

CONCEPTUAL MODELS

AQUATIC ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Bob Hall)

The GRYN contains a diverse group of lakes, both natural and human-made. There are numerous glacier-carved lakes in high alpine areas of the Teton Range, and several large lakes formed from tectonic processes. Bighorn Canyon contains a large impoundment, and the top 8 m of Jackson Lake is regulated by a dam at its outlet. The large lakes contain substantial biological and economic resources. For example, Yellowstone lake has the largest population of Yellowstone cutthroat trout (*Onchorhynchus clarki bouvieri*) (Gresswell and Varley 1988). These lakes are used extensively for recreation, such as boating and fishing. Bighorn and Jackson Lake are used for water storage.

River ecosystems are equally diverse in the GRYN. Rivers range from large lake outlets (e.g. Snake and Yellowstone rivers, to many high-mountain streams, and geothermally influenced rivers in the Madison drainage and South Boundary area of YNP. High variation in groundwater source, parent material, and topography lead to high variation in the types of streams within GRYN. In terms of ecosystem functions such as whole stream metabolism and nitrogen processing, streams within GTNP are more variable than 11 streams within different biomes ranging from the tropics to Alaska (Hall and Tank 2003).

In this narrative I will only consider the aquatic part of rivers as the riparian section is covered elsewhere, though stressors to streams and lakes can come from habitat damage to the riparian zone.

Drivers

Lakes are formed by exogenous processes (glacial scour, plate movement, dams, differential cooling of lava in the case of Yellowstone lake), and these processes shape the morphometry of the lake which, in turn will determine most aspects of its function. Climate plays a large role in temperature, hydrology and mixing regime of

lakes. Human activities can affect lakes by altering hydrology, climate, nutrient load and biotic assemblages. Drivers for rivers are similar to those for lakes, except with the fundamental difference that rivers morphology is a function of the hydrology (driven by climate) of the river and geology of the drainage basin as channel structure changes through time. Changes in climate will affect hydrology and temperature of rivers, and humans can strongly impact rivers by altering hydrology, geomorphology and biotic assemblages.

Stressors and impacts to ecological processes

A. TEMPERATURE:

Climate change may be an important stress to Yellowstone ecosystems over the long term. Lakes can be used as bellwethers of climate changes and will likely be affected by global climate change. Long term records of ice-out on lakes suggest warming of lakes (Likens 2000, Magnuson 2000) and effects of climate change in the watershed, e.g. increased fire frequency, may alter lake dynamics (Schindler et al. 1996). Increasing temperature will affect biota of rivers directly, e.g. by limiting distribution of coldwater species (Rahel et al. 1996). Alternatively increased temperature could provide for faster growth rates of fish in rivers and lakes, including invasive lake trout (Hill and Magnuson 1990), which may change predator-prey dynamics in lakes.

B. WATER LEVEL AND RIVER HYDROLOGY:

Lakes that are hydrologically managed (e.g. Jackson Lake, Bighorn lake) will have fluctuating water levels that can potentially alter lake food webs and ecosystem function. Lakes are linked to their shoreline and receive a fraction of their energy inputs from allochthonous inputs, coarse woody debris which provides habitat, and may control terrestrial predator interactions (Schindler and Scheuerell 2002). Changing water level may decrease allochthonous inputs and may limit access of the lake by terrestrial predators (e.g. otters).

Rivers can be altered hydrologically from dam operations (e.g. Snake River), which can alter biotic assemblages (Stanford and Ward 1989). Water removal for irrigation can reduce instream flows and flood peaks in the summer, (e.g. Gros Ventre River, Bighorn River, Shoshone River, and Spread Creek). Additionally climate change may alter stream hydrology (Poff 2002) which will affect all aspects of river ecosystem function (Meyer et al. 2000, Firth and Fisher 1995) ranging from food web interactions (Power et al. 1995) to nutrient cycling.

C. SEDIMENTATION AND GEOMORPHOLOGY:

An important stress, covered in the riparian narrative.

