Savanna - Landscape and Regional Ecosystem Model

Model Description

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Table of Contents

List of Figures. ............................................................... v

Section I. Introduction and Model Overview. ........................................ 1
  Introduction. .................................................................. 1
  Spatial Structure. ......................................................... 1
  Submodel Overview...................................................... 3
  Savanna Modeling Objectives. ......................................... 4

Section II. Weather Data Input and Generation. ................................... 6
  Data Input and Generation. ............................................ 6

Section III. Soil Water Submodel. .................................................. 9
  Soil Water Simulation. ................................................... 9

Section IV. Snow Submodel. ................................................... 12
  Simulating Snow. ....................................................... 12

Section V. Net Primary Production Submodel. ..................................... 13
  Light Penetration and Interception................................... 13
  Potential Transpiration Rates........................................ 14
  Realized Net Primary Production. ..................................... 15
  Nitrogen Uptake.......................................................... 17
  Leaf Growth Initiation.................................................. 17
  Biomass Allocation - Herbs and Shrubs. ........................... 17
  Biomass Allocation - Trees. ........................................... 19
  Tree Biomass Growth and Size Class Increments. ............... 19
  Phenology................................................................. 20
  Tissue Senescence and Mortality. ..................................... 21

Section VI. Plant Population Submodels. ........................................ 22
  General Approach. ........................................................ 22
  Biomass-Based Seed Germination and Establishment. .......... 23
  Simple Demographic Seed Dynamics and Establishment. ....... 23
  Plant Mortality. .......................................................... 25
  Plant Sizes and Cover. .................................................. 25
  Transfers Among Tree Size Classes. ................................ 27

Section VII. Plant Fire Responses.................................................. 28
  Simulating Fire Responses............................................ 28

Section VIII. Herbivory Submodel. ............................................... 30
  Available Forage. ........................................................ 30
Diet Composition................................................................. 31
Forage Intake Rate.............................................................. 35

Section IX. Ungulate Energy Balance, Weight Change and Condition Index. ............ 35
Simulating Ungulate Energy Balance........................................... 35

Section X. Ungulate Population Submodel.................................... 38
Simulating Populations............................................................ 38

Section XI. Ungulate Distribution Submodel.................................. 40
Simulating Ungulate Distribution............................................... 40
The Water Discharge Map....................................................... 42

Section XII. Wolf Submodel.................................................... 44
Simulating Wolves................................................................. 44

Literature Cited........................................................................... 46
List of Figures

Figure 1  Overall Model Structure. ................................................ 1
Figure 2  Spatial Structure of the Model. ........................................... 1
Figure 3  Water Model. .......................................................... 9
Figure 4  Daily - Weekly Water Allocation Scheme. .......................... 9
Figure 5  Light and Water Model - Vertical and Horizontal Spatial Structure. .............. 13
Figure 6  Transpiration - NPP Linkage. .......................................... 14
Figure 7  Allocation of NPP .................................................... 18
Figure 8  Establishment Models. ................................................ 23
Figure 9  Tree Population Model. ................................................ 27
Figure 10 Ungulate Energy Balance - Population Model Linkage ................. 30
Figure 11 Ungulate Distribution Model. ........................................... 40
Figure 12 Wolf Population Model. ................................................ 44
Section 1. Introduction and Model Overview

Introduction

Savanna is a spatially explicit, process-oriented model of grassland, shrubland, savanna and forested ecosystems. The Savanna model simulates processes at landscape through regional spatial scales over annual to decadal time scales. The model is composed of hydrologic, plant biomass production, plant population dynamics, ungulate herbivory, ungulate spatial distribution, ungulate energy balance, ungulate population dynamics and wolf predation submodels (Figure 1). Since Savanna is process-oriented rather than empirical or rule-based, it aims toward realistic, general and explanatory representations of ecological change as opposed to descriptions of ecological states or prescribed responses.

Every simulation model has a certain level of tradeoff between mechanistic detail and model simplicity. While highly aggregated or simplified models are easier to use, they are less realistic, less generalizable, and less explanatory. On the other hand, highly mechanistic models are more difficult to implement and the marginal costs of added complexity are high. Highly resolved models are more computationally demanding, which may prohibit their implementation at large spatial or long temporal scales. Therefore, Savanna treats ecological processes at an intermediate level of resolution. The time step of the Savanna model is a week, which allows simulations over longer time scales and larger spatial scales. This time step allows Savanna to simulate landscapes composed of 100-1000 grid cells over 5-50 year time spans in a reasonable amount of time on the current generation of microprocessors.

Spatial Structure

The Savanna model has a hierarchical, three-scaled spatial structure (Figure 2). It is spatially explicit (ie. it is sensitive to spatial position) at the landscape scale. It is spatially inexplicit at patch scales. Grid-cells cover landscapes or regional-scale ecosystems. Grid-cell size is scaled to the spatial extent of the simulated ecosystem.

Within grid-cells the model is sensitive to the proportions of grid-cell area covered with "subareas" which correspond to fixed distributions of physical factors like topography and soils. Within subareas, the model simulates vegetation patches or "facets". These are defined by covers of herbaceous plants, shrubs and trees. Therefore facet cover is a dynamic outcome of vegetation growth and mortality. Facet locations are not modeled, only the fractions of subareas that are covered by the facets.

Within classes of facets and subareas, the model simulates plant growth and soil water budgets. The results are scaled-up to the grid-cell level by multiplying by the fractions of the grid-cell area covered by each patch type. For example, if the model simulates 100 g per square meter of plant biomass on a facet, and the facet occupies 25% of the grid cell, then the total plant biomass contributed by that facet to the grid cell is 25 g per square meter. Essentially, scaling-up
Figure 1
Figure 2
is nothing more than area-weighted averaging. Thus, the model does not delimit the exact locations or boundaries of the subareas or facets, only the fractions of ground that they cover. In other words, the model is spatially inexplicit at patch scales.

Water is redistributed at the sub-grid scale by modeling runoff and runon. By simulating water movements among landscape positions, the model accounts for effects of patch-scale landscape structure on soil water storage and subsequent plant growth. Runon potentially recharges deeper soil layers, thus affecting the balance between deep and shallow rooted plant species, and the length of the period during which water is available to support plant growth. Similarly, variations in ecological responses among slope/aspect classes can be important, in which case these classes should also be recognized as subareas.

Patches dominated by trees, shrubs and herbaceous plants on each runoff, runon or other landscape position are dynamic. The area of land 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 mortality essentially creates "gaps" which are then reclassified as herbaceous. The explicit positions and numbers of gaps are not simulated, only the their total area. By definition (of the tree and shrub facets), tree and shrub establishment can only occur on the herbaceous facet. There, herbaceous plants may inhibit tree and shrub establishment.

Tree and shrub vegetation covers are defined in terms of rooted area; ie. 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. A centimeter of water in the soil, for instance, corresponds to 10,000 cm$^3$ of water on one square meter of ground. When plants use $x$ grams of water per square meter, $y$ cm should be removed from their rooting volume. Rooted area per plant may be either smaller or larger than canopy area. If it is larger, then plants will be implicitly spaced so that canopies do not overlap. If rooted area is smaller than canopy area, then canopies may be implicitly overlapping. Although tree rooted area defines tree cover, understory shrubs and herbaceous plants are assumed to share the soil volume exploited by the overstory tree. Thus on tree covered facets, trees, shrubs and herbaceous plants all compete for the same soil resources.

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. The second layer is generally the deepest layer that is exploited by herbaceous roots. The bottom layer is generally occupied only by 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.
Submodel Overview

Savanna is comprised of several interacting submodels (Figure 1). Each of these is described in detail elsewhere in this document. Here, however, a brief overview is provided of submodel functions and interactions.

Savanna is driven by monthly weather data. Precipitation data may be spatially explicit, or it may be spatially inexplicit mean values for the ecosystem. Non-spatially explicit monthly temperature data from a base station at known elevation are corrected for grid cell elevations according to temperature lapse rate. A snowmelt submodel simulates snow water content and depth. Snow crusting is stochastically related to temperature.

The water budget submodel simulates soil moisture dynamics and use on each patch type on each grid cell. Soils map data are used, in conjunction with soil properties for each soil type, to determine soil water holding capacities of each subarea on each grid cell. The water budget includes terms for precipitation, interception, runoff, runon, infiltration, deep drainage, bare soil evaporation, and transpiration.

The light submodel simulates shading within and among plant canopies. On tree covered facets, incident radiation first passes through the tree canopy, then the shrub understory and finally the herbaceous understory. Light extinction follows an exponential decay function, dependent on leaf area indices.

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 efficiency. Thus, for each gram of water used by plants, a certain amount of biomass is produced. Biomass is allocated to leaves, stems and roots. Plant tissues die due to water or temperature stress or phenological stage, and they turn over at a nominal rate that reflects their maximal longevities. The NPP submodel also simulates plant nitrogen uptake and losses due to herbivory and tissue mortality.

Plant population submodels simulate plant establishment, size, and mortality. Herbaceous plant establishment is represented by modeling seed biomass dynamics while shrub and tree establishment are modeled in simpler demographic terms. Establishment is affected by herbaceous standing crop, water and temperature. The herb and shrub population models simulate a single variable-size class while the tree model simulates six fixed-size classes of plants. Mortality occurs at a nominal rate accentuated by water and temperature stress. The population submodels are explicitly linked to the NPP model.

A fire response submodel simulates plant responses to fire in terms of biomass change, changes in plant size, and changes in plant numbers. Fire severity maps specify the spatial distributions of these responses.

The herbivory submodel simulates ungulate foraging. Forage intake is determined by diet selection, forage abundance, forage quality, and snow cover. Diet selection is based on preference indices and relative forage abundances.

The ungulate energy balance submodel simulates body weight of the mean animal of each species, based on differences between energy intake and energy expenditure. Energy intake depends on forage biomass intake and forage digestibility. Expenditures depend on body weight
and travel patterns. The body weight of the mean animal is used to derive an animal condition index, which affects ungulate population dynamics.

The ungulate spatial distribution submodel simulates how animals are dynamically distributed among grid cells over the simulated landscape or region. Animals are redistributed monthly in relationship to habitat suitability. Habitat suitability is dynamically affected by changing forage distributions as well as topography, water, vegetation structure and management.

The ungulate population dynamics submodel is a stage-structured model with five age/sex classes: newborns, immature females, immature males, mature females and mature males. Birth rates and death rates are affected by animal condition indices. Animals may be culled from their respective populations in a prescribed or rule-based manner.

Finally, the wolf submodel simulates wolf predation and wolf population dynamics. Predation rate responds to prey density. The wolf population then responds to its prey intake.

**Savanna Modeling Objectives**

The Savanna model is oriented towards simulating spatially extensive ecosystems occupied by herbivorous ungulates, however, it can also be used to simulate vegetation change in the absence of herbivores. The Savanna model can be used to simulate multispecies plant communities, but it is really designed to simulate interactions among plant functional groups such as sun-adapted herbs, shade-tolerant herbs, shrubs, deciduous trees and evergreen trees. The explicit linkages among water and nutrient pools, primary production processes and plant population dynamics provide answers to a number of questions than would be difficult to address with either a population dynamics model or a biomass model alone. For example, does competition for water and light affect relative numbers and sizes of different functional groups of plants? Similarly, since ungulate population dynamics are affected by forage intake rate, levels of herbivory are tightly coupled to ungulate densities. Ungulate carrying capacity depends strongly upon this linkage, whether carrying capacity is defined in terms of maximum sustainable stocking rate or in terms of a naturally regulated balance between plants and ungulates.

In contrast to an annual time step model, Savanna is suited to simulate seasonal dynamics, by virtue of its weekly time step. Seasonal dynamics are important when it is necessary to predict vegetation standing crop and resultant fuel loads, for example. Seasonal dynamics are important when it is critical to evaluate and managing ungulate populations in relation to inter-seasonal forage dynamics. Seasonal "bottlenecks" of low forage availability or vegetation susceptibility, such as during winter or dry seasons, may be critical. On the other hand, the weekly time step is less precise than a daily time step. Savanna is well-suited for simulations of one to fifty years, although longer and shorter runs are certainly possible.

The vertical spatial structure of the model among soil layers and among different canopy layers is suited to address questions about resource partitioning of soil resources, competition for soil resources, and competition for light resources. For example, the hypothesis that trees and grasses coexist in savannas due to soil moisture partitioning among soil depths may be examined.

