90-110 g m⁻² and leaf mass was 13-15 g m⁻².

In the extended simulation, sagebrush increased and leveled off at 8% cover (Figure 34F). Willow cover fluctuated between 35-42%. Cover values of other shrubs cycled, with no apparent trends.

Spatial Distributions of Plant Biomass, Net Primary Production, and Woody Cover

Tree canopy cover prior to 1988 (Figure 35) reflected the initial conditions (Figure 10), and little change in the subsequent initializing runs. After 1988, tree cover was obviously reduced in burned forests.

Overstory (not including shrubs in forest understories) shrub cover was lowest in shrub grasslands and in dry forests on the west side (Figure 36). Intermediate values were estimated for *Vaccinium* dominated forests, due to the presence of the shrubs in open patches and between tree rooting zones. Highest shrub covers occurred in forests with lowest tree covers. The 1988 fires

increased overstory shrub cover in many areas, as formerly understory shrubs were converted to overstory shrubs with the loss of the tree overstory. This does not indicate that total overstory plus understory shrub cover increased, however.

Herbaceous biomass was heterogeneously distributed (Figure 37). The most obvious feature of the simulated biomass maps is the higher productivity of the open grasslands and shrublands of the northern range and Hayden and Pelican Valleys. A decrease in biomass in the lower elevation portion of the northern winter range was predicted as a result reduced precipitation. The most productive areas of the park for herbaceous plants were clearly Hayden and Pelican Valleys, and Gardners Hole (the southwest arm of the northern winter range). Scattered areas of higher biomass in open meadows can be seen on the Mirror Plateau between the northern range and Pelican Valley. The hot springs vegetation near Firehole River is also productive, but not as extensive. There was essentially no difference in herbaceous biomass of open grasslands and shrublands before and after 1988. In forested areas, the 1988 fires decreased herbaceous biomass some areas and increased it in others (Figure 38).

Predicted spatial distributions of herbaceous biomass were largely consistent with the biomass data model, however there were differences in the details of the distributions (Figure 39). Both models agreed on the ranges of values for grasslands of the northern range, and Hayden and Pelican Valleys, hot springs areas in the Firehole area, and other similar areas. They also both predicted much lower values for forested areas. The predicted distributions of the ecosystem model were generally more heterogeneous than those of the biomass model, most likely reflecting the greater complexity of the ecosystem model and the greater number of factors underlying the predictions. The area of relatively high herbaceous biomass was predicted to extend over a greater portion of the northern range in the ecosystem model than in the biomass model. The ecosystem model also predicted more high biomass areas north of the northern range. The reduced biomass at very high elevations, clearly shown in white on the biomass model output map, is not as clearly discernable in the ecosystem model output map, largely due to the lower resolution of the latter. However there was general agreement in these high elevation areas. The ecosystem model predicted very low biomass ($<80 \text{ kg ha}^{-1}$) in more locations than the biomass model. The distinction between wet forests and other forests west of Lake Yellowstone in the biomass model was not as clearcut in the ecosystem model.

A comparison of simulated herbaceous green biomass to NDVI in non-forested areas (Figure 40) shows broad-scale agreement, particularly in that lower biomass values were simulated at lower elevation along and outside the northern park boundary. Just across the northern boundary where the road exits lies the town of Gardiner. Roads and buildings there likely lowered the NDVI signature. Low NDVI values relative to model predictions occurred in some grid-cells on the northern winter range.

The distribution of herbaceous root biomass was similar to that of aboveground biomass (Figure 41). Root:shoot ratios generally ranged from 2-3, with higher values in areas supporting coarse graminoids.

Herbaceous aboveground net primary production distribution was, as might be expected, similar to that of herbaceous biomass (Figure 42). However, there was greater divergence between high and low production areas.

Herbaceous biomass varied considerably across the northern range (Figure 43). In general the upper winter range was more productive than the lower winter range. Low productivity cells around the margins of the range are forests. The high productivity sedge bog habitats along the bottoms of the Lamer River and Slough Creek valleys are readily distinguished. High productivity grid-cells also corresponded to the riparian grid-cells that were randomly distributed along streams. (Recall that fine-grained riparian habitats were not included in the YNP habitat map, nor were fine-grained willow patches.)

Sedge bogs and riparian areas similarly explained patches of high productivity in Hayden Valley (Figure 44). The low production areas surrounding the open grasslands represent forest margins, with less herbaceous biomass. Tree islands in Hayden Valley were also less productive.

In Pelican Valley (Figure 44) production was high in the numerous sedge bogs along the Pelican River. The areal extent of moderately productive grasslands was less than in Hayden Valley. As in Hayden, production was reduced in the forest margin surrounding the valley.