D. SOLUTE CONCENTRATIONS:

Solutes include all dissolved solids in water, which strongly affect lake ecosystems. Drought and fire change cation import to lakes (e.g. Schindler et al. 1996). High mountain lakes may be subject to acidification if they are poorly buffered; however western mountains tend to have lower acid inputs than Northeastern US Mountains. In the Snowy Range, SE Wyoming, despite low acid-neutralizing capacity of lakes, acidification is not yet evident because pH of precipitation is higher than that in the Eastern US (Reuss et al. 1995).

E. NUTRIENT LOADING:

Eutrophication from excess nutrients is a pervasive stress on many lakes and rivers in the US by increasing primary production, changing biotic assemblages and lowering water clarity; estimating the effects of this eutrophication has a long history (Smith 1998). Local development and atmospheric deposition can cause nutrient loading even in large mountain lakes such as Lake Tahoe. For example, increased N loading to Lake Tahoe has increased primary production and decreased water clarity (Goldman 1988). The effect of excess nutrients to rivers is much less well known; experimentally increased P loading to a tundra river increased primary productivity, moss biomass and secondary production (Peterson et al. 1993). Phosphorus is often considered the limiting nutrient for lakes and streams, however it is now recognized that nitrogen often limits production as well (Elser et al. 1990). Nitrogen is most likely to be the limiting nutrient for most lake ecosystems within the GRYN; almost all streams in GTNP are N limited (J. L. Tank and R. O. Hall unpublished data). Planktonic algae responded greatly to N additions in experimental bioassays showing that N was primarily limiting in Yellowstone and Jackson lakes (Interlandi and Kilham 1998), thus we suggest that N will be a more important pollutant than P in the GRYN.

In the West, there are areas with high N loading from atmo-

spheric deposition, particularly near cities and areas downwind from power plants or intensive agriculture Fenn et al. 2003b). Loch Vale in Rocky Mountain National Park receives 3-5 kg N ha⁻¹ y⁻¹, (Baron et al. 2000), and this N has been implicated in changing the phytoplankton assemblages in these lakes (Wolfe et al. 2001). Lakes in the GRYN are fairly low-nutrient (Interlandi et al. 1999) thus they are likely to respond to small increases in nutrients similarly to Tahoe. Indeed, eastern Idaho and the Teton Range are projected to have high rates of N deposition (Fenn et al. 2003b). Primary sources would most likely be atmospheric deposition or from local inputs from towns and settlements within the parks. High mountain lakes could be most susceptible because they can receive high N loads from atmospheric deposition, and many lakes in the west have high nitrate concentrations (Fenn et al. 2003a), although there are almost no data represented in their paper from western Wyoming, despite large high elevation areas with crystalline bedrock that is potentially susceptible to increased nitrate loading. Although N deposition rates are low in areas far from cities (e.g. west slope of Colorado Rockies, Baron et al. 2000), deposition could increase as NO_x emissions and local development increases (see Vitousek et al. 1997).

Rivers upstream of Bighorn canyon run through agricultural areas have elevated nutrient loads and N and P (Water Resources Division, National Park Service 1998), which might contribute to the eutrophic nature of Bighorn Lake (Lee and Jones 1981).

F. EXOTIC SPECIES:

Exotic species are one of the most pervasive environmental problems in the US and the GRYN has received some well-publicized invasions that can potentially alter aquatic ecosystems. Lake trout (*Salvelinus namaycush*) have invaded Yellowstone Lake and may lower native cutthroat trout populations (Stapp and Hayward 2002a, Ruzycki et al. 2003) and may extend to predators outside the lake (Stapp and Hayward 2002b). Lake trout can consume 14% of juvenile cutthroat trout (*Onchorhynchus clarki*) populations per year, even when numbers are controlled by gill-netting. Whirling disease has also invaded rivers in Yellowstone which may impact cutthroat trout populations (Ruzycki et al. 2003). New Zealand mud snails (*Potamopyrgus antipodarum*) have invaded many rivers in the GRYN and are likely having severe impacts. In Polecat Creek, New Zealand mud snails constitute 90% of invertebrate biomass, and represent the largest fluxes in the nitrogen cycle (Hall et al. in review). Secondary production of mud snails in Polecat Creek is one of the highest rates