The horizontal spatial structure facilitates analyses of vegetation responses to broad-scale climatic, topographic and soils gradients or mosaics. For example, how are vegetation and ungulate distributions and interactions related to soils and topography? The finer but non-
spatially explicit spatial scales are useful where smaller scale spatial heterogeneities are thought to have important effects on ecosystem processes. For example, what are the landscape-scale consequences of water redistribution over catenas? While it is theoretically possible to simulate a landscape at a patch-scale spatial resolution, it is not practical. For example, to simulate a landscape using grid cells which are small enough to distinguish runon, runoff, wooded, non-wooded patches, a 1000 m$^2$ grid-cell size may be barely sufficient. At that resolution, it would take 100,000 grid-cells to simulate a relatively small 100 km$^2$ landscape. Multi-year simulations are quite feasible when ecosystems are composed of about 100-2500 grid-cells. More grid-cells can be simulated, but the time required to perform multi-year simulations becomes unreasonable. Therefore, Savanna is suited to conduct long-term simulations at coarse spatial scales, or short-term simulations at highly resolved spatial scales.
Section 2. Weather Data Input and Generation

Data Input and Generation

Weather inputs to the model are monthly precipitation (mm), average maximum temperature and average minimum temperature. Monthly precipitation maps can be used in place of the monthly precipitation data. Alternatively, spatially interpolated rainfall values for each grid cell can be computed as the simulation progresses based upon base station precipitation data and monthly regressions of precipitation against base station elevation. Stochastic weather can optionally be generated from the monthly weather data.

The scheme for stochastic weather generation is to pick weather years at random from the monthly weather data. There may be as few as one weather year on the file, which would then be comprised of the long-term monthly means. Normally distributed random variation is then added to the monthly weather for that year. The coefficients of variation are specified as $C_{vppt}$, $C_{vtnn}$, and $C_{vtmx}$ for precipitation, minimum and maximum temperatures. While random noise is added monthly, the simulated weather patterns will reflect the intra-annual patterns in the observed weather data set. This scheme does not represent weather cycles over years. If this scheme proves too limited, more sophisticated weather generators can be used to generate the monthly weather data.

If the study area is large or has significant topographic relief, then monthly precipitation maps, or dynamic spatial interpolation should probably be used. The scheme for generating monthly precipitation data with dynamic spatial interpolation accounts for elevation effects (Coughenour 1992). The algorithm tests for significant relationships between elevation and precipitation on a monthly basis. If the relation is significant, it is used to improve the estimate derived from squared inverse distance weighted spatial interpolation. This algorithm is implemented directly in the model, but this or similar algorithms may be used to generate monthly precipitation maps.

Regressions of rainfall on elevation are performed for each month. For each grid point (cell), the four nearest weather stations are located and the distances ($D_i$) to these stations are computed. Precipitation data for each of the four stations are used to estimate precipitation at the unknown point, based on the difference in elevation between the weather station and unknown point and the observed increase in precipitation with elevation. Thus, for the $i$th known precipitation datum ($i=1,2,3$ or 4) and the $j$th unknown grid point,

$$P_{pte_{ij}} = P_{pti} + B(E_j - E_i)$$

where $P_{pti}$ is the known precipitation amount, $E$ is elevation, $B$ is the slope of the precipitation vs. elevation regression equation, and $P_{pte_{ij}}$ is the precipitation estimate. Each of the four estimates ($p_{pte_{ij}}$, $i=1,2,3$ or 4) is weighted by the inverse square of the distance ($1/D_i^2$) to derive an estimate for the $j$th unknown point. If the precipitation vs. elevation regression produces a
Spatial variations in temperature and water vapor pressure are computed during a model run based upon elevations in a digital elevation model, the temperature lapse rate ($T_{lapse}$), and the elevation of the monthly weather data station ($T_{relev}$). Minimum and maximum temperatures are assumed to lapse at the same rate.

Stochastic precipitation data can be generated that show typical spatial patterns of precipitation patterns characteristic for the system. This is achieved by first generating a random monthly precipitation value for a base station as described above. The mean value of precipitation over the system is computed from the base station data based on a regression equation with parameters $Pptreg_1$ and $Pptreg_2$. The stochastically generated base station datum is transformed to that system mean, which is then distributed spatially. Then, the model searches the data base of monthly precipitation maps to find a map having the most similar monthly mean precipitation. The spatial patterning of precipitation on that map is used to distribute precipitation in the system. The system mean is preserved the calculation of its spatial distribution.

Mean monthly values of daily global shortwave radiation ($Rad_{gl\_monthly}$, W/m$^2$/d) and relative humidity ($Relh_{monthly}$, fraction) are used throughout a simulation. Photosynthetically active radiation ($Rad$) is 0.5 of global radiation. Units are transformed as mmol/m$^2$/s = .0045W/m$^2$.

Daytime saturation vapor pressure (g H$_2$O/m$^3$) is calculated from temperature as

$$E_{sat}=4.89+0.33T_{day}+0.0695T_{day}^2 \quad T_{day}>5.0$$

$$E_{sat}=6.33T_{day} -0.748T_{day}+0.0301T_{day}^2 \quad T_{day}>5$$

where $T_{day}$ is daytime temperature. Daytime vapor pressure is then

$$E=Relh\times E_{sat}$$

Since temperature varies with elevation, so does $E$. Daytime temperature is calculated from $T_{max}$ and $T_{min}$ as

$$T_{day}=0.606T_{max} +0.394T_{min}$$

while night temperature is

$$T_{night}=0.394T_{max} +0.606T_{min}$$

Potential evapotranspiration (PET) rate is calculated using the Priestly-Taylor equation (Priestly and Taylor 1972).

$$\lambda\text{PET} = Ptcoeff\times(T_{avg}+3.0)\times Rad_{gl}$$

where

$$\lambda=4.188(-0.575T_{avg}+597.3)$$

is the latent heat of vaporization and $Rad$ is global shortwave radiation (mean daytime flux density in W/m$^2$ during the daylight hours). The parameter $Ptcoeff$ must be calibrated for each
The size of an individual precipitation event, ie. rainfall per day, strongly affects runoff and bare soil evaporation. Therefore there is a need to translate the monthly precipitation data into the number and sizes of rain days per week. To accomplish this, the model stochastically determines the number of rain days in each week. The mean number of rainy days per month is estimated from a regression equation of number of precipitation days against monthly precipitation, with parameters $Strmn_1$ and $Strmn_2$. The probability of a rainy day is

$$P_{strm} = \frac{N_{strm}}{M_{dry}}$$

which is the number of storms in a month divided by the number of days per month.

On a rainy day within a week, the amount of rainfall is stochastically determined by sampling from a gamma distribution with mean equal to the monthly precipitation divided by the number of storms per month. The shape parameter of the gamma distribution is encoded into the model as 7.0. While iterating over each day in a day-within-week sub-loop, randomly deciding whether it is a rainy day based upon $P_{strm}$, the total precipitation in the week is summed as well as the number of precipitation days. This process yields a stochastic estimate of the fraction of monthly precipitation that falls in each week ($P_{ptwk}$), the number of storms ($N_{strmw}$), and mean storm size in each week ($P_{ptst}$). The actual monthly precipitation value is not altered in this process, it is merely distributed over weeks.
Section 3. Soil Water Submodel

Soil Water Simulation

Soil profiles are divided into three layers (Figure 3). The total simulated soil depth ($S_{dep}$, cm) is usually the maximum plant rooting depth. The depth of the herbaceous rooting zone ($H_{dep}$) generally defines the bottom of the second layer while the third and deepest layer is often only used by large woody plants. The middle layer is occupied by roots of both trees and herbaceous plants. The top layer depth must be at least as deep as the depth of bare soil evaporation ($E_{dep}$, cm), but also may be slightly deeper ($D_{ep}$). When appropriate, the top layer may be used to represent soil volume where there are very few tree roots. Layer thicknesses, along with volumetric field capacity ($F_{cp}$), 1.5 Mp wilting point ($W_{lt}$), porosity ($S_{mo}$) are used to calculate soil moisture holding capacities and maximum quantity of water available to plants in each layer.

The runoff curve number method of the U.S. Soil Conservation Service is used to calculate runoff. This approach is widely used and is simple to implement. The full algorithm is given in Wight et al. (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. Tables of typical curve condition numbers can be found in Wight et al. (1987), and USDA (1972). Values range from 40 (sand with high vegetation cover) to 95 (wetland or dense clay with little vegetation cover). The model interpolates between the low vegetation cover runoff curve number ($C_{ni}$) at a leaf area index (LAI) of zero and a high vegetation cover number ($C_{ni}$) at an LAI of four.

The runoff curve approach requires daily rainfall data to implement while the Savanna model operates on a weekly time step with monthly rainfall data. For this reason the runoff response from a randomly chosen mean rain day per week is simulated (Figure 4). The rainfall on that day is $P_{ptst}$ (see weather submodel). Total volume ($m^3$) of runoff in a grid cell is calculated as

$$Runvol = \sum_{nfac} \sum_{nsub} Runoff_{nfac,nsub} \times F_{cvr_{nfac}} \times S_{bcvr_{nsub}} \times C_{ellsz} \times 10^{-4}$$

where Runoff is cm of runoff from facet $nfac$ of subarea $nsub$, $F_{cvr}$ is the fraction of the subarea covered by the facet, $S_{bcvr}$ is the fraction of the grid cell covered by the subarea, and $C_{ellsz}$ is km$^2$ of grid cell. This total runoff volume is distributed among runon subareas as

$$Runon = Runvol \times \frac{S_{bcvr_{nsub}} \times 1}{R_{ocvr} \times C_{ellsz} \times S_{bcvr_{nsub}} \times 10^{-4}}$$

to find cm of runon ($Runon$) for each subarea, where $R_{ocvr}$ is total runon subarea cover. This formula distributes total runoff among runon subareas in proportion to their covers. The quantity
Figure 3
of runoff from the runon area is calculated using the same approach, where the effective rainfall per day includes actual rainfall plus runon. Runoff from the runon areas would be exported from the grid cell or routed into a stream flow submodel. Runoff from the runon area is calculated using effective daily precipitation, which is equal to the sum of actual precipitation (cm) plus run-on (cm).

Bare soil evaporation is simulated using the Ritchie (1972) model, which is also used by Wight et al. (1987). The Ritchie model must be implemented using a daily time step. It is applied here on a weekly basis, by calculating the evaporation following a mean weekly rain day. The approach is to calculate the fraction of rainfall that evaporates in a mean weekly rain day, then apply that fraction to the weekly rainfall total (Figure 4). Dummy soil water layers are first initialized with values equal to the current soil water contents (Figure 3). Water from precipitation and runon less runoff is infiltrated into the top dummy soil layer. Crack flow and water in excess of field capacity is drained from each dummy layer. The total water available for evaporation is the fraction \( \frac{E_{dep}}{S_{thck}} \) of water in the top dummy layer. Evaporation proceeds in two stages. During the first stage it is limited only by PET while in the second stage it is limited by soil water content. Evaporation may proceed for at most \( N_{dymx} \) days where

\[
N_{dymx} = \frac{N_{dymn}}{\min(1, N_{strvw})}
\]

is the mean number of days between rainy days plus the rainy day itself. Total weekly evaporation \( (B_{sevw}) \) is found as evaporation per storm times number of storms per week. The maximum bare soil evaporation rate is

\[
B_{sev_{\text{max}}} = PET \times \text{Min}(e^{-LaixK}, Gr)
\]

where \( LaixK \) is total plant leaf area index times extinction coefficient as computed in the light interception submodel. The value \( Gr \) is the "mulch factor" (typically 0.5-1.0), the minimum reduction in PET due to surface litter shading (Wight et al. 1987).

Precipitation that does not runoff is routed to the dummy subsoil layers with crack flow and a simple "tipping bucket" model. The fraction of water input to layer one that is routed to layer two is \( Crack_1 \) and the fraction of that amount that is routed to layer three is \( Crack_2 \). Then, water is drained into successively deeper layers, filling each with drainage from the layer above, up to field capacity. Excess water above field capacity is drained. This approach is applied with the mean weekly rain day to determine the fraction of rainfall that is routed to each layer \( (P_{infl}) \).

Each week, the actual water infiltration into the soil is found as

\[
P_{t} = ((P_{t wk} \times P_{t}) + R_{runon})(1. - S_{run}) + (S_{nf} - S_{run})
\]

where \( P_{t wk} \) is the fraction of monthly precipitation that occurs in the current week, \( P_{t} \) is monthly rainfall, \( S_{run} \) is fraction of runoff during a mean rainy day, and \( S_{nf} \) and \( S_{run} \) are inputs and runoff due to snow melt. The maximum quantity of water available to plants in each soil layer for the week is

\[
A_{l} = (S_{wtr} - W_{ltp}) + P_{t}(P_{infl})
\]

where \( S_{wtr} \) is cm of water in layer \( l \) and \( W_{ltp} \) is the cm of water held at 5 MPascal. The total
Figure 4
water available to a given plant species is the sum of $Avlwat$ over all layers where the plant is rooted (i.e., layers 1-2 for herbaceous, layers 1-3 for woody). The ratio of total available water to weekly PET is

$$Avwpet_{nrl} = \frac{\sum_{i=1}^{nrl} Avlwat_i}{P_{et_{wk}}}$$

where $nrl$ is number of rooting layers. $Avwpet$ is used to affect plant growth and death (see plant submodels).