In the Madison River/Cougar Creek area along the western boundary of the park (Figure 45), low productivity dry forest habitat was interspersed with high productivity willow/sedge and riparian habitats along streams. In the Firehole River area (Figure 45) the most productive cells were in riparian habitats. The areas of intermediate productivity were located in hot springs vegetation habitats.

Shrub ANPP was lowest on the open shrub-grasslands and highest in the forests, particularly those with intermediate tree canopy cover (Figure 46). Low values also occurred in the low elevation forest near the western boundary. Values ranged from 35-70 g m⁻²yr⁻¹ in that forest area, to 50-130 g m⁻²yr⁻¹ in the shrub-grasslands, to 200-300 g m⁻²yr⁻¹ in some of the forests. The difference between total shrub ANPP pre- and post-1988 was not as pronounced as the difference in overstory shrub cover (Figure 34). The ANPP maps include both understory and overstory shrubs while the shrub canopy cover maps include only overstory shrubs.

Tree ANPP (Figure 47) was as expected, higher where there was higher tree cover. Fires reduced tree ANPP, despite the regeneration that was taking place. Tree ANPP was in the 40-100 g m⁻²yr⁻¹ range in burned forests, while in unburned forests it varied between 100-400 g m⁻²yr⁻¹.

Total ANPP, the sum of herbaceous, shrub, and tree ANPP's, was generally higher in forests than in the shrub-grasslands, with dense moist forests being most productive (Figure 48). Total ANPP in forested areas was largely in the 200-400 g m⁻²yr⁻¹ range, with ANPP in wet forests reaching 500-700 g m⁻²yr⁻¹. Shrub grassland ANPP was in the 100-200 g m⁻²yr⁻¹ range except on the lower northern range where it was less than 100 g m⁻²yr⁻¹.

Total ANPP was reduced by the fires of 1988, mainly due to the loss of large trees (Figure 49). The reduction was mainly in the 50-100 g m⁻²yr⁻¹ range except in some of the formerly productive forests where the reduction was in the 100-300 range. The fractional reduction was mainly in the 10-25% range, but in some areas on the western side the reduction was 50-60%.

Biomass and ANPP in Relation to Habitat - Comparisons to Observed Values

Observed herbaceous biomass data from the synthesis in Table 3 were summarized as means for each habitat type in different locations (Table 17). Outputs from the model for those habitats and locations were extracted from model output maps using a GIS procedure that calculated means and spatial standard deviations for the grid-cells in each category. This permitted a comparison of observed and predicted biomass values.

There was good agreement between observed and predicted biomass for dry and moist grasslands and shrublands on the northern range and moist grasslands and shrublands in Hayden Valley. Predictions for Hayden Valley dry grasslands were higher than the mean, but well within the range of observed data. Predicted dry grassland biomass for the Firehole/Madison area was similar to observed ungrazed biomass but much higher than observed grazed biomass.

Simulated biomass values for tufted hairgrass meadows on the upper northern range and in the Firehole area were in agreement with data. Simulated biomass in Hayden Valley was below observed values, however. In mesic habitats such as sedge meadows, riparian and willow/sedge on the northern range, predicted values were greater than mean observed values, but were well within the range of observed values. In Hayden Valley, predicted values were lower than observed, but still within the range of observed values.

Simulated biomass in Hayden Valley tended to be below values observed by Olenicki et al. (2003). They observed means of 87 g m⁻², 122 g m⁻², 194 g m⁻², and 279 g m⁻² biomass in dry, moist sage/fescue, tufted hairgrass, and mesic grasslands and shrublands respectively. The model predicted on average 80 g m⁻², 112 g m⁻², 130 g m⁻² and 208 g m⁻², and respectively. The predicted values were within range of max and minimum observations, with the exception of tufted hairgrass. The prediction for moist sage/fescue habitats was well within range, and this was by far the most prevalent habitat type in Hayden Valley with 65 km², as compared to 9 km² of mesic habitats, 2 km² of tufted hairgrass, 1 km² of dry grassland/sagebrush and 1 km² of hot springs vegetation.

There was a discrepancy between observed and predicted biomass for hot springs vegetation in the Firehole/Madison area. While the model predicted values that were only slightly below the ungrazed biomass quantities inside grazing cages, on average, there was only one fourth as much biomass observed outside grazing cages as inside cages (Dawes 1996).

Comparison were made between the biomass data model and the simulation model for each habitat type (Table 18). Mean values from the data model output map were determined

using a GIS. There was good agreement for Idaho fescue/bluebunch wheatgrass, tundra, and big sagebrush/Idaho fescue habitats. The simulation model predictions were below data model predictions for Idaho fescue/hairgrass and sedge meadow habitats. Simulation model predictions were above data model predictions for hairgrass and big sagebrush/Idaho fescue/geranium habitats. While the data model was based upon data, it also contained a number of assumptions, so must be taken as an approximation. Thus, it is possible that the simulation model is more correct than the data model. The point of this comparison was to identify where there could be problems with either model.