ever recorded for an aquatic invertebrate (Hall et al. in preparation). It is not likely that these will be the last invasions, as Simberloff and Von Holle (1999) suggest that invasions beget more invasions; evidence in the Great Lakes suggests that this hypothesis is true, as the invasion rate is increasing non-linearly (Ricciardi 2001).

Potential Indicators

Indicators can be integrative assessments of biological condition (Karr 1981, 1999) (i.e. looking for the effect). Measuring biotic condition is important because it represents the impact that managers and visitors to the parks care about: Are there fish to catch? Is there wildlife to observe? Is the lake clear? Also, biota can indicate multiple stressors and often provide better information on change than hard-to-measure stressors (such as episodic pollution events (Karr 1999)). Alternatively we can examine the stressor itself. Measuring changes in the stressor (if possible) is important for 2 reasons: One is that it may be possible to detect change in the stressor long before there is an impact to ecological processes. For example, N inputs or temperature may increase before the biotic assemblage responds. Invasion of an animal to a new ecosystem can be detected more easily than the impact to native populations or ecosystem processes. The other reason is that measuring the stressor may help to understand causes of observed biological changes. If lake clarity decreases concomitantly with nutrient loading, then increased nutrients are a strong causal hypothesis for this biological change.

a. Nitrogen inputs

Justification: Atmospheric nitrogen input is a stressor that, if high enough, could increase primary production in lakes and streams. Given that most N loading to Yellowstone and Teton Parks is via atmospheric inputs (as opposed to urbanization or agriculture), measurement of nitrogen concentrations in precipitation may detect early changes to these inputs. There are few NADP sites in the GRYN and the one in Yellowstone is a low elevation where concentration and of nitrate and volume of precipitation are expected to be low. There are few high-elevation sites for N deposition in the intermountain west (Fenn et al. 2003b), thus inputs on N and changes of those inputs are relatively unknown for the GRYN.

Examples of specific measures: Annual wet and dry deposition of N at a few high and mid elevation sites within the GRYN.

b. Nitrogen concentrations in aquatic ecosystems

Justification: Atmospheric nitrogen input is a stressor that, if high enough, could increase primary production in lakes and streams. High alpine watershed lose most of their nitrogen during snow-melt (e.g. Reuss et al. 1995), and losses are proportional to inputs (Williams et al. 1996), despite processing of N in the shallow soils. Stream monitoring can detect long-term trends in deposition (Likens et al. 1996), and may provide a means to detect watershed-level response to N additions (Williams et al. 1996).

Examples of specific measures: Temporal sampling of stream water N throughout the year in Teton Range streams, Bighorn River and Lake and possibly some Yellowstone rivers. Surveys of N concentrations in lakes.

c. Water Temperature

Justification: Global climate change may increase temperatures of lakes and streams which may alter animal habitat and interactions. Additionally, geologic change (e.g. earthquake in Firehole River basin) may alter groundwater inputs with corresponding temperature changes in rivers. Measurement of temperature may be able to detect these changes which can be linked to any biological changes.

Examples of specific measures: Hourly recording of temperature in lake epilimnia and rivers via inexpensive recording thermometers. Ice out dates for major lakes.

d. Surface hydrology

Justification: Hydrology of lakes and rivers in the GRYN can change from direct human modification (e.g. impoundments, water abstraction) or via changes in climate (Meyer et al. 1999). This monitoring is already occurring for several of the rivers in GRYN, e.g. Snake, Bighorn, Madison, Yellowstone, and 2 of the lakes, Jackson and Bighorn.