At the end of each weekly time step, the weekly soil water budget for each layer is updated with

$$S_{lwat}(t+1) = S_{lwat}(t) + (P_{t} \times P_{hfl}) - Transp_l$$

where $S_{lwat}(t)$ is cm soil water at time $t$ and $Transp_l$ is total plant transpiration from layer $l$. Weekly bare soil evaporation ($Bsevw$) is also subtracted from the top layer. The tipping bucket model is then applied to drain any water still remaining in excess of field capacity.

A water table may be specified, but the model has no capability to simulate water table depth. The depth of a water table ($W_{table}$, cm) may be specified for each soil type. Based on that, the quantity of water in each soil layer due to the presence of the water table is determined. Throughout a simulation, soil water in the layer containing the water table surface cannot be less than the sum of water table water plus water held at 5 MP in the unsaturated portion of the layer. Layers below that remain saturated.
Section 4. Snow Submodel

Simulating Snow

The quantity of water in the snowpack (Snowat) of each facet on each subarea depends on the rate of snow input and the rate of melt. Weekly precipitation is snow if $T_{\text{ave}} < Psntmp$. The rate of melt depends on temperature. Melting during night and day are modeled individually. Thus

$$\text{Ssnow}_{\text{day}} = \text{Rmelt} \times (T_{\text{day}} - T_{\text{mltmn}}) \times \frac{\text{DayIn}}{24}$$

$$\text{Ssnow}_{\text{nite}} = \text{Rmelt} \times (T_{\text{nite}} - T_{\text{mltmn}}) \times (1 - \frac{\text{DayIn}}{24})$$

where $T_{\text{mltmn}}$ is the minimum temperature for melting, $R_{\text{mltmx,month}}$ (mm/°C/d) is maximum melt rate in each month. Melt rate is specified for each facet of each subarea. The rate of melt can vary among facets due to differences in plant shading, slope or aspect. Water is lost from the snowpack by evaporation at 0.87 times the PET rate, where 0.87 accounts for the latent heat of fusion.

Snow depth is calculated as

$$\text{Snowdep} = \frac{\text{Snowat}}{S_{\text{dntmp}}(T_{\text{avg}})}$$

where $S_{\text{dntmp}}$ gives cm of snow depth per cm of snow water as a function of daily average air temperature.

Snow crusting is predicted stochastically. Crusting may occur during particular weather patterns of high temperatures followed by refreezing, or from wind. The occurrence of such weather during a month cannot be deterministically predicted from monthly temperatures. Thus, the 0-1 probabilities of a crust developing during a month are given by the functions $P_{\text{crust,month}}(T_{\text{avg}})$ for each month. Crusting is predicted on a weekly basis and there is currently no assumption that crusting in a given week is more or less likely if there was a crust in the previous week. While temperatures vary among grid cells due to elevation, the occurrence of a weather pattern that causes snow crusting potentially affects the entire study area at landscape and subregional scales. Thus, crusting can be based solely upon the base station monthly temperature. Alternatively, crusting may be patchy, with no synchronization among grid cells. The option to model crusting as a synchronous or patchy process is specified by a flag $\text{indcrust}$. Regardless of whether crusting is synchronous or patchy, the effect of local grid cell temperature on crusting is taken into account. The presence of a crust in a grid cell is denoted by the value of the flag $\text{Ncrust}$, where a value of 0 means no crust, 1 means crust.
Section 5. Net Primary Production Submodel

Light Penetration and Interception

The light penetration component of the NPP model simulates mean incident light in the tree, shrub and herbaceous plant canopy layers (Figure 5). Light penetration through plant canopies is modeled using Beer's Law. The products of leaf areas and extinction coefficients are summed across species and tissue types.

\[
L_{ai} = \sum_{nsp=1}^{nsp} L_{ai_{nsp}} \times R_{adk_{nsp}}
\]

The light intensity below the canopy is

\[
R_{ad} = R_{adin} \times e^{-L_{ai}}
\]

where \( R_{adin} \) is incident light intensity at the top of the canopy, \( L_{ai_{nsp}} \) is the leaf area index of plant type \( nsp \) and \( R_{adk_{nsp}} \) is its extinction coefficient. Canopies are divided into three functional group layers containing tree, shrub and herbaceous leaf areas, respectively. Incident radiation at the top of the herbaceous or shrub layer is reduced by overstory shading. The overstory of herbaceous plants includes tree and shrub leaf areas while the overstory of shrubs just includes tree leaf area. Beer's law is used to calculate the radiation that passes through the overstory, which is then used as incident radiation to the next lower canopy layer.

The three functional group layers are each broken into three sublayers and Beer's Law is applied to each. The functional group leaf area is distributed among the \( n \) sublayers in the proportions \( Pr_{lai_{n}} \). The mean radiation intensity within each sublayer is estimated as the mean of the radiation intensity at the top and bottom of the sublayer. The mean radiation in each functional group layer is the mean over the sublayers.

Light is distributed among the tree size classes and tree species. The total leaf area that is above each size and type of tree is computed from the heights of the tops and bottoms of the canopies of the tree size classes in the stand. Total leaf area above a tree size class is used to compute incident light to that class. The total leaf area between the bottom and top of the canopy of each tree size class is used to compute mean incident radiation intensity within the canopy.

Trees in the wooded facet of a grid cell subarea are assumed to be randomly mixed rather than organized into patches of single species and/or size classes at whatever spatial scale is being simulated. This affects the extent to which smaller trees are shaded by taller trees. The accuracy of this assumption depends on the spatial scale of the grid cells. If the grid cells are of the same size or smaller than typical tree "stands" (even or uneven aged), then the assumption is accurate. If the grid cells are much larger than typical stands, then the assumption breaks down. The consequent loss in accuracy may or not be important, depending on modeling objectives.

The incident radiation on trees depends on the degree of clumping of the trees. If a tree is located within a tree clump, then the incident radiation can be computed using the leaf area index
Figure 5
of the clump, or equivalently, the leaf area index of the wooded facet (ie. m$^2$ leaf per m$^2$ facet area). If, on the other hand, trees are widely spaced, particularly at low woody canopy covers, then the incident radiation should be computed from the leaf area index of the subarea (ie. m$^2$ leaf per m$^2$ subarea). The Savanna model is not designed to predict the degree of clumping at this fine spatial scale. Thus, the degree of clumping must be specified with the function $Trclmp(Wdcvr)$, which describes the fraction of trees located within clumps vs. the woody canopy cover on a subarea. $Trclmp$ must, however, have a value of 1.0 at $Wdcvr$ of 1. Thus

$$Radir = (Radcl \times Trclmp(Wdcvr)) + Radsp \times (1 - Trclmp(Wdcvr))$$

where $Radcl$ and $Radsp$ are mean incident radiation intensities for clumped and spaced trees respectively using computed LAIs of the wooded facet on the subarea.

### Potential Transpiration Rates

Savanna computes potential net primary production as the product of a computed rate of water use through transpiration and water use efficiency (Figure 6). Stomatal conductance (g H2O/mg leaf/sec) is calculated as

$$Cs = Csmx \times Efwp(Awpet) \times Eflp(Rad) \times Efslp(T_{dag}) \times \min[Efpn(Pnb), Efslr(Stre)]$$

where $Csmx$ is maximal conductance.

The 0-1 function $Efnp$ describes how $Cs$ decreases as plant nitrogen concentration ($Pnb$) decreases.

The 0-1 function $Efwp$ reduces $Cs$ due to water stress. $Awpet$ is the ratio of available water (mm/d) to potential evapotranspiration (mm/d). $Awpet$ is used rather than actual soil water content for two reasons. First, during the weekly time step a significant amount of water may be added to the soil, which would not otherwise be usable until the next week. Second, the amount of water that is available in a layer during a week may exceed the soil water holding capacity of the layer due to within-week cycles of rain-days followed by plant water uptake. Third, scaling to PET accounts for drought stress effects on daily stomatal closure. Use of $Awpet$ has also worked well over monthly time steps (Century Model, Parton et al. 1994).

Eflp is a 0-1 function of light intensity. The mean radiation in a sublayer is used to compute the effect of light on photosynthesis and transpiration as

$$Eflp = \frac{u \times Rad}{\sqrt{1 + (a \times Rad)^2}}$$

where $a$ is the initial slope of the function $Eflp$ of $Rad$ (mmol/m$^2$/sec). The unitless function $Eflops$ ranges in value from 0-1. Thus the units of $a$ are the inverse of those of $Rad$, ie. m$^2$sec/mmol.

The 0-1 function $Efslr$ is included to represent the possibility that photosynthesis may be enhanced as the rate of root resource supply per unit of shoot mass increases (Coughenour 1991). An effective shoot:root ratio is calculated as
\[ S_{re} = S_{rr} \times Ensr(Pnb) \]

where Ensr is parameterized so that \( S_{re} \) decreases as plant nitrogen increases. This accentuates the positive effect of low shoot:root ratio on photosynthesis in high nitrogen plants. Efsr and Ensr are only parameterized to have effects when justified.

Eftp is a 0-1 function of daytime temperature (\( T_{day} \)),

\[
Eftp = \left( \frac{T_{max} - T_{day}}{T_{max} - T_{opt}} \right) \times \left( \frac{T_{day} - T_{min}}{T_{opt} - T_{min}} \right)
\]

where \( T_{opt}, T_{max}, T_{min} \) are the optimal, maximal and minimal temperatures for photosynthesis.

The transpiration rate (mm/d) is then

\[ Transp = C_s \times V_{def} \times Dayln \times 0.0036 \times Gbiom \]

where \( V_{def} \) is vapor pressure deficit (g H2O/m³), \( Dayln \) is daylength (hours), \( Gbiom \) is green leaf mass (g/m²) and the constant 0.0036 converts units.

\[
0.0036 = 3600 \text{(sec/hr)} \times 10^3 \text{(mg/g)} \times 10^{-6} \text{(m³/cm³)} \times 10^{-3} \text{(mm/gH₂O/m²)}
\]

Transpirational water demand from soil water layers is distributed just as available soil water is distributed

\[
T_{deml} = Transp \times \frac{Avlwat_i}{\sum_{l=1}^{nlay} Avlwat_l}
\]

where \( Avlwat_l \) is available water in soil layer \( l \) and \( nlay \) is the deepest soil layer with roots.

**Realized Net Primary Production**

The sum of potential plant water demands of all the plants that are rooted in a soil layer of a given facet may exceed the actual quantity of water that is available due to the use of a weekly time step. With a daily time step, stomates would gradually close as soil water is depleted. An approximate solution is derived by assuming that each plant's competitive ability for water is proportional to it's potential rate of water use, ie. it's "sink strength" for water uptake. Thus, when total plant water demands in a layer exceed available water,

\[
\sum_{\text{nap}=1}^{\text{nnap}} T_{deml_{\text{nap}}} > Avlwat_l
\]

then the available water is partitioned among competitors in proportion to their demands

\[
A_{\text{transl}_{\text{nap}}} = \frac{T_{deml_{\text{nap}}} \times Avlwat_l}{\sum_{\text{nap}=1}^{\text{nnap}} T_{deml_{\text{nap}}}}
\]
where \( A_{\text{trans}}_{\text{l,sp}} \) is actual water uptake from soil layer \( l \) by plant species \( \text{sp} \) (mm \( \text{H}_2\text{O}/\text{d} \)). Otherwise, if total water demands do not exceed available water, then the actual water uptake equals the potential. Finally, actual net primary production rate (g/m\(^2\)/d) is

\[
N_{\text{pp}} = \sum_{l=1}^{\text{lay}} A_{\text{trans}}_{\text{l,sp}} \times W_{\text{ue}}_{\text{sp}}
\]

where \( W_{\text{ue}} \) is the water use efficiency (g/m\(^2\)/mm \( \text{H}_2\text{O} \)) of the plant species.