Percent forb in the herbaceous layer ranged from 29-28% for most shrub grasslands and tufted hairgrass meadows (Table 19). This was comparable to the median value for such habitats in Table 7. In sedge meadows there was 5-6% forbs, which was lower than the single data point in Table 7. In tundra there was 50% forbs, but there were no data. As pointed out earlier, there is currently no empirical basis for predicting variations in forb abundances in different habitats.

Predicted herbaceous biomass was summarized by elevation zone and soil substrate (Table 20). Habitats were differentiated into dry, moist, and wet based upon descriptions given in Despain (1990). Moist habitats included Idaho fescue/sagebrush/sticky geranium and silver sage/Idaho fescue. Wet habitats included tufted hairgrass, hot springs, sedge bogs, willow, and riparian habitats.

In dry habitats, biomass consistently declined with increasing elevation on rhyolitic soils. However in dry habitats with andesitic soils, biomass increased with elevation between 1700 m and 2400 m, and above 2400 m it decreased with elevation. In moist habitats, biomass increased with elevation between 2000 m and 2400 m, but declined with elevation above 2400 m. In wet habitats with rhyolitic soils biomass increased with elevation between 2000 m and 2400 m and declined above 2400 m. On andesitic soils biomass declined with elevation throughout. Productivity was on average 20% greater on andesitic soils than rhyolitic soils in dry and moist habitats. In wet habitats biomass was 66% greater on andesite than on rhyolite.

Effects of substrate varied with elevation. There was only a 5% increase on andesitic soils in dry habitats at 1700-2000 m, but a 28% increase at 2000-2800 m. Above 2800m the effect reversed. In moist habitats biomass was 41-44% greater on andesite at 2000-2200 m and 2600-2800m, but only 5-8% greater at 2200-2600 m. In wet habitats there was only a 24% increase on andesite at 2200-2400 m, but 55-80% increases at 2000-2200 m and 2400-2600 m.

Predicted herbaceous biomass in forested habitats ranged from 12 g m⁻² in whitebark pine/*Vaccinium* to 77 g m⁻² in wet forests (Table 21). In the common lodgepole pine(LP)/*Vaccinium* habitats biomass was in the 20-28g m⁻² range. In Douglas fir (DF) biomass was 54-59 g m⁻². The LP/meadowrue habitat was also productive, with 70-77 g m⁻². ANPP was consistently higher than standing biomass, mostly due to transfer of shoots to litter, since forests are grazed lightly. The predicted values are generally comparable to the limited set of observed values in Table 4.

Notably, there were no real differences in mean herbaceous biomass before and after the 1988 fires. Biomass and ANPP were greater after the fire in LP,DF/pinegrass, DF/deciduous shrub and wet forests. In the common LP/*Vaccinium* habitats there was little change. Thus, despite the fact that herb biomass appeared to decline in some forests with low biomass initially (Figure 38), these small declines were compensated by increases elsewhere.

A comparison of herbaceous biomass estimates from the simulation and data models at different elevation zones revealed agreements in some cases and discrepancies in others (Table 22). In Douglas fir, the data model predicted decreasing biomass with increasing elevation. However, the simulation model predicted no decline with elevation in Douglas fir. Simulation model biomass actually increased between the 1700-2000 m and 2000-2200 m elevation zones. Data model and simulation model predictions for Douglas fir were similar at 2000-2200 m, however in the 1700-2000 m zone the data model predictions were higher than the simulation model predictions and the reverse was true in the 2200-2400 m zone. In lodgepole pine, the data model again predicted decreasing biomass with increased elevation. The simulation model predicted a decline with elevation. Simulation model predictions were greater than data model predictions except in the 2000-2200 m zone, and the divergence was greater at higher elevations.

In Douglas fir forests that burned in 1988, the simulation model predicted higher biomass at low elevations and higher biomass at high elevations (Table 23). There was little difference in simulated biomass pre and post-fire in Douglas fir. However in lodgepole pine and whitebark pine there was less biomass post-fire. Wet forest herbaceous biomass was greater post fire. Agreement was good between the data model and the simulation model for Douglas fir, Whitebark pine, and lodgepole pine at 2000-2200 m. However above 2200 m the simulation model predicted more biomass than the data model in lodgepole pine. The simulation model predicted less biomass than the data model in wet forests.

Shrub cover varied among different habitats and locations (Table 24). There were few observed values to compare to (Table 8). Outside exclosures on the upper northern winter range in 1988, a mean of 14.2% cover was observed while the model simulated 14.4% cover in 1969-1988 and 12.5% cover in 1989-2001. On the lower winter range, 0.9% cover was observed outside exclosures while the model predicted 5.6% cover in 1969-1988 and 6.8% cover in 1989-2001. Inside exclosures, 6.5% cover was observed suggesting the difference could be due to the fact that mule deer and antelope browsing on sagebrush in that area were not represented in the model. Mean willow cover in 1986-1988 on the northern range was 25% (Table 9). The model predicted 33% for 1988-2001.