Specific measures: Lake water level and large river discharge.

e. River morphology and habitat assessment (as specified in riparian narrative)

f. Algal species composition and biomass

Justification: Increased nutrients or changes to the food web (e.g. Carpenter et al. 1985) may change algal biomass, water clarity and species composition. Research in Yellowstone Lakes has shown that diatom species compositions predictably respond to slight changes nutrients according to their physiology (Interlandi et al. 1999) and these changes in assemblages may be sensitive

indicators to nutrient inputs and associated climate change (Kilham et al. 1996). Algal species in high-elevation lakes can also signal changes in nutrient concentrations (Wolfe et al. 2001).

Specific measures: Chlorophyll a concentrations of algae in lakes. Secchi disk measurements (a measure of water clarity). Algal (mostly diatoms and some cyanobacteria) assemblage structure.

g. *Cutthroat trout responses to exotic predators.*

Justification: Exotic lake trout and whirling disease can potentially lower densities of native Yellowstone cutthroat trout in Yellowstone Lake; these effects may cascade to streams and predators outside of the lake (Stapp and Hayward 2002).

Specific measures: Long-term quantification of Yellowstone cutthroat trout density, age structure, spawning and recruitment in Yellowstone Lake and its tributaries.

h. *River invertebrate assemblages.*

Justification: Stream invertebrate assemblages may change in response to exotic species, sedimentation, nutrient load or predator population change. Stream invertebrates are often used as measures of water quality (Karr 1999) and is the current approach used by the state of Wyoming for water quality analyses (King 1993). They are sensitive indicators of change and they can integrate physical stressors that might otherwise be difficult to measure, and these changes can relate to changes in ecosystem function (Wallace et al. 1996). There are several approaches to using invertebrates to measure water quality; two current methods either develop a set of additive metrics (Kerans and Karr 1994), a local examples is Wyoming index of biotic integrity (WYIBI) (Stribling). Another method uses multivariate approaches to estimate predicted invertebrate assemblages which can be compared to measured assemblage structure e.g. Hawkins et al. (2000). Long term monitoring of invertebrates may be able to detect change in response to exotic mud snails, and new, unforeseen invasions

Specific measures: Invertebrate assemblage structure, following approaches of current bioassessment methods.