\( W_{\text{ue}} \) often decreases with increasing plant size due to greater maintenance respiration costs and possibly other processes. Tree relative growth rates decline with increasing size at least partly due to an increase in respiratory costs of maintaining nongreen tissues and changes in allocation (Shugart 1988, p. 50). For this reason, tree growth equations of forest models (eg. Shugart 1988), dictate that the tree volume increment per unit leaf area is

\[
\frac{d(D^2H)}{dt} = \frac{1}{La} \left( r \left( 1 - \frac{DH}{D_{\text{max}} H_{\text{max}}} \right) \right)
\]

where \( D \) is tree diameter and \( H \) is tree height, \( La \) is leaf area per tree and \( r \) is maximal relative growth rate. Even if diameter increment does not decline with size, the annual tree mass increment per leaf area per year may necessarily decline with increasing tree size in order to be consistent with morphometric relationships. Herb and shrub \( W_{\text{ue}} \) are

\[
W_{\text{ue}} = W_{\text{ue max}} \times E_{\text{swue}}(\text{Relsz})
\]

where \( E_{\text{swue}} \) is a declining function of relative plant size \( \text{Relsz} \),

\[
\text{Relsz} = \frac{\text{Size}}{\text{Size}_{\text{max}}}
\]

where \( \text{Size} \) and \( \text{Size}_{\text{max}} \) are the current and maximal root biomass per plant. The scaling factor for tree \( W_{\text{ue}} (E_{\text{swue}}) \) is specified for each tree size class.

\[
W_{\text{ue,n}} = W_{\text{ue max}} \times E_{\text{swue,n}}
\]
Nitrogen Uptake

Uptake of inorganic soil nitrogen (g N/m²/d) is represented as a Michaelis-Menton function of soil inorganic N concentration (Nₗ g N/m²)

\[ N_{up} = \frac{U_{pmx} \times \text{Roots} \times \text{Enup} \times \text{Enpup} \times \text{Epup} \times \left( \frac{N_{l} \times U_{pmx}}{N_{l} + U_{pnkm}} \right) \times T_{avg}^{Enup} \times T_{avg}^{Epup} \times Phen}{N_{l} + U_{pnkm}} \]

where \( U_{pmx} \) is maximal uptake rate (g N/g root/d), \( U_{pnkm} \) is the Michaelis half-saturation constant (g N/m²), \( \text{Roots} \) is total root mass density (g/m²), \( \text{Proot} \) is proportion of total roots in soil layer \( l \), \( \text{Enup} \) is a 0-1 function of plant N concentration, \( \text{Etup} \) is a 0-1 function of average daily temperature (\( T_{avg} \)), and \( \text{Upnup} \) is a 0-1 function of phenophase (\( Phen \)).

The weekly time step can create situations when the total plant demands for N exceed the available soil N supply. An approximate solution is found by apportioning N uptake among species in proportion to their demands.

Leaf Growth Initiation

Initial leaf growth by perennial plants after a dormant season requires translocation of biomass from perenniating stems and belowground tissues. The rate (g/m²/d) of reserve use by herbaceous plants and shrubs is

\[ Gr_{inr} = \text{Roots} \times Trnmx \times E_{grmb} \times Awpet_{awr} \times T_{avg} \times Phen \]

where \( Trnmx \) is maximum fraction of root mass (Root g/m²) per day, \( E_{grmb} \) is a 0-1 function of temperature, \( E_{awmb} \) is a 0-1 function of the ratio of available water in the top two soil water layers to potential evapotranspiration (\( Awpet_{awr} \)) and \( Ephres \) is a function of phenophase (\( Phen \)). Although the rate is expressed relative to root mass, \( Gr_{inr} \) is supplied by stems vs. roots in proportion to their biomasses.

Tree reserve use rate (g/m²/d) is

\[ Gr_{inr} = \text{Rfstm} \times W_{grm} \times Awpet_{awr} \times T_{avg} \times Ephres \]

where \( \text{Rfstm} \) is maximum ratio of leaf to stem mass, and \( W_{grm} \) is biomass (g/m²) of stems (branch plus bole). Thus for trees, \( Trnmx \) expresses the fraction of maximum leaf mass that can be generated from the use of stored reserves per day.

Biomass Allocation - Herbs and Shrubs

Net primary production of herbs and shrubs is allocated first between shoots and roots, and then shoot growth is allocated among leaves, stems and reproductive tissues (Figure 7a).

Belowground growth of herbaceous plants and shrubs is calculated as

\[ R_{gr} = N_{pp} \times Pr_{rt} \times E_{sr} \times E_{w} \times E_{al} \times E_{nl} \times E_{nl} \times E_{pal} \times Phen \]

where \( Pr_{rt} \) is maximum fraction of \( N_{pp} \) that can be allocated to roots, \( Esrb \) is a 0-1 function of
Figure 7a

Allocation of NPP

Figure 7b

Allocation of NPP
shoot:root ratio ($S_{rr}$), $E_{w}$ is a 0-1 function of the ratio of total available water to PET ($A_{wpet}$), $E_{n}$ is a 0-1 function of plant nitrogen concentration ($P_{n}$), and $E_{p}$ is a function of phenophase ($P_{h}$). The remainder of $N_{pp}$ is used for shoot growth ($S_{gr}$).

\[
S_{gr} = N_{pp} - R_{gr}
\]

Herbaceous shoot growth is allocated to leaves in the proportion $P_{rlf}$ and to reproduction in the proportion $P_{rfl}$, while the remainder is allocated to stems. Thus, leaf growth ($G_{rlf}$ g/m$^2$/d) is

\[
G_{rlf} = S_{gr} \times P_{rlf}
\]

and stem growth ($W_{dgr}$) constitutes the balance.

\[
W_{dgr} = S_{gr} \times (1 - P_{rlf} - P_{rfl})
\]

Allocation of aboveground growth ($S_{gr}$) by shrubs depends on the current fraction of shoots that are leaves. When growth begins, it is assumed that allocation to leaves has highest priority until the morphometric leaf:stem ratio is attained. Thereafter, allocation to leaves is in the morphometric proportion. Thus

\[
D_{fl} = P_{rlf} \times (W_{wood} + G_{biom}) - G_{biom}
\]

is the current deficit of leaf mass relative to the morphometric leaf mass, and

\[
S_{grl} = \min(D_{fl}, S_{gr}) \quad D_{fl} > 0
\]

\[
S_{grl} = P_{rlf} \times S_{gr} \quad D_{fl} \leq 0
\]

is allocations of shoot growth to leaves to meet the leaf mass deficit if there is one, or it is the allocation to leaves in the proportion $P_{rlf}$ if there is not.

**Biomass Allocation - Trees**

Tree NPP is allocated first to leaves (Figure 7b). Any additional NPP is allocated to root and wood according to morphometric stem:root ratios and the current distribution of trees among size classes. Allocation to leaves in trees is similar to that of shrubs: there is a priority to produce leaves until the morphometric leaf:stem ratio is attained. While tree shoot:root allocation is not affected by water in this model, an effect of water is introduced to regulate leaf:stem ratio. Thus the leaf mass deficit is

\[
D_{fl} = (R_{lfs} \times W_{wood} \times E_{wgr(A_{wpet})}) - G_{biom}
\]

where $R_{lfs}$ is the morphometric leaf:stem ratio, accounting for the current tree size class distribution and $E_{wgr}$ describes the fraction of maximal leaf:stem ratio that should be present as a function of the ratio of available water to PET. Leaf growth is then

\[
S_{grl} = \min(D_{fl}, N_{pp}) \quad D_{fl} > 0
\]

\[
S_{grl} = 0 \quad D_{fl} \leq 0
\]

which will maintain leaf mass at the morphometric, water-limited proportion on a weekly basis.
As leaf:stem ratio increases to the morphometric value, \( Npp \) will be increasingly allocated to stems and roots. Therefore root:shoot allocation in trees is entirely dependent on the proportion of \( Npp \) that is needed to produce leaves.

Traditionally, tree growth is measured in terms of annual increments of stem biomass or diameter. To be consistent with these measurements, tree stem and root masses are incremented on an annual basis. The excess \( Npp (g/m^2) \) remaining after weekly leaf and reproductive growth is accumulated over the course of a year in \( Npp_{exc} \).

\[
Npp_{exc} = \sum_{n=1}^{52} (Npp_n - Grlf_n)
\]

for the 52 weeks in a year. At the end of the year it is allocated between stems and roots.

Stem and root biomass proportions vary morphometrically with tree size. Thus, allocation between wood and roots must vary as the tree size class distribution changes. While wood and root masses for each and every tree size class are not tracked, the morphometric proportion of wood biomass in the population can be calculated as a weighted average over the size classes,

\[
Frwood = \frac{\sum_{n=1}^{6} Frwood_n \times Basal_n \times Tnum_n}{\sum_{n=1}^{6} Basal_n \times Tnum_n}
\]

where \( Basal_n \) is basal area per tree of size class \( n \), \( Tnum_n \) is tree density (trees/km\(^2\)) and \( Frwood_n \) is the fraction of wood per tree for each size class.

Wood growth (g/m\(^2\)/y) is calculated from the difference between the morphometric proportion and the actual proportion of wood per tree,

\[
Wdgr = (Frwood \times (Wood + Roots + Npp_{exc})) - Wood
\]

where the quantity in brackets is total tree mass including the current \( Npp \). \( Wdgr \) cannot exceed \( Npp_{exc} \) nor can it be less than 0. The remainder of \( Npp_{exc} \) is allocated to root growth (\( Rtgr \)).

**Tree Biomass Growth and Size Class Increments**

The total wood growth of trees, computed above, is allocated among tree size classes. In turn, the biomass increment of each size class determines how many trees are promoted to the next larger size class.

Total \( Npp \) must be allocated among size classes because the model does not calculate \( Npp \) for each and every tree size class. It is assumed that the fraction of total \( Npp \) that originates from a size class is determined by the fraction of total leaf area in the class, the size-specific water use efficiency (\( Wue \)) of the class, and the light-constraint on the photosynthetic rate of the class.
Thus, the fraction of total \( Npp \) originating from (and allocated to) a given size class \( n \) can be calculated as

\[
Frlai_n = \frac{Frleaf_n \times Sbsize_n \times Tnum_n}{\sum_{n=1}^{6} Frleaf_n \times Sbsize_n \times Tnum_n}
\]

\[
Frltp_n = \frac{Frlai_n \times Eflp(Rad_n) \times Eswuets_n}{\sum_{n=1}^{6} Frlai_n \times Eflp(Rad_n) \times Eswuets_n}
\]

where \( Frlai_n \) is the fraction of leaf area in each size class, \( Frleaf_n \) is the leaf:stem ratio for each size class, \( Sbsize_n \) is the stem mass per tree, \( Tnum_n \) is the tree density (trees/km2), \( Eflp(Rad) \) is the effect of light on stomates and photosynthesis, and \( Eswuets_n \) is the scaling factor that decreases \( Wue \) in larger plants. The increment in wood and root mass for each size class is then

\[
Tgrw_n = Wgr \times Frpsts_n
\]

\[
Tgrr_n = Rtgr \times Frpsts_n
\]

**Phenology**

Growth is initiated after a dormant (cold or dry) season if the current phenophase is the dormant phase (0) and the effects of water and temperature on leaf growth initiation \( Ewgrmb(Awpet) \) and \( Etgrmb(T_{avg}) \) are greater than zero. When growth is initiated, an accumulator begins to sum total degree-days, i.e. the product of daily average temperature times time in days.

Degree days are converted into a phenological stage that ranges in value between 1 (early vegetative growth phase), 2 (late vegetative growth phase), 3 (begin flowering), and 4 (complete flowering and seed set). Phenophase 0 is dormancy. When dormancy is broken, phenophase is set to 1. Phenophase is computed from degree days as

\[
Phen_{ns} = Phenod_{ns} (Phendd_{ns})
\]

where \( Phenod_{ns} \) is total degree days for species \( nsp \) since it initiated growth. The function \( Phenod_{ns} \) relates phenophase to degree days.

Phenology is reset to the dormant phase (0) if either of the following conditions are met:

\[
T_{avg} < Phrstm_{ns}
\]

\[
Awpet_{ns} < Phrswc_{ns}
\]

where \( Phrstm \) is a low temperature, and \( Phrswc \) is a low ratio of available water to PET. If both of the following are true phenology will also be reset to 0.
\[ \text{Phen}_{\text{mp}} = 4 \]

\[ \text{Month} = \text{Mpres}_{\text{mp}} \]

Mpres is the month of the year when phenology will be reset provided a growth cycle is completed, irrespective of temperature or moisture stress.

**Tissue Senescence and Mortality**

Plant tissues senesce at rates affected by water stress, temperature, and phenology. Tissue death rate per day is

\[ \text{Death}_i = \text{Biom}_i \times \text{Max}(\text{Drwat}_i(\text{Awper}), \text{Drtmp}_i(\text{T}_{\text{mp}}), \text{Drphn}_i(\text{Phen})) \times \text{Endr}(\text{Pnb}) \]

where \( \text{Biom}_i \) is biomass of the \( i \) tissue type (leaves, stems or roots), \( \text{Drwat}_i \) is death rate as a function of the ratio of available water to PET, \( \text{Drtmp}_i \) is death rate as a function of temperature, and \( \text{Drphn}_i \) is death rate as a function of phenophase. \( \text{Endr} \) can be used to alter death rates as a function of plant nitrogen concentration. Coarse and fine root death rates are distinguished. A fraction \( \text{Pcmsg} \) of root mass is assumed to consist of coarse roots and the remainder is fine roots. Coarse roots senesce at a fraction \( \text{Driftc} \) of the rate of fine root senescence.