Overstory plus understory shrub ANPP and overstory cover values for all grid-cells in each habitat type are shown in Table 25. In forests, total shrub ANPP varied from 96-258 g m⁻²yr⁻¹ in all but wet forests. There were increases in some habitats after the fires and decreases in others. In wet forests total shrub ANPP was only 14 g m⁻²yr⁻¹ before fires but 77 g m⁻²yr⁻¹ after fires. In dry and moist non-forested habitats ANPP varied from 21 to 41 g m⁻²yr⁻¹, with no effects from the fires. Mean ANPP in willow was 232-248 g m⁻²yr⁻¹ while in riparian habitats it was 124-163 g m⁻²yr⁻¹. The latter had less willow cover, and had more area located at higher elevations.

Tree ANPP in lodgepole pine declined with stand age prior to 1988 (Table 26). However post-fire, the regenerating stands (LP0) had lower ANPP than older stands, probably because they were in an earlier stage of regrowth than pre-fire LP0 stands, and plants were still quite small. It is expected that ANPP will rapidly increase in post-fire LP0 stands the plants get larger. In post-fire LP1-LP3 stands, ANPP declined with stand age. A similar pattern held for Douglas fir except there was little decline in ANPP between DF2 and DF3. After 1988, the regenerating DF0 stands were still lower in ANPP than older stands. The DF/non-forests (NF) stands had lower ANPP simply because they had fewer trees. Whitebark pine (WB) stands in the first stage (WB1) were most productive, with declining production in stages 2 and 3 (WB2, WB3). Regenerating whitebark pine stands post-fire were least productive. Spruce-fir stands in stages 0 and 1 (SF0, SF1) had similar ANPP values pre-fire. Post-fire stands in stage 0 were least productive. ANPP declined markedly in stage 3 both pre- and post-fire.

Tree ANPP was maximal between 2000 m and 2600 m elevation (Table 27). At colder, higher elevations tree cover was also less. At lower elevations tree productivity declined as did tree cover. There was also more overstory shrub cover in the lowest elevation zone. Shrub cover increased with elevation above 1700 m. Total overstory plus understory shrub ANPP (Table 27) increased with elevation, partly due to the increase in overstory shrub cover.

On all slopes greater than 10%, aspect has little effect on graminoid ANPP (Table 28). Forb ANPP was greater on south facing slopes. Shrub ANPP was greatest on north and west slopes. Tree ANPP was greater on north and east slopes. Differences in shrub and tree ANPP among aspect positions were due to differences in shrub and tree cover. On non-forested slopes at all elevations, graminoid and forb ANPPs were lowest on northern slopes and greatest on east and south slopes (Table 29). Shrub ANPP was greatest on west slopes and lowest on east slopes. On non-forested slopes below 2000 m elevation, graminoid and forb ANPPs were greatest on north and east facing slopes (Table 30). Shrub ANPP was greatest on north facing slopes.

DISCUSSION

Comparisons Between Simulated and Observed Herbaceous Biomass

Simulated biomass and ANPP levels were generally consistent with data over a wide range of habitat types and productivities. The simulated patterns of biomass distribution on the landscape and over seasonal and interannual time scales were realistic. However, comparisons between observed and simulated values are not always straightforward due to subtleties in the ways that data were collected. Because the simulation included grazers, comparisons must be made between observed grazed biomass and simulated grazed biomass. These comparisons were favorable on the northern winter range and for the most prevalent habitat types in Hayden Valley. In Hayden Valley the model under-predicted hairgrass biomass by 25% and sedge meadow biomass by 11%, however these areas comprised only 2 km² and 9 km² respectively.

The discrepancy between simulated and observed biomass in Madison/Firehole hot

spring vegetation was likely due to an imperfect comparison. On average, Dawes (1998) found 68% less biomass outside than inside grazing exclosures (fixed cages) in 1996, and 84% less in 1997. However, out of 92 paired comparisons of biomass inside vs. immediately outside each exclosure, only 11 were significant ($p < 0.05$) and 12 were near significant ($0.05 < p < 0.1$). Five of the significant and two of the near significant differences were in May, reflecting winter offtake rather than summer utilization and plant growth. In July and August, there were no differences in biomass inside versus outside of fixed cages in 1996, and only 2 out of 12 comparisons in 1997 were significant. The mean observed biomass value given in Table 17 included and was thus influenced by Dawes' May values, while the model value was for August only. Thus, the simulated value represented summer plant growth and offtake, while the observed value was heavily influenced by winter offtake. Fine-scale spatial variability in grazing likely also contributed to the discrepancy. Some locations may have experienced heavier grazing pressure, yet the outcomes at these locations could have been averaged out at the 1 km² resolution of the model.