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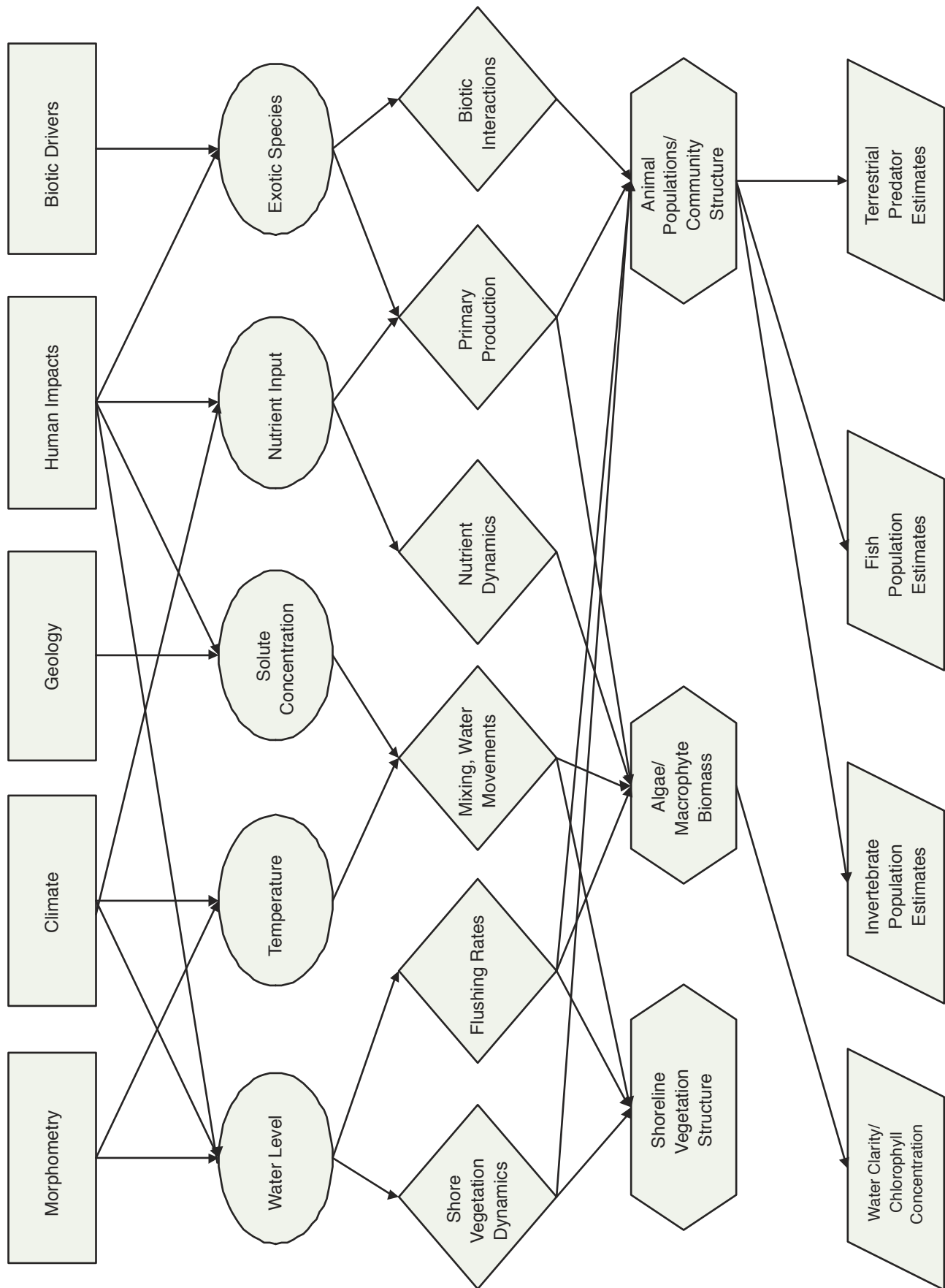


FIGURE I Lake model.