When tissues die, a fraction of the nitrogen follows and the rest stays in the plant,

\[ \text{Ndeath}_i = \text{Death}_i \times \text{Ssn}_i(\text{Pnb}) \times \text{Pnb} \]

where \( \text{Ndeath}_i \) is nitrogen death (gN), \( \text{Death}_i \) is biomass death (gB), \( \text{Ssn}_i(\text{Pnb}) \) is sink strength as a function of plant N:B ratio \( \text{Pnb} \). Stems (or wood) and coarse roots have a quantity of N, expressed as \( \text{Wdnc} \) gN/gB, that is lost during senescence irrespective of \( \text{Pnb} \), while the remainder of the N is affected by \( \text{Pnb} \) as in the equation above.

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 at the rate

\[ \text{Trsd} = \text{Dbiom} \times \text{Max}(\text{Falr}, \text{Esnwdf}(\text{Snowat})) \]

where \( \text{Dbiom} \) is standing dead biomass, \( \text{Falr} \) is minimal transfer rate, and \( \text{Esnwdf} \) is a rate that is a function of snow water content (\( \text{Snowat} \)). Dead roots and tree stems are not simulated in the current model.
Section 6. Plant Population Submodels

General Approach

Herbaceous plant population sizes are modeled on a facet basis (e.g. number of plants per m² in the understory of a wooded facet, or number per m² on the non-wooded facet). There is a single plant size class; however plant size varies in response to tissue growth and mortality.

Shrub populations are modeled on a subarea basis (i.e. number of plants per ha of subarea). Shrubs in the understory of trees are referred to as such. Shrubs not growing beneath trees are referred to as overstory shrubs. Overstory shrub cover defines the shrub facet. Shrub population dynamics are computed using a weekly time step. The shrub population model simulates a single size class, however plant size is variable.

Tree population dynamics are also modeled on a subarea basis (i.e. number of plants per km² subarea). Tree cover defines the wooded facet. The tree population on each grid cell subarea is divided into six size classes. Except for establishment, tree population dynamics are simulated with an annual time step, at the end of month twelve.

There are three main points of connection between the primary production submodel and the plant population submodel; seed germination, plant size determination, and plant mortality. The latter two are relatively straightforward. When plant biomass increases relative to plant number, plants must be increasing in size. When plants die, live tissue biomass is converted to dead tissue biomass.

Seed germination can be represented in biomass or demographic terms. If a biomass-based approach is used, seed size must be known (g/seed). Uncertainty is introduced in successfully predicting seed biomass production, and thus biomass allocation to seeds in the primary production submodel. A demographic approach can be, but is not necessarily, simpler. It is potentially simpler because mass balance does not have to occur. Thus, an establishment rate can be specified in terms of numbers of new plants per extant seed bearing plant without having to track the various fates of seed biomass (i.e. allocation of NPP, plant to soil transfer, death, viability decay, establishment, failed establishment). These various fates could be tracked in terms of seed numbers, but they do not have to be tracked in a simple demographic model.

In past experience, it has proven easier to express shrub and tree recruitment in simple demographic terms than to express it in terms of the biomass of seeds that germinate and become established. However, a more complex approach is needed to simulate dynamics of short-lived or annual herbaceous plants. For instance the time lags associated with seed development and transfer to soil can lead to significant errors if not explicitly simulated. Seed bank dynamics must be modeled explicitly to account for loss of viability, time lags, and potential declining plant abundance due to overgrazing and loss of seed production. Therefore, the model is configured to simulated herbaceous seed dynamics in biomass terms and tree/shrub establishment in simple demographic terms.

Biomass-Based Seed Germination and Establishment
The biomass-based seed model tracks seed biomass from allocation of NPP to seeds on the plant, to seeds in the soil, to establishment (Figure 8a). Seed biomass production and germination are calculated in the net primary production (NPP) submodel. Seed biomass on the plant ($\text{Seed}_p$ g/m$^2$) is distinguished from the seed biomass in the soil ($\text{Seeds}_d$ g/m$^2$). Seeds are transferred from the shoots to the soil at a rate $S_{d_{f_{rlt}}}$ (d$^{-1}$). Soil seeds also originate from an external seed source at a rate $\text{Seed}_r_{n_{sp}}$ g/m$^2$/yr, thus representing a seed rain that originates from outside the study area. Soil seed viability decays at the rate $S_{d_{thrt}}$ (d$^{-1}$). Seeds that become inviable are removed from the soil seed bank.

Seed germination proceeds at a rate (g/m$^2$/d)

$$Grinis_{n_{sp}} = \text{Seeds}_{n_{sp}} \times \text{Germ}_{n_{sp}} \times E_{g_{m_{rb}}(T_{avg})} \times E_{w_{r_{mb}}(A_{w_{pet}})}$$

where $\text{Germ}_{rb}$ is maximal daily germination rate, and $E_{w_{r_{mb}}}(A_{w_{pet}})$ and $E_{g_{m_{rb}}}(T_{avg})$ are functions of available water:PET ratio and average daily temperature. These functions allow growth initiation from root and stem reserves. Newly established seed biomass is converted to leaf and root tissue in equal proportions.

The number of plants that are established due to germination is

$$E_{str_{n_{sp}}} = Grinis_{n_{sp}} \times \text{Seed}_{p_{n_{sp}}} \times E_{h_{r_{beb}}(n_{sp})} \times (H_{erb_{m}})$$

where $\text{Seed}_{p_{ng}}$ is the maximum number of established plants per gram of germinating seed biomass, and where $E_{hr_{beb}}$ is a 0-1 function of total live plus dead herbaceous standing crop of all species ($H_{erb_{m}}$ g/m$^2$). The function $E_{hr_{beb}}$ simulates shading or other competitive effects from established plants.

**Simple Demographic Seed Dynamics and Establishment**

In a simple demographic mode, establishment depends on the number of plants already established, abiotic factors, and "competition" from herbaceous plants (Figure 8b). Shrub establishment in a month, from seed or vegetative spread, is

$$Sh_{estb} = Sh_{num} \times G_{erm_{rs}}(S_{h_{bsz}}) \times E_{gr_{ms}}(T_{avg}) \times E_{w_{r_{ms}}}(A_{w_{pet}}) \times E_{h_{rb}_{es}}(H_{erb_{m}}) \times E_{c_{ov}}$$

where $\text{Sh}_{num}$ is number of shrubs per hectare, $G_{erm_{rs}}$ is the maximum number of new shrubs established per month as a function of shrub size $S_{h_{bsz}}$, $E_{gr_{ms}}$ is a 0-1 function of temperature, $E_{w_{r_{ms}}}$ is a 0-1 function of the ratio of available water to PET, $E_{hr_{bes}}$ is a 0-1 function of herbaceous plant biomass $H_{erb_{m}}$, and $E_{cov}$ is the fraction of a subarea that is available for shrub establishment. $E_{cov}$ for overstory shrubs is

$$E_{cov} = 1 - W_{d_{cov}} - S_{cov}$$

while for understory shrubs it is

$$E_{cov} = W_{d_{cov}} - S_{cov}$$
Establishment Models

a) Biomass-based Seed Germination

NPP

Seeds on Plant

Seeds in Soil

Viability Decay

Establishment

Leaf Root

b) Simple Demographic Establishment

Water, Temperature, Herb. Biomass

Establishment

Leaf Root

Plant Number
where $Wdcvr$, $Shevr$ and $Shevru$ are fractions of ground on a subarea covered by trees, overstory and understory shrubs, respectively.

Tree establishment from seed or vegetative spread depends on the number of mature seed producing trees as

$$Tresth = \sum_{n=1}^{6} Tnum_n \times Germr_n \times Etgrmt(T_{ave}) \times Ewgrmt(Awpet) \times Ehbet(Herbm) \times Ecov$$

where $Tnum_n$ is tree number per km² in size class $n$, $Seedrt_n$ is maximum number of trees that can be recruited into the population per month from the seeds produced by a tree in size class $n$, $Etgrmt$ is a function of temperature, $Ewgrmt$ is a 0-1 function of the ratio of available water to PET, $Ehbet$ is a 0-1 function of herbaceous biomass g/m² on the herbaceous facet.

$Ecov$ is the fraction of the subarea available for tree establishment.

$$Ecov = 1 - Wdcvr - Shevr$$

Thus, if the rooting space on a subarea is fully occupied by shrubs and trees ($Shevr$ and $Wdcvr = 1$), then recruitment can only occur if root gaps open up due to tree mortality or shrub mortality. This does not mean that establishment cannot occur under tree or shrub canopies because wooded facet cover is defined in terms of woody root biomass, not crown closure (see below). It is possible to have free root space even if there is full crown closure, if the rooting volume covers less ground area than a tree crown. If so, then trees will assumed to be closely spaced, with overlapping crowns. New trees will be assumed to be recruited with that spacing. The tree spacing function used in the light interception submodel ($Trclmp$) can also dictate which tree species will tend to be located within clumps or closely packed stands (see Section 5.1).

Larger trees shade smaller trees in the stand - it is assumed that trees in different size classes and species groups are intermixed rather than organized into separate patches in a given grid cell (see light submodel). Similarly, the parameter $Cvpgr$, which defines areal cover per gram of shrub roots can be defined so that shrub canopies overlap (ie. there is a potentially large leaf area per unit of ground occupied by shrub roots). While trees can be clumped, as described by the $Trclmp$ function (see light submodel), clumped trees are still assumed to be well mixed.

**Plant Mortality**

Plant mortality is modeled differently for herbs, shrubs and trees due to differences in their time scales, absence or presence of size classes, and the different factors that control mortality in each group.

Herbaceous plant mortality rate is

$$Dthnum_{nag} = Plnum_{nag} \times Max(Drwatp(Awpet), Drttmp(T_{ave}), Drphnp(Phen))$$

where $Plnum$ is plant density (number/m²), $Drwatp$ is death rate (d⁻¹) vs. available water to PET ratio, $Drttmp$ is death rate (d⁻¹) vs. temperature and $Drphnp$ is a death rate (d⁻¹) vs. phenophase.
Shrub mortality rate is

\[
\text{Shdth} = \text{Shnum} \times \text{Max} \left[ \text{Drwals}(\text{Awpet}), \text{Drumpah}(T_{\text{awp}}) \right]
\]

where \( \text{Shnum} \) is plant density (number/ha), \( \text{Drwats} \) is death rate \((\text{mo}^{-1})\) vs. the ratio of available water to PET.

Tree mortality occurs at a size-specific nominal rate, to which is added an additional mortality due to slow growth (stress). Thus

\[
\text{Tdth}_n = \text{Tnum}_n \times (\text{Drinr}_n + \text{Drslow}(\text{Dincr}_n))
\]

where \( \text{Drinr}_n \) is nominal mortality \((\text{yr}^{-1})\) and \( \text{Drslow}(\text{Dincr}) \) is slow growth mortality rate vs. diameter increment for size class \( n \). Slow growth mortality of trees in size class 6 is computed using \( \text{Dincr} \), since trees in class 6 cannot increase in size, by definition.

**Plant Sizes and Cover**

Mean root biomass per plant is a measure of herbaceous plant size,

\[
\text{Rsize} = \frac{\text{Roots}_{nsp}}{\text{Plnum}_{nsp}}
\]

where \( \text{Roots} \) is root biomass \((\text{g/m}^2)\). In the net primary production submodel herbaceous plant growth stops if root mass per plant attains the maximal value \( R_{\text{szm}x_{nsp}} \). This is particularly important for annual plants because it dictates a maximal standing crop that is dependent on the number of seeds that successfully germinate and establish.

Overstory shrub cover \((\text{m}^2 \text{ rooted area per } \text{m}^2 \text{ subarea})\), which defines the shrub facet, is calculated as

\[
\text{Shcvr} = \sum_{nsp=1}^{nssp} \text{Grmsa}_{nsp} \times \text{Cvpgr}_{nsp}
\]

where \( \text{Cvpgr}_{nsp} \) is the constant \( \text{m}^2 \text{ cover per gram of root biomass for shrub species } nssp, \) and \( \text{Grmsa}_{nsp} \) is grams of shrub roots per \( \text{m}^2 \) subarea of shrub species \( nssp \). Understory shrub cover is also expressed in terms of the fraction of subarea that is covered \((\text{m}^2 \text{ rooted area per } \text{m}^2 \text{ subarea})\).

\[
\text{Shcvru} = \sum_{nsp=1}^{nssp} \text{Grmsa}_{nsp} \times \text{Cvpgr}_{nsp}
\]

Shrub species \( nssp \) is only included if it is an understory species. Understory shrub cover is computed for output only. It does not define a facet. To find cover in the tree understory, \( \text{Shcvru} \) must be divided by \( W_{\text{dcvr}} \).