Comparisons could be made between observed ungrazed biomass and predicted ANPP, which includes grazing offtake. However there are two problems with this comparison. One is that exclosed peak biomass may be less than ANPP outside exclosures due to stimulation of growth by herbivory. Stimulation of plant growth by herbivory is discussed in further detail elsewhere (Coughenour 2005a). The other is that the transfer of biomass to litter inside the exclosures causes ungrazed biomass to be less than ANPP. In either case, simulated ANPP would be greater than observed ungrazed biomass. Modeled ANPP was indeed consistently greater than ungrazed biomass due to both factors.

There were limited data for herbaceous biomass in forests, and no data for ANPP. However, comparisons between simulated and available observed values were favorable. As expected, biomass was lower in forests than in open grasslands and shrublands at comparable elevations, indicating that the model was successful in predicting the effects of trees on resource availability to the herbaceous understory. Higher biomass was predicted for Douglas fir than lodgepole pine forests, which was consistent with three of the four data points for Douglas fir. This was probably due to generally longer growing seasons at the elevations Douglas fir is found at, deeper soils with higher water holding capacity, and higher soil fertility in Douglas fir habitats compared to lodgepole pine habitats. Herbaceous biomass in mature lodgepole pine was predicted to be 36 g m⁻² averaged across elevation zones while Hansen et al. (2000) found a mean of 24 g m⁻². However the variance among modeled grid-cells was large, with the standard deviation being 50% of the mean. There is also a potential that biomass collections in forests tended to avoid forest clearings and open patches over larger scales. For example if forest stands, perhaps with small open patches, were interspersed with larger open patches, sampling might be restricted to the forests on the grounds that the large open patches are not forests. In contrast, the model did not distinguish patches of less than 500 m x 500 m or 1 km x 1 km in size.

Factors Controlling Herbaceous Biomass and ANPP Distributions

In agreement with previous field studies (Merrill et al. 1993, Hansen et al 2000), the

model predicted significant changes in herbaceous biomass and ANPP with elevation. Herbaceous and tree ANPP declined at the lowest elevations due to reduced precipitation, and they declined at the highest elevations due to reduced temperatures and shorter growing seasons. Like the ecosystem model predictions, NDVI, and data model predictions declined at low and high elevations. At low elevations, the negative effects of decreased precipitation on ANPP were stronger than the positive effects of warmer temperatures. At high elevations, the negative effects of cold temperatures were stronger than the positive effects of increased precipitation.

The elevation trends predicted by the ecosystem model in non-forested habitats were in agreement with trends in precipitation, NDVI, and the biomass data model (Table 16). NDVI was maximal at 2200-2400 m. This is also the elevation band in which the model predicted the most productive non-forested areas would be located (Table 20). In contrast to the trend found by Hansen et al. (2000) in forested habitats, the model did not predict lower understory biomass in lodgepole pine forests at <2200 m than at >2400 m. Hansen et al. found twice as much herbaceous biomass in mature forests and three times more biomass in clearcuts at <2200 m than at >2400 m, purportedly due to warmer temperatures and longer growing seasons. In Douglas fir forests however, the model did predict less understory biomass at <2000 m than at > 2000 m.

Much of the predicted heterogeneity of herbaceous biomass among sites in was tied to the assumed redistribution of water on the landscape. Topographic variation results in variably sized areas of runoff and runoff - runoff areas receive surface and subsurface water from varying upslope areas. Variation in contributing upslope areas in turn, results in spatial variation in the amount of water subsidy and thus plant growth. Although SAVANNA is capable of redistributing runoff and subsurface drainage according to the distribution of topographic similarity index (TSI) and thus contributing upslope areas, that feature was not used here because it was beyond the scope of this study to test that submodel. Instead, the simple approach of specifying time-varying water tables in mesic habitats was used, and this was the mechanism responsible for the much higher production in sedge, willow, riparian, hairgrass, and wet forest habitats. This assumption, and the results, are consistent with field studies where multiple topographic positions have been examined (Coughenour 1991, Frank and McNaughton 1992, Merrill et al. 1993, Wallace et al. 1995, Singer and Harter 1996, Hansen et al. 2000). The field studies have shown that mesic, moist, and dry habitats differ both in species composition and in biomass. Although variations are visually apparent, unfortunately, none of the studies have provided data on soil moisture variability.

Soil properties play a fundamental role in affecting primary productivity and in explaining variations at multiple spatial scales. Variations in soil depth and texture were paramount, as they determined variations in soil water holding capacity (Figure 6B). There are broad and fine scale patterns of water holding capacity across the region. Many of the forest soils are thin and coarse textured in contrast to the deeper and heavier soils of most of the grasslands and shrublands. Despite high water inputs from snowmelt, on the coarse textured soils, much of the snowmelt likely leaches beyond the rooting zone. A much higher amount of water is likely retained on the fine textured soils.