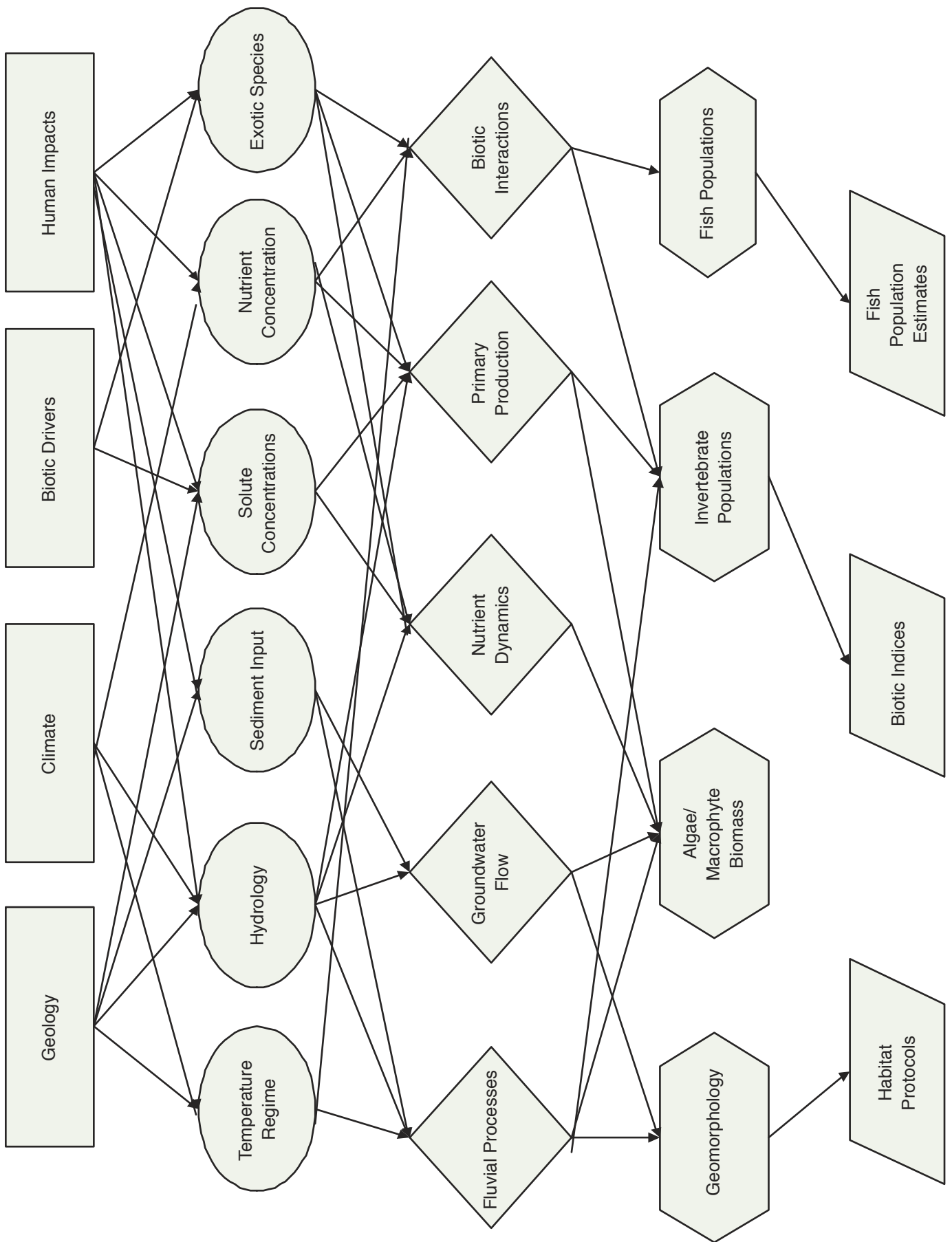


FIGURE 2 River Model.

ALPINE-TIMBERLINE ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Duncan Patten)

Although the alpine and timberline ecosystems are closely linked, they represent quite different sets of dynamic processes which result in potentially different indicators. Consequently, to understand these systems and model them to address possible indicators (vital signs), they are treated in many of the discussions below and in conceptual models (Figures 3 and 7) as separate, but interrelated, systems.

The alpine ecosystem is one of the smallest in area within the GRYN. It occurs only at high elevations on summits, slopes and ridges above the local timberline (Billings 1988). The environments of the alpine ecosystem often are extreme with intense radiation, cold temperatures and wide temperature fluxes, extreme wind velocities, thin air, and often long-lasting snow and ice. Substrates in the alpine may be barren, rocky outcrops which create highly exposed environments, while other areas may have well developed soils, or substrates that are constantly being altered by frost action. Consequently, plants that survive in these extremes tend to grow near the ground, often in mats but also as isolated plants. Their productivity results from the combined stress of alpine environments (Scott and Billings 1964).

The sharpest environmental gradient in mountains is the ecotone between alpine and forest, the timberline zone. This ecotone is broadly defined as the upper limit of trees, a response to environmental stress (White 1996). It is related to the declining amount of biologically useful thermal energy with summer temperatures dictating the length of the growing season (Billings 1974). Physical factors such as weather, temperatures, snowdrifts, and soil conditions control whether woody forest species will establish and survive at high elevations. Trees growing at timberline grow at the same rate as several hundred meters below timberline (Paulsen et al. 2000), although isolated trees above the extensive timberline ecotone may have very slow growth, in part, because of foliage loss to wind and other factors. Treeline vegetation is sensitive to many environmental factors. Over a half century period, Klasner and Fagre (2002) saw changes in timberline forests in Glacier National Park with forests below the timberline becoming more dense and krummholz (twisted wood) stands becoming fragmented near trails.