Since root mass defines the cover of the overstory shrub facet, the biomass densities of shoot and other state variables per \( \text{m}^2 \) of facet area may change in response to changes in total root mass and facet cover on the subarea. Thus, biomass densities per \( \text{m}^2 \) facet are recomputed. For example a new value of green leaf mass per \( \text{m}^2 \) facet is found as
where $G_{\text{lmsa}}$ is grams of leaf per m$^2$ subarea.

$$G_{\text{lmsa}} = G_{\text{biom}, \text{old}} \times Shc_{\text{v}, \text{old}}$$

were, $G_{\text{biom}, \text{old}}$ is green biomass per m$^2$ facet prior to its recomputation.

Tree cover is defined in terms of the rooting volume of individual trees. The effective diameter of a rooting area can be assumed to be the inverse of tree density when trees are at maximal density. Since thinning curves describe the relationship between density and tree size, these can be used to compute effective rooting area radii for each tree size class. The effective rooting area diameter $R_{\text{diam}}$ (m) can be read in directly, or the parameters for the thinning curves of ln(trees/ha) vs. ln(kg/tree) or trees/ha vs. ln(kg/tree) can be read-in and used to compute $R_{\text{diam}}$. Thus

$$W_{\text{dvr}} = \sum_{n=1}^{6} \sum_{n\text{mp}=1}^{\text{max}} T_{\text{num}, n\text{mp}} \times (\pi \times R_{\text{diam}}^2) \times 10^{-6}$$

summing over species and size classes on a sub area where $T_{\text{num}}$ is numbers of trees per km$^2$. As with shrubs, the tree facet is defined by tree rooted area, so the root mass per m$^2$ facet may remain nearly constant, changing only when tree size class distribution changes and when each size class has a different root mass density in the rooted area.

**Transfers Among Tree Size Classes**

Trees are transferred to larger size classes based upon biomass production (Figure 9). Some fraction of the trees in a size class must be promoted to the next larger size class when biomass is added through tree growth, since the biomass per tree in each size class remains constant, by definition. The increase in biomass per tree (g wood/tree) of size class $n$ is calculated as follows.

$$\Delta_{\text{bwt}} = \frac{T_{\text{grw}, n}}{T_{\text{num}, n} \times 10^{-6}}$$

The fraction of trees in a size class that must be promoted is

$$F_{\text{tr}}, n = \frac{\Delta_{\text{bwt}}, n}{S_{\text{bsize}, n+1} - S_{\text{bsize}, n}}$$

where $S_{\text{bsize}, n}$ is the defined tree size (g wood/tree) of size class $n$. The actual number of promoted trees is thus
Tree Population Model

Figure 9
The diameter increment of a size class can be calculated as

\[ D_{\text{incr}} = \frac{D_{\text{elbtr}}}{W_{dpmn}} \]

where \( W_{dpmn} \) is the biomass increment per mm of stem diameter increase, calculated from morphometric relationships.
Simulating Fire Responses

Simulated plant responses to fire include removal of aboveground biomass and plant mortality. The fire severity index that is read from a fire map is translated into plant biomass mortality. The total quantity of biomass that is combusted during a fire is calculated by first summing the total biomass density on a subarea ($g/m^2$ facet $x m^2$ facet/$m^2$ subarea), performing the removals, calculating the remaining biomass after plant mortality and combustion, then finding the difference between the total biomass on the subarea before and after the fire.

Herbaceous plant responses to fire are determined by the parameters $F_{cmbs}$ and $F_{rdth}$, which are the fraction of aboveground biomass combusted (live and dead) and individual plants killed by a fire of severity $n_{sev}$. Root mass is killed in the same fraction as are individual plants.

The fraction of shrub aboveground biomass that is combusted is $S_{frbrn}$, while the fraction of shrub plants killed is $S_{frdr}$. The cover of overstory shrubs is also reduced by the fraction $S_{frdr}$. All plants on a subarea are the same size so cover and numbers must change in parallel. Total overstory root mass per $m^2$ subarea is mass per $m^2$ shrub facet (rooted area) times $m^2$ facet per $m^2$ subarea. Root biomass per $m^2$ of overstory shrub facet does not change: it is a constant specified by $C_{vpgr}$ ($g/m^2$ facet).

Fire impacts on trees are represented through tree mortality and size reductions. The fraction of trees in each size class that reverses by one size class is $F_{rrv1}$, while the number that reverse by two size classes is $F_{rrv2}$, and the number that revert to the smallest size class is given by $F_{rrv0}$. The fraction of tree boles in a size class that is killed by a fire is $F_{dr}$. Trees may respond to fire by producing new shoots (suckering). The number of sucker plants that are produced per fire killed tree is $S_{crt}$. Tree suckers are put into the smallest size class. Thus, although $F_{dr}$ fraction of tree boles die, a fraction $S_{crt}$ of those may be replaced by new boles.

Following a fire, replacement trees are recruited into the population in proportion to the numbers that were killed. This is necessary since the simple demographic model of tree recruitment (Figure 9) is based on living trees only - it does not simulate seed banks. Furthermore, enhanced seed germination after fire due to increased light, serotiny or other factors is not accounted for. Accordingly,

$$Estab = Firegrm \times Dth$$

where $Estab$, is number of newly established trees (per km$^2$), $Dth$, is number of trees that were killed by fire in the $n$ size class and $Firegrm$, is number of new trees per fire-killed tree.

Changes in tree cover ($W_{dcvr}$) on a subarea are brought about as the tree density on a subarea is reduced and as trees are moved from larger to smaller size classes. This is because tree cover is calculated from the product of tree number times the ground area over an individual tree’s rooting volume. Total root mass due to tree death is calculated from the reduction in cover
and numbers of individuals. The tree biomass density per m$^2$ wooded facet changes as the tree size class distribution changes. Each size class has a unique root and stem density per m$^2$ rooted area.

When tree or shrub cover are lost due to fire, through mortality of plants and reductions in plant size and root mass, former understory plants and biomass that survive the fire are transferred to a different facet. Understory herbs are transferred to the herbaceous or overstory shrub facet while surviving understory shrubs are transferred to the overstory shrub facet. In the current structure of the model, however, understory plant types may not occur on the non-understory facets. Therefore, the plants may need to be reclassified into a new type. The parameters $pfwdhb_{nsp,nfac}$ and $Pfwdsb_{nsp,nfac}$ are arrays storing the indices of the plant types that plant type $nsp$ on facet $nfac$ (2-tree, 3-tree) are reclassified to. This limitation will be relieved in future model version which will allow all plant types to occur on all facets.
Available Forage

Ungulate forage intake rate and diet composition both depend upon the distribution and abundance of available forage (Figure 10). Available herbaceous forage is simply standing crop minus ungrazable biomass. For example available green leaf is

$$T_{avg} = G_{biom} - U_{ngrzb}$$

where $G_{biom}$ is current leaf density and $U_{ngrzb}$ is ungrazable leaf biomass density. Stem and dead leaf availabilities are calculated similarly.

Available green shrub leaf is calculated as

$$T_{avg} = (G_{biom} \times E_{shsz} \left( \frac{Sh_{bssz}}{Sh_{smx}} \right)) - U_{ngrsz}$$

where $Sh_{bssz}$ is the simulated mean size of shrubs (g/plant) and $Sh_{smx}$ is the maximum size. Current stems, old stems and dead leaf availabilities are calculated similarly. The function $E_{shsz}$ expresses declining availability due to small plant size. Biomass density (g/m$^2$) cannot reflect this effect because a given g/m$^2$ standing crop may be achieved with many small plants or fewer large plants.

Available tree forage is computed based on tree sizes. Available green leaf is

$$T_{avg} = \sum_{n} G_{biom_{n}} \times P_{rl_{n}} \times A_{vlbr_{n}}$$

where $P_{rl_{n}}$ is the fraction of leaf mass in size class $n$, which is computed from tree sizes and their distribution among size classes. The parameter $A_{vlbr_{n}}$ is the fraction of forage in each tree size class available to an ungulate. Availability of dead leaves, old stems and wood and current stems are computed similarly. The distribution of browsing impact on tree stems ($P_{rdw_{n}}$) is distributed among tree size classes in proportion to available stem mass. $P_{rdw}$ is used elsewhere (see below) to calculate the fraction of plants that revert to smaller size classes due to browsing.

Forage availability is affected by the fraction of plants that are buried,

$$F_{bury} = 1 - e^{\frac{Pl_{ht} \left( S_{nodep} \right)}{P_{rl_{n}}}}$$

where $Pl_{ht}$ is plant height (cm), $S_{nodep}$ is snow depth (cm), and $E_{snw}$ is a parameter (Jenkins et al. 1990). Some ungulates dig or crater, thus buried forage is not necessarily unavailable. Available forage after cratering ($T_{avgc}$) is

$$T_{avgc} = T_{avg} \times (1 - F_{bury} \times E_{snwfr} \left( S_{nodep} \right))$$

where the function $E_{snwfr} \left( S_{nodep} \right)$ is applied to the buried fraction of the forage. $E_{snwfr}$
Figure 10
describes the effect of snow depth on foraging rate, and thus "effective" availability of the buried fraction. If an ungulate cannot dig, then $E_{snowfr}$ equals zero at all snow depths. If an animal can dig to 40 cm, then $E_{snowfr}$ equals zero only at 40 cm depth.

**Diet Composition**

The ungulates in a grid cell, as predicted by the distribution submodel, choose among patches (facets) and plant types within patches in that cell to achieve a preferred diet composition. Diet composition is determined by using preference weightings, similar to Ellis et al. (1976). In this approach, diet composition is affected by the relative availability of different forage types as well as by preferences or avoidances. A preference-weighted rank value of a forage is

$$Prfb_{nsp,nsub,nfac} = Prfw_{nsp} \times Tavg_{nsp,nsub,nfac} \times Cvrfac_{nsub, nfac}$$

where $Prfw_{nsp}$ is the preference weight parameter for the $nsp$ plant type, $Tavg_{nsp,nsub, nfac}$ is the g/m$^2$ facet in facet $nfac$ on subarea $nsub$, and $Cvrfac_{nsub, nfac}$ is the fraction ground (in the grid cell) covered by the facet. Thus, $Prfb$ responds to the total abundance of forage in a grid cell as well as preference. $Prfb$'s are normalized by summing over all plant species and facets in a grid cell, to yield $Prfd$, the fraction of the item in the diet.

$$Prfd_{nsp,nsub, nfac} = \frac{Prfb_{nsp,nsub, nfac}}{\sum_{nsp} \sum_{nsub} \sum_{nfac} Prfb_{nsp,nsub, nfac}}$$

Thus, if all preference weights equal 1.0, plants will be taken exactly in proportion to their availabilities. Preference weights can take any value greater than or equal to zero, since the final rankings ($Prfb$) are normalized.

Animal foraging days in a grid cell are distributed among forage types in the proportions $Prfd$. Animal-days of foraging in each facet is then

$$Hn_{forf, nsp, nsub, nfac} = Hpop \times Prfd_{nsp,nsub, nfac} \times Dtmn$$

where $Hpop$ is total animals in the grid cell and $Dtmn$ is the number of days per time step (week).

**Forage Intake Rate**

The effect of forage abundance on forage intake rate is represented as a Type II functional response. This is expressed as

$$Fr=\frac{Foragg}{Foragg+Frkm}$$

$$Fr=\frac{Foragb}{Foragb+Frkm}$$

where $Frkm$ and $Frkm$ and the forage densities (g/m$^2$) at half of the maximum daily intake
rates, and \textit{Foragg} and \textit{Foragb} are the total densities of graze and browse in an entire grid cell. Total available graze abundance in a grid cell is

\[
\text{Foragg} = \sum_{nsp} T_{nsp,mb,rfac} \times C_{rfac,mb,rfac}
\]

which includes only herbaceous plants. Only items having \textit{Prfwt}_{nsp} greater than \textit{Prfresp} threshold are included, thus potentially limiting the calculation to important dietary items. Browse abundance (\textit{Foragb}) is calculated similarly, by summing over shrubs and trees.

These then, are the aggregate responses to the total densities of graze and browse. Responses to individual forage species abundances are not distinguished since it seems unlikely that \textit{Frkmb} and \textit{Frkmg} parameters for the functional response equation would be known at the species level.