Broad and fine scale variations in soil fertility also affected primary production. There was a broad scale differentiation of subregions with respect to this substrate difference (Figure 6C), which likely contributed to broad scale differences in NPP. Andesitic soils are more fertile than rhyolitic soils (Trettin 1986, Despain 1990, Rodham et al. 1996) and substrate differences did affect simulated plant growth (Tables 20,21). Because total soil carbon and nitrogen were greater in the andesitic soils, there was greater N mineralization. This in turn increased plant growth to the extent that N was limiting. The soil fertility effect was modified by elevation, with less of an effect at low and high elevations. The fertility effect would be greatest in areas with more optimal moisture and temperature conditions if soil fertility acts multiplicatively with the effects of moisture and temperature.

Differences in ANPP on different aspect positions could have been due to variations in incident solar radiation.

- need to look in more detail at radiation effects on plants, snow, water balance
- finer scale variations related to topo, not captured here, runoff, snowblow, etc.
- effect of snow cover on grow season length

For example, north facing slopes have been shown to have higher NDVI's than south facing slopes (Burrough et al. 2001), which is most likely a consequence of radiation. A relevant question is whether the ecosystem model captured this effect? The model simulated higher total green biomass on north slopes than south slopes, but this was due to the higher tree cover on north slopes, which was part of the initial conditions. The model does not currently account for the effect of slope angle on incident photosynthetically active radiation, but it does account for slope angle effect on evaporation and transpiration, which would reduce water use efficiency.

Interannual Variability in Herbaceous Biomass and ANPP

Interannual variability in precipitation has been considered to be the most likely source of interannual variation in herbaceous biomass production. However, this effect has not been well documented in empirical research in Yellowstone N.P. Coughenour and Singer (1996) carried out correlations and regressions of biomass on precipitation using data from early "volume plots" 1935-1950. They found a significant correlation of total biomass with water year precipitation and spring precipitation but only with correlations (R^2 's) of 0.28 and 0.18 respectively. They used data from from three years of more recent studies (Coughenour 1991, Singer 1995) to focus on green biomass, which would be more sensitively related to precipitation. Green biomass outside exclosures was weakly correlated to spring precipitation ($R^2=0.24$) while green biomass inside exclosures was more significantly related to winter precipitation ($R^2=0.52$) and weakly related to water-year precipitation ($R^2=0.28$). The clarity of the results are undermined by the weak correlations, the lack of a correlation between water-year precipitation and green biomass outside exclosures, and the lack of a correlation between winter precipitation and total biomass in the volume plots. A more subtle problem may be that effects of spatial variability may be confounded with effects of temporal variability. Biomass on the lower winter range near Gardiner, Montana was matched to precipitation in Gardiner, while biomass on the upper winter

range was matched to data from Mammoth, Tower, and Lamar and data from both lower and upper winter range were included in the correlations and regressions. Thus, effects of precipitation may have been largely a result of the well documented differences in herbaceous biomass and cover between upper and lower winter range, which are an outcome of cumulative differences in precipitation over longer time periods. Similarly, Merrill et al. (1993) found no significant correlation between annual precipitation and green biomass sensed in Landsat remote sensing data between 1972 and 1987. They only found a negative relationship between the date of the Landsat scene and green biomass, reflecting the normal curing of herbaceous plants as the soil dries out during the summer (July-September). Interestingly, they found that in a year with high precipitation, green biomass could actually be reduced by the extended duration of the snow pack. Thus, the only two attempts to document a relationship between interannual precipitation and biomass have been relatively inconclusive.

It is not inconsistent with data, therefore, that the model predicted little interannual variation in total biomass or ANPP despite variance in interannual precipitation. The single exception was the simulated response to the dry conditions in summers of 1988. The model predicted a 1 year delayed response, with lower production in 1989, not in 1988. This is consistent with data. Coughenour (1991) observed higher total biomass in 1988 than in 1987. Frank and McNaughton (1992) observed lower ANPP in 1989 than in 1988. They suggested that the 1988 drought may have caused plant or root mortality, in summer of 1988, which diminished productive potential in 1989. They correctly pointed out that the spring of 1988 was actually well above average in precipitation. The drought only began in June. This suggests that total biomass production is mostly affected by spring, and possibly winter precipitation. Summer precipitation contributes little to ANPP, but it is important in other ways. The model simulated an early curing of herbaceous plants in 1988, that is a transfer of tissues from green to senescent, accompanied by a decline in tissue nitrogen concentration. The model also simulated increased root mortality, or at least an inability of the plants to supply photosynthate to roots at a rate equal to the rate of root turnover. What was unique about 1988 was that spring moisture was well above average, but there was little moisture during early-mid summer and the soils dried out when plants normally replenish root biomass. As a result the plants entered winter of 1988/1989 with lower root biomass. Dry conditions occurred again in summer of 1989, and because of the low starting point, roots declined to even lower levels. A common misconception is that the drought of 1988 resulted in less forage biomass for elk, which contributed to increased elk mortality in winter of 1988/89. Based upon a careful examination of the model outputs and available data, however, this is not correct. Instead, total ANPP was not reduced in 1988, but the dry summer of 1988 did result in an early curing of forage and lower forage quality, which then likely reduced forage digestibility and total digestible energy intake.