Forage intake rates for each species of graze and browse are

\[
\text{Fintkg}_{nsp} = C_{rnx,ns} \times Fr_{nsp} \times E_{snw,ns} \times E_{cntk,Cond} \\
\text{Fintkb}_{nsp} = C_{rnx,ns} \times Frb \times E_{snw,ns} \times E_{cntk,Cond}
\]

where \textit{Fintkg}_{nsp} and \textit{Fintkb}_{nsp} are kg forage per kg body weight per d (kg/kg/d) intake of graze and browse of the \textit{ns} plant type, \textit{Crmx}_{nsp} is maximum intake rate (kg/kg/d) of plant type \textit{ns}, and \textit{Ecintk} is a 0-1 function that decreases intake rate when animals are very near their maximum body weights i.e. when condition index \textit{Cond} is near 1.0. Maximum intake rates (	extit{Crmx}_{nsp}) are specified for each plant type.

The net effect of snow on intake rate is expressed by \textit{Esnow}.

\[
E_{snw,ns} = (1 - F_{bury,ns}) + (F_{bury,ns} \times E_{snwft,Snodelp})
\]

The 0-1 function \textit{Esnwft,Snodelp} which is the effect of snow depth on forage intake rate of buried forage, is only applied to the fraction of forage that is buried by snow (\textit{Fbury}). The fraction that is not buried is not affected.

Total forage intake rate per animal cannot exceed a rate that is limited by forage quality. This is due to the fact that digestion can be limited by rate of passage through the rumen, which can decline when forage quality is low. Grazers are more affected by this limitation than browsers, because the latter have rumens that are adapted to "skim" the high quality material, even from low quality food items. Thus

\[
\text{Intkmx}_{nsp} = C_{rnx,ns} \times E_{nintk,ns} (N) \times E_{dintk,ns} (Digest) \\
\text{Intkg}_{nsp} = \min(\text{Fintkg}_{nsp}, \text{Intkmx}_{nsp}) \\
\text{Intkb}_{nsp} = \min(\text{Fintkb}_{nsp}, \text{Intkmx}_{nsp})
\]

where \textit{Intkmx} is the maximum quality limited intake rate, \textit{Intkg} and \textit{Intkb} are intake rates of graze and browse. The 0-1 function \textit{Eintk}(\textit{N}) expresses the reduction in intake rate due to low nitrogen (protein) content, the 0-1 function \textit{Edintk}(\textit{Digest}) expresses the effect of low
digestibility. Both effects may not be needed, since digestibility and nitrogen concentrations are often correlated. Digestibility of dead leaf, old stems and current annual stems are given by the parameters $D_{\text{digst}}$, $W_{\text{digst}}$, and $C_{\text{digst}}$. Green leaf digestibility is given as a function ($G_{\text{digst}}$) of green leaf nitrogen content $G_{nb}$ which varies with phenology and plant nitrogen content (see plant production submodel).

Total intake per animal (kg) can be found by multiplying $Int_{kg}$ or $Int_{kb}$ (depending on whether the forage is graze or browse) by body mass (kg). Total kg/d of intake of the graze forage on each facet is

$$Int_{kg \text{ facet}} = Int_{kg \text{ facet}} \times C_{\text{wtg}} \times H_{\text{for facet}}$$

where $C_{\text{wtg}}$ is body mass (kg) and $H_{\text{for facet}}$ is animals (or animal foraging days) using the forage type $nsp$ on facet $nfac$ and subarea $nsub$. A similar equation is applied for browse items. Total digestible dry matter intake is found by summing forage intake times digestibility over plant tissue types. Total kg nitrogen intake is found by summing forage intake times nitrogen concentrations over tissues.

Offtake of graze per unit of ground area (grams per m$^2$ facet per d) is then

$$Off_{\text{kg facet}} = \frac{Int_{kg \text{ facet}}}{Area_{\text{facet}}} \times 10^3$$

where $Area_{\text{facet}}$ is the m$^2$ ground area covered by the facet. Browse offtake is calculated similarly. The biomass that is wasted (not consumed but transferred to litter) is a fraction $Waste$ of $Off_{\text{kg}}$.

The distribution of browsing impacts over tree size classes ($Pr_{\text{dw}}$, calculated above) is used to calculate changes in tree size class distribution. The wood offtake per tree (kg/tree) is

$$Off_{\text{tree n}} = \frac{Pr_{\text{dw n}} \times Off_{\text{kw n}} \times W_{\text{dcvr}}}{T_{\text{num n}}} \times 10^6$$

where $Off_{\text{kw n}}$ is g wood offtake per m$^2$ woody facet, $Pr_{\text{dw n}}$ is the fraction of wood browsing taken from size class $n$, $W_{\text{dcvr}}$ is m$^2$ tree cover per m$^2$ subarea, and $T_{\text{num n}}$ is tree density (number per km$^2$ subarea). The number of trees per km$^2$ that must revert by one size class to maintain constant tree size in a class is

$$Rev_{\text{t n}} = \frac{Off_{\text{tree n}}}{(S_{\text{size n}} - S_{\text{size n-1}}) \times T_{\text{num n}}}$$

where $S_{\text{size n}}$ is kg per tree of size class $n$.

An additional impact of herbivory is plant mortality, i.e. reduction in the number of plants. Plants die due to physical damage caused by trampling or uprooting. Morality rate is assumed to be related to animal density. The fraction of herbaceous or shrubby plants that are killed per week is

$$H_{\text{kill}} = P_{\text{kill n}} \times H_{\text{dens}} \times 0.0192$$

where $P_{\text{kill}}$ (animal/km$^2$/y) is fraction per animal per km$^2$ per year, $H_{\text{dens}}$ is animal density (number/km$^2$) and 0.0192 is year per week. Tree mortality rate per year in size class $n$ is found
similarly. The base rate $Tkilc_n$ (animal/km$^2$/y) is given for each size class.

$$Tkilc_n = Tkilc_n \times Hdens$$
Section 9.  Ungulate Energy Balance, Weight Change and Condition Index

Simulating Ungulate Energy Balance

The weight dynamics of ungulates are predicted by modeling their energy balance (Figure 10). Weight is gained when energy intake exceeds requirements and it is lost when intake is less than requirements.

Metabolizable energy intake from forage consumption is computed as

\[ F_{me} = T_{cons} \times Digest \times E_{metab} \]

where \( T_{cons} \) is kg total forage intake per animal per day, \( Digest \) is the mean digestibility of the forage, \( E_{metab} \) is the product of the gross energy content of digestible plant matter and the metabolizability. For example Minson (1981) reports 18.0 MJ metabolizable energy per kg digested forage and 0.81 metabolizability, which yields an \( E_{metab} \) of 14.58. Renecker and Hudson (1985) report an \( E_{metab} \) value of 15.60 (20.0x0.78) for moose while 15.5 is employed by Watkins et al. (1991) for elk. \( T_{cons} \) is calculated by summing total kg forage intake across all grid cells and dividing by population size. \( Digest \) is computed by dividing total digestible forage intake (see herbivory model) by total dry matter intake, accounting for differences in digestibility among forage types.

There are two main options for calculating energy requirements. The first, described below, is a relatively simple approach where a typical base energy requirement is specified, and where additional costs of travel and lactation may be added on \( (irqop=0) \). The second option \( (irqop=1) \) is to calculate energy requirements in more detail, including costs of thermoregulation as a function of temperature. An activity budget is specified by month. The equations for the second option are found in Hobbs (1989) and will not be listed here.

Energy requirements consist of a "base cost" metabolic energy demand per unit body weight per day \( (C_{reqme}) \). To this may be added energetic costs of travel and lactation. If travel and lactation costs are computed (set by flag \( Irqop \)), then \( C_{reqme} \) includes basal metabolism, posture, and eating costs only. Otherwise, \( C_{reqme} \) includes all costs. If travel and lactation costs are computed, then milk offtake may be simulated (a pastoral or milking model is needed) or specified (flag \( Imkop \)). The total milk energy yield is really the loss after milk is consumed by young, since the energy they consume is not lost from the population. Travel costs may be calculated either from specified mean travel distances and slopes or from simulated values based on simulated mean distance to water (flag \( Itrvop \)). If simulated mean distance to water is used, a function \( T_{vdswt}(Distwt) \) must be provided, which gives actual travel distance as a function of straight-line distance to water \( (Distwt) \).

The costs of horizontal and vertical travel are

\[ E_{trvh} = Dish \times Cwtkg \times Trvch \times 0.001 \]

\[ E_{trvv} = Disv \times Cwtkg \times Trsvc \times 0.001 \]
where $Dish$ and $Disv$ are horizontal and vertical travel distances (km across and km upwards), $Cwtkg$ is body weight (kg/animal), $Trvcsh$ and $Trvcsv$ are travel costs (J metabolic energy per kg body weight per meter, and the 0.001 converts meters to km. Lactation costs are computed as

$$Elac = \frac{Fmlkm \times Emilk}{Rneml}$$

where $Fmlkm$ is the fraction of the total herd body mass lactating, $Emilk$ is the net energy required per lactating animal per day, and $Rneml$ is the efficiency coefficient, the fraction of metabolizable energy that is converted to net energy. The efficiency coefficient for lactation is empirically related to digestibility as

$$Rgenl = (0.35 \times 0.81 \times \text{Digest}) + 0.420$$

where 0.81 is the fraction of digestible forage that is metabolizable and $\text{Digest}$ is digestibility (see Coppock et al. 1986, ARC 1980).

Total metabolizable energy required (MJ/d) is then

$$Rqmn = (Cwtkg x Creqm) + Esrv + Esv + Elac$$

If energy intake ($Fme$) exceeds requirements ($Creqm$), then weight gain rate (kg/animal/d)

$$Delwt = (Fme - Rqmn) \times \frac{Rneml}{26.0}$$

where 26.0 is the MJ net energy used per kg of body weight gained (ARC 1980) and $Rneml$ is the ratio of net to metabolizable energy for lactation, as above, which is assumed to apply for weight change as well (Coppock et al. 1986). If energy requirements ($Fme$) exceed intake ($Creqm$), the weight loss rate (a negative value) is

$$Delwt = (Fme - Rqmn) \times \frac{Rneml}{26.0 \times 0.84}$$

where the 0.84 is the efficiency of energy metabolism from weight loss. The total weight change rate (kg/d) of the mean animal in the population is

$$Tdelwt = \sum_{narea} Delwt_{narea} \times \frac{Hpop_{narea}}{Hpop_{opt}}$$

where $Hpop_{narea}$ is population number in grid cell $narea$ and $Hpop_{opt}$ is total population size. This is added to the current weight of the mean animal ($Cwtkg$) in the population. Mean body weight cannot exceed the maximum, nor to be less than the minimum body weight of the mean animal given the current age/sex class distribution.

Animal condition index ($Cond$) is a dimensionless number between 0.0 and 1.0, the ratio of deviation below maximum weight ($Bwmx$) to the difference between maximum and minimum weight ($Bwmn$). At $Cond$ of 0.0 animals are at the minimum weight while at $Cond$ of 1.0 animals are at maximum weight.
Changes in the age/sex class distribution of the animal population dictate that the expected minimum and maximum body weights for the mean animal must change as well. For example, if the entire population was comprised of newborns the expected mean body weight would be much different than if the entire population was mature males. The expected mean body weight of the mean animal is

\[ \text{Cond} = \frac{\text{Cwtkg} - \text{Bwmm}}{\text{Bwnx} - \text{Bwmm}} \]

where \( Pagsx_n \) is the proportion of the population in age/sex class \( n \) and \( Bodsz_n \) is the specified "normal" body weight of an animal in an age/sex class. The expected minimum and maximum body weights are

\[ \text{Bwtnn} = \text{Bwtxp} \times \text{Bwtnnn} \]
\[ \text{Bwnx} = \text{Bwtxp} \times \text{Bwtnmx} \]

where \( Bwtnn \) and \( Bwtnx \) are the ratios of minimum and maximum body weights to the mean body weight. Each time step \( \text{Bwtxp} \), \( \text{Bwtnn} \) and \( \text{Bwtnx} \) are recalculated based on the current age/sex distribution. To ensure that the body weight of the mean animal is consistent with the current age/sex distribution, the mean body weight is recalculated as

\[ \text{Cwtkg}_{\text{new}} = \text{Bwtnn} + [\text{Cond} \times (\text{Bwnx} - \text{Bwnn})] \]

which preserves the current value of \( \text{Cond} \). If, for example, all the mature animals in a population are suddenly removed, then this ensures that the current condition index is preserved while changing the mean body weight to reflect the predominance of immature animals.
Section 10. Ungulate Population Submodel

Simulating Populations

The ungulate population model is an age/sex class model wherein birth and death rates respond to animal condition index (Figure 10). There are five age/sex classes: 1 - newborns (unsexed), 2 - immature females, 3 - immature males, 4 - mature females, 5 - mature males. Newborns are defined as animals younger than the time since last birthing season (i.e. less than one year old if there is one birthing season per year). Immatures are defined as animals older than newborns, but not as old as the youngest females that can give birth. Matures are animals at least as old as the youngest females that can give birth.

Births occur in one or two specified birthing month(s) ($Monbr_1$ and $Monbr_2$). If there is a single birth season, $Monbr_2$ is set to zero. The number of animals born in a birth month is

$$\text{Birth} = \text{Ans}_i \times \text{Ecbirth}(Conges)$$

where Ecbirth($Conges$) is birth rate per mature female ($Ans_i$) per birth season as a function of the mean value of the condition index ($Conges$) over a gestation period. The length of the gestation period is $Conges$ months. On the month of a birth the month of lactation ($Lacmo$) is set to 1, and incremented monthly thereafter.

Each birth month, the last cohort of newborns is transferred to the immature classes. A fraction $Permal$ are moved to the male immature class while the rest are moved to the female immature class.

If there is a single birthing season per year animals are moved from the immature to the mature classes on the month designated as the ageing month ($Monage$). The fraction transferred ($Pmatyr$) is calculated from

$$Yrim = \frac{Mpart}{12} - 1$$

$$Pmatyr = \text{Min}(1, \frac{1}{Yrim})$$

where $Yrim$ is the number of years an animal is in the immature class and $Mpart$ is the months of age at the first birth given by a female. One year is subtracted from $Mpart/12$ since animals are in the newborn class for one full year. If there are two birthing seasons per year (e.g. small animals like goats) then at each birth month one half of the immatures are transferred to the mature class.
Mortality is also a function of condition index. The number of animals dying per month in each age/sex class is

\[
Dthr_1 = An_{s1} \times Clvdth(Min[\text{Cond}, \text{Conges}])
\]

\[
Dthr_2 = An_{s2} \times Yngdth(\text{Cond})
\]

\[
Dthr_3 = An_{s2} \times Yngdth(\text{Cond})
\]

\[
Dthr_4 = An_{s4} \times Fmldth(\text{Cond})
\]

\[
Dthr_5 = An_{s5} \times Buldth(\text{Cond})
\]

where the functions Clvdth, Yngdth, Fmldth and Buldth give the monthly death rates for newborns, immatures, mature females and mature males as a function of condition index. In the case of newborns, if the condition index over the gestation interval (\text{Conges}) is lower than \text{Cond}, it is used, since the condition of the mother over the gestation period affects birth weight.
Section 11. Ungulate Distribution Submodel

Simulating Ungulate Distribution

The ungulate distribution model predicts how ungulate populations are distributed among grid cells in the study area in relation to the distribution of habitat suitability (Figure 11). Distributions are recalculated once per month. Rather than modeling the explicit movements of animals, the model simply redistributes the entire population in relationship to the spatial distribution of habitat suitability. This approach is much faster computationally, and requires less information, than modeling individual animal movements. It works best where there is spatial mixing among animals over the study area or where subpopulations do not diverge in their condition indices due to lack of mixing among them. Subpopulations could, however, be individually simulated in separate model runs, or treated as individual species in one run.

The suitability of habitat in a grid cell is potentially affected by many factors, including forage, water, and tree cover. Suitability indices for each factor are calculated based on the current state of forage, water and cover in the grid cell and these are combined to yield an overall grid cell suitability index. Any or all of the habitat variables discussed below may or may not be used as indicated by flags on the parameter file.

Animals are redistributed in direct proportion to the distribution of habitat suitability indices among grid-cells on a monthly basis. The indices ($Hsi$) are computed as

$$Hsi_{narea} = \frac{Hsf_{narea} \times Phys \times Prefar \times Pwat \times Noise}{\sum_{narea} Hsf_{narea}}$$

where $Hsf$ is the initial function value, then normalized over all grid-cells to find $Hsi$. $Pforage(Tforage)$ expresses a 0-1 suitability index for forage abundance. $Tforage$ ($g/m^2$) only includes vegetation that is in the animals diet. $Pwat$ is the 0-1 suitability index for water. $Phys$ is the 0-1 suitability index of the physical habitat and $Prefar$ is an index for a preferred area. The index $Prefar$ is included to represent preference for certain locations provided there is a certain level of forage present there. If the mean forage abundance within a preferred area ($Prfhbg_{narea}$ $g/m^2$) is greater than $Prfgmn_{narea}$, then the value of $Pprefar$ will equal $Prefam_{narea}$, otherwise $Prefar$ equals 1.0 for every grid cell. A map of the preferred area must be provided which consists of 0's for the non preferred grid cells and 1's for the preferred grid cells. Noise is a term to introduce randomness into spatial distributions. Noise is computed as a multiplier ranging in value from $xnsmn$ to $xnsmx$. A 0.0-1.0 range would introduce a lot of noise. A 0.9-1.0 range would introduce a little.

Physical habitat suitability is modeled as
Figure 11
Phys = Min(Slp, Elv, Shd, Thc) \times Frc \times Psnw(Sdep)

where $Frc$ is a 0-1 measure of the suitability imposed by an externally forced distribution (e.g., fencing), $Slp$ is a 0-1 index of slope suitability, $Elv$ is a 0-1 measure of elevation suitability, $Shd$ is a 0-1 index of the shade suitability, $Thc$ is a 0-1 index of physical accessibility in relation to thicket cover. $Psnw(Sdep)$ is a function of snow depth in cm.

The index $Frc$, can represent a number of effects, such as forcing a herd into a fenced area over a certain period of time or responses to a perceived threat from predation. Maps of the distribution of a 0-1 force ranking over the area may simply be filled with 0s and 1s to denote unaccessible and accessible habitat, or they may be filled with 0-1 rankings.

Shade and thicket covers are computed from the amounts and size distributions of tree woody canopy cover. Cover of trees with canopy bottoms taller than 2 m ($Shcv$) is considered shade. Cover composed of trees with canopy bottoms less than 2 m tall is considered thicket ($Thcv$). Functions $Pshcv$ and $Pthcv$ describe the 0-1 suitabilities as functions of fraction woody ground cover.

$$Shd = Pshcv_{nw}(Shcv)$$

$$Thc = Pthcv_{nw}(Thcv)$$

The functions $Pelev(Elev)$ and $Pslope(Slope)$, which yield 0-1 indices of suitability vs. average grid cell elevation and slope.

$$Slp = Pslope(Slope)$$

$$Elv = Pelev(Elev)$$

Ungulate habitat use is often limited by the distribution and quality of water. Different season types of water sources may be considered; seasonal wells, permanent wells, and perennial streams. Each of these may be classified as either mineral or fresh. For each type of water source, two maps must be provided, one describing the minimum distance to a water source (km) and the other the effective discharge rate (m$^3$/d/grid cell).

The effects of distance to water and water quality on habitat suitability are represented by

$$Pwtr_{nw} = \sum_{nw} Pdisw_{nw}(Distmn_{nw, jmn}) \times Eminr_{nw, jmn} \times Eseas_{nw}$$

where $Pdisw$ provides a 0-1 preference value as a function of minimum distance to water ($Distmn$) for each of the $nw$ types of water sources. The variable $Eminr$ reflects preference for fresh or mineral water. It is computed from the parameter $Minrlrw_{nw}$ which ranges in value from 1.0 (use only fresh water), to 2.0 (no preference) to 3.0 (use only mineral). $Eseas$ is an 0-1 effect of rainfall on water discharge rate in seasonal and permanent wells. Seasonal wells are affected by total mm rainfall in the last three months by the function $Ef3w(Ppt3m)$. Permanent wells decrease in value in response to total rainfall in the last 12 months by the function $Ef12w(Ppt12m)$. 

51
After animals have been distributed in relationship to the distribution of $Hsi$, it is possible that animal density distributions may not be supportable by available water discharge. The total requirement for water in a grid cell is

$$Wd\text{dem}t = \sum_{nscn} Hpop_{nscn} \times Watreq_{nscn}$$

where $Watreq$ is the m$^3$ of water required per animal type $nscn$ per day and $Hpop$ is total number of animals in the grid cell. The total supply of water in a cell is

$$Ws\text{upl}t = \sum_{n} Watdsc_{n} \times Eseas_{n}$$

If the demand exceeds the supply ($Wd\text{em}t > Ws\text{upl}t$) the fraction of animals of each type that can be supported is found as

$$F_{\text{sup}nscn} = \left(\frac{Ws\text{upl}t_{nscn}}{Wd\text{em}t_{nscn}}\right) \times Hpop_{nscn}$$

and the number that can be supported is then

$$Popsup_{nscn} = F_{\text{sup}nscn} \times Hpop_{nscn}$$

The population is set to $Popsup$ and the excess ($Hpop - Popsup$) is put into a pool of dispersers ($Dispr_{nscn}$). The animals in the disperser pool are then distributed in the system in relationship to the distribution of the suitability of habitat with unused water.

$$Hsid_{nscn} = Hsi_{nscn} \times (Ws\text{upl}t_{nscn} - Wd\text{em}t_{nscn})$$

It is possible to furthermore set an upper limit on the density of animals in any given grid cell despite the distribution of $Hsi$. This might occur for example if animals regulate their density in terms of spacing, or if humans regulate animal density. If the density of animals in a grid cell exceeds $Hdem\text{mx}_{nscn}$, the excess animals are added to a disperser pool ($Dispr_{nscn}$). The animals in the disperser pool are then distributed in the system in relationship to the distribution of suitability of habitat below the density limit.

$$Hsid_{nscn} = Hsi_{nscn} \times (Hdem\text{mx}_{nscn} \times Cellsz_{nscn} - Hpop)$$

### The Water Discharge Map

One algorithm that can be used to develop the effective discharge map works as follows. Calculate a weight for each grid cell that is the sum of the discharge from all water points (eg wells) within a maximum travel distance from the cell. Normalize that weight among cells. Then distribute the total discharge in the system among grid cells in proportion to the normalized weighting factor. Thus, the availability of discharge is distributed over the map depending on travel distances. If a grid cell is within travel distance and the actual discharge in the cell is zero, the effective discharge will nevertheless be greater than zero.
Section 12. Wolf Submodel

Simulating Wolves

The wolf submodel simulates wolf predation on ungulates and resultant wolf population dynamics (Figure 12). It is basically the model developed by Boyce and Gaillard (1991) to analyze potential wolf reintroduction into Yellowstone Park (see also Boyce [1993]).

Wolf population dynamics are modeled with the equation

$$\text{Wolf}_{t+1} = \text{Wolf}_t \times e^R$$

which is the logistic equation for population growth, with an intrinsic rate of increase (or decrease) of $R$. The value of $R$ is derived from

$$R = \sum_n \left( \frac{\text{Prkill}_n \times \text{Rnumr}_n}{\text{Wolf}_n \times \text{Wolf}_k} \right) - 0.68$$

where $\text{Prkill}_n$ is the number of prey killed per wolf per year, $\text{Rnumr}_n$ is a constant giving the increase in $R$ per prey animal killed, and $\text{Wolf}_k$ is the maximum number or carrying capacity of wolves in the system. $\text{Wolf}_k$ can be calculated from pack size ($\text{Packsz}$ animals) and pack territory size ($\text{Terrsz}$ km$^2$) and area of the simulated system ($\text{Simkm}^2$ km$^2$).

$$\text{Wolf}_k = \frac{\text{Packsz}}{\text{Terrsz}} \times \text{Simkm}^2$$

The number of prey animals killed depends on the relative densities of prey and wolves. A multispecies disk equation, modified to incorporate a Type III functional response is used.

$$\text{Prkill}_n = \frac{\text{Attack}_n \times \text{Prden}_n \times \sum \text{Prden}_n}{1 + (\text{Attack}_n \times \text{Handtm}_n \times \left( \sum \text{Prden}_n \right)^2)}$$

Here, $\text{Prden}_n$ is the density of the $n$th prey species (number/km$^2$), $\text{Attack}_n$ is the attack rate and $\text{Handtm}_n$ is the handling time. $\text{Attack}$ is the probability of encountering and attacking a prey per unit of prey density (animals/km$^2$) per unit time (yr). While Boyce and Gaillard (1991) give $\text{Attack}$ in units of probability per prey animal per time, this may be converted to prey density units (probability per animals/km$^2$/yr) by dividing their values by the area of the system they were modeling (830 km$^2$). Handling time ($\text{Handtm}$) is the minimal time (y) it takes to find, capture and eat prey.

It is useful to compare this form of the disk equation with the single prey species Type III functional response,
Figure 12
where $F_{max}$ is the maximum number of prey killed per predator per year and $W_{prey}$ is the prey density (number/km$^2$) at the inflection point of the curve. We can relate parameters in the disk equation to those in the Type III response curve as follows.

$$\text{Handt}_m = -\frac{1}{F_{max}}$$

$$\text{Attack} = -\frac{1}{W_{prey}^2 \times \text{Handt}_m}$$

These equations are used to calculate $\text{Handt}_m$ and $\text{Attack}$ from $W_{prey}$ and $F_{max}$. 
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