The model predicted even drier soil conditions in the winter of 1986/1987. The soil dried to a very low level in the fall of 1986. This did not affect plant growth in 1986 because the plants had already entered dormancy. Subsequent snowmelt in spring of 1987 replenished soil moisture. There was a dry period in summer of 1987, but it was later in the summer than in 1988. As a result, plant growth in 1987 was little affected either by dry soil conditions in winter 1986/1987 or in late summer 1987. The comparison of events in 1987 and 1988 reveals the importance of

the timing and thus duration of summer dry-down. It is significant that shifts in the timing of precipitation can bring about such results given that the system is otherwise rather insensitive to variations in total annual precipitation.

Tree and Shrub ANPP

Simulated forest shrub ANPP was lower than values calculated by Hansen et al. (2001). While shrub ANPP in simulated lodgepole pine was $166\text{--}258\text{ g m}^{-2}\text{yr}^{-1}$, Hansen et al. derived $51\text{--}82\text{ g m}^{-2}$ shrub ANPP in mature lodgepole pine forests and $37\text{--}188\text{ g m}^{-2}\text{yr}^{-1}$ in burned lodgepole forests. They calculated ANPP by dividing total biomass by eight years, assuming that to be the average age of the plants. A problem with that approach is that leaf turnover occurs annually in deciduous shrubs, so leaf ANPP would be underestimated eight-fold. Based upon their ANPP values the biomass values would have been $414\text{--}616\text{ g m}^{-2}$ in mature lodgepole. In comparison, the model here simulated approximately 230 g m^{-2} stem plus 110 g m^{-2} leaf in *Vaccinium* and 230 g m^{-2} stem and 25 g m^{-2} leaf in deciduous shrub understories. Thus, it is likely that cover of understory shrubs was different in the lodgepole forests studied by Hansen et al. study from the forests modeled here. Differences in species composition would also contribute to different predictions.

Differences between observed and simulated tree ANPP could arise from differences in tree density or age class structures in simulated and observed forests. The model was not run for a long enough time period here to test predictions of tree density dynamics. Instead, simulated tree densities were largely influenced by initial conditions. Simulated tree ANPP in mature lodgepole pine forests (LP2-LP3) was $172\text{--}202\text{ g m}^{-2}\text{yr}^{-1}$. In close agreement, Hansen et al. (2000) found $142\text{--}211\text{ g m}^{-2}\text{yr}^{-1}$. Pearson et al. (1987) measured $250\text{--}320\text{ g m}^{-2}\text{yr}^{-1}$ in mature even-aged lodgepole pine stands and 150 g m^{-2} in uneven aged stands in Wyoming. Hansen et al. (2000) calculated that $220\text{--}280\text{ g m}^{-2}\text{yr}^{-1}$ was likely in the study by Pearson et al. (1987). Binkley et al. (2003) found a wide range of $130\text{--}488\text{ g m}^{-2}$ ANPP in old growth spruce/fir forests in Colorado, probably largely reflecting variations in stand density. Reed et al. (1999) found $14.3\text{ g m}^{-2}\text{yr}^{-1}$ in a low density 9-year old stand and 381 g m^{-2} in a high density 9-year old stand. Thus, the simulated mean of 131 g m^{-2} for LP0 for 1989-2001 is mid-way between the observed values for low and high density stands. Douglas fir productivity was $236\text{--}256\text{ g m}^{-2}\text{yr}^{-1}$ while Hansen et al. (2000) found $348\text{ g m}^{-2}\text{yr}^{-1}$ in a single stand. Differences in tree density and cover between that stand and the forests modeled here are unknown, but could account for the difference.

The fact that the model predicted decreasing ANPP with increasing stand age is significant. Declining ANPP with stand age is commonly observed, and the potential causes are much discussed (Gower et al. 1996, Ryan et al. 1997). Causes could involve decreased photosynthesis to respiration ratios, increased nutrient limitation, changes in root/shoot allocation, or decreased hydraulic conductivity from soil to leaf in larger trees. An in-depth study of the causes behind model predictions is beyond the scope of this study, however it is likely that all of the mechanisms except the hydraulic conductivity change played a role in the model predictions.

Implications for Ungulates

Predicted spatio-temporal patterns of herbaceous biomass have implications for grazing ungulates. Bison and elk seasonal ranges were outcomes of the dynamic distributions of available forage. Available forage in this ecosystem is strongly influenced by snow cover. The model predicted dynamic snow depth distributions, which then affected habitat selection and forage intake rates. It was assumed that animals move in response to snow cover due to the effect of snow on forage intake rate, as well as mobility. Accumulated snow depth at the end of winter in combination with air temperature, determined the date of final snowmelt, and subsequently, the time of herbaceous green-up. After snow melt, air temperature is most likely the final determinant of green-up date. It has been observed that elk move up-slope in spring, following a “green-up wave” (Frank and McNaughton 1992). The model predicted the progression of this “wave” through underlying processes. The simulated timing of snowmelt occurred at later dates at higher elevations due to increased snow accumulation and colder temperatures. The model also predicted higher leaf N concentrations in early phenological stages, so the most nutritious forage would occur during the period immediately following green-up. Thus, the model predicted waves of forage quality as well as forage quantity that would drive elk and bison migrations.

The distribution of forage during summer months would likely have differential effects on elk and bison ranges. Given that bison are pure grazers and have a high preference for graminoids, their summer ranges would be limited to grasslands such as those in Hayden and Pelican Valleys, or high elevation grasslands such as those found on Mirror Plateau. Their larger body size also requires that they forage in more productive grasslands so as to obtain a sufficient rate of intake to meet their greater energy demands. In contrast, elk are mixed feeders so they could be less constrained to grasslands, and their smaller body size would allow them to exploit less productive grasslands such as those found on ridges. The model predicted that most of the forests, excluding wet forests, produce little herbaceous forage. The prevalent *Vaccinium* shrubs are very low in digestible energy and would not be palatable. Coarse forest grasses such as pinegrass are also widespread, but have low palatability. Forests with understories comprised of other shrub species and forbs would be suitable elk habitats, however.

During winter, suitable habitats would be those which have ample supplies of herbaceous forage and snow depths that are not so deep as to prevent forage intake through cratering. These are the two attributes that primarily define the northern winter range. While elk are limited to conditions on the northern range, the tolerance of bison for deeper snow is probably a primary reason why they winter in the higher elevation Hayden and Pelican Valleys, and in the Firehole area. The presence of thermal areas both on thermally warmed ground, and along thermally warmed rivers and streams in these areas also provide important refugia during severe winter conditions (Meagher 1973). The model simulated these areas by exposing the snow pack to warmer than ambient temperatures, thus resulting in shallower snow depths and improved foraging conditions.

Uncertainties and Data Gaps

In order to increase predictive capabilities for plant biomass and net primary production in Yellowstone N.P. and adjacent ungulate ranges, it would be advantageous to focus on the following areas.

- 1) Landscape scale herbaceous biomass sampling covering a wider range of habitats and topographic positions would be very useful. Certain areas of YNP, particularly the northern range, have been well studied. Other areas such as Hayden Valley and the Firehole/Madison River area have only been studied during the last few years. Other areas important to ungulates have still not been studied, including Pelican Valley, Mirror Plateau, and Gardiners Hole. There is a need to be able to extrapolate herbaceous biomass from landscape variables, which depends upon an .
- 2) Surprisingly little information is available to characterize forest understory biomass, shrub cover, or plant functional group composition. While forest understory species composition has been characterized (Despain 1993), abundances have not. A study is required to relate understory biomass to habitat variables to enable extrapolation across the landscape.
- 3) Tree and overstory shrub cover maps are needed. An attempt was made herein to estimate tree cover from winter NDVI values, however more accurate methods could be employed, particularly methods based upon high resolution aerial photography. It is possible for example, to grid the landscape at 500 m resolution and estimate tree and shrub cover for each grid cell using a dot count approach. Another approach would circumscribe polygons of similar cover visually, and estimate cover in each polygon with dot counts or trained visual estimation. In particular, maps for willow and sagebrush cover are needed.
- 4) The modeling experiments here did not explicitly consider landscape water redistribution except through modeling runoff and prescribing water table depths in certain habitats. In a future modeling project, the redistribution should be modeled more explicitly. It would be beneficial to more adequately characterize the redistribution of water on the landscape due to runoff, runoff, and basal flow. There is insufficient data about water table dynamics in various habitats that are subsidized through surficial or subsurface water flows. A study of soil moisture by depth in relationship to landscape position, vegetation type, and precipitation would enable water regimes to be more adequately characterized across the landscape based upon GIS data.
- 5) While excellent soils map has been developed for YNP and surrounding areas, there is a need for matching data on soil carbon and nitrogen contents.
- 6) Maps of thermally warmed ground including areas along thermally warmed streams, along with studies of soil and air temperatures, and snow depth dynamics in such areas, would improve capabilities for predicting primary production. The length of the growing season is expected to be markedly enhanced by the shorter duration of snow cover and

higher temperatures.

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