Drivers and Related Stressors

Extreme environments of the alpine and timberline areas are com-

mon elements in these two systems allowing a combined discussion of the drivers. The drivers fall into five major categories: climate, geology, fire, human activities and biotic factors.

Climatic drivers or natural stressors are the most obvious set of parameters controlling processes at high elevations in the GRYN. At high elevations several factors become limiting and dominate physiological and growth processes of organisms (Tranquillini 1979). Temperature extremes with wide fluctuations play an important role both for organism survival but also physical processes. High radiation levels at high elevations can cause the ground surface to heat up during the day followed by rapid nighttime cooling. Extreme cold temperatures dictate physiological processes and are considered one of the primary causes of timberline, that is, only plants with metabolic systems that can function at very cold temperatures during the short alpine growing season can grow at these elevations. Temperature extremes may function synergistically with other natural stressors to create even more extreme conditions. For example, wind combined with low temperatures may limit high elevation forest growth.

Wind is a constant force in the alpine environment. It may cause alpine temperatures to become more extreme by breaking down the boundary layer formed on physical and biological surfaces. Consequently, low temperatures become more "penetrating" and potential for freezing increases, while daytime highs on ground and other surfaces may be far above ambient temperatures. Wind may bring warmer temperatures from lower elevations to the alpine. Wind also drives ice and snow which scour and abrade surfaces and plant tissues, and causes snow to accumulate. Snow drifts often do not melt until well into the alpine growing season limiting early phenological stages of alpine plants.

The thin air at high elevations results in two different environmental drivers. Thin air allows a greater amount of solar radiation, especially in the ultraviolet (UV). UV-B can differ by a whole order of magnitude between a dry environment at sea-level and high alpine environments (Caldwell et al. 1980). Alpine plants have adapted to high UV by either absorbing it in the epidermis or reflecting it off leaves or other plant parts. Thin air also means lower partial pressure of gases, CO₂ being the one of concern. Low CO₂ levels control photosynthetic rates, and yet, photosynthetic efficiency of alpine plants is often greater than low-elevation plants tested within the same low CO₂ atmosphere.

Drought is a climatic factor that can influence both composition of alpine plant communities and timberline. Alpine zones range from

very wet to dry. Both extremes may produce conditions with low water availability, however, moisture gradients do create concomitant vegetation gradients in the alpine zone (Oberbauer and Billings 1981).

Fire is not a common driver in alpine ecosystems; however, in the past it was common in GRYN forests and thus played a role in modifying timberline forests. Forest fires in the montane and subalpine forests often reached to timberline destroying living timberline trees, or burning dead and down trees at that elevation zone. Evidence of the location of timberline may have been destroyed or reduced by fires reaching timberline. Remains of burned trees are used to determine extent of timberline forests. Dendrochronological techniques are used to date remnants of timberline forests allowing establishment of dates of forest encroachment into the alpine or withdrawal from alpine/timberline ecotones.

Disease is a natural occurrence in most ecosystems; however, disease and insect infestations, although cyclical, can alter the structure of alpine and timberline vegetation. Several types of conifer insect infestations and diseases have altered timberline forests, for example, bark beetle and bud worm. The cyclical nature of these diseases and infestations do not permanently alter the forest as it normally recovers at the end of the cycle.

High elevation ecosystems are permanently under environmental stress as environments at these elevations do not allow robust vegetation development, either in the alpine or at timberline. Climate, geology, fire, human activities and biotic factors all play a role in creating stressful conditions. Here the term stressful applies not only to the normal extremes at these elevations but also to changing environments that may be natural or of human origin.

Climate and the resulting local weather conditions constantly influence alpine and timberline ecosystems. Many of these conditions are discussed above; however, long-term climatic cycles may ameliorate timberline environments and allow trees to grow at higher elevations. On the other hand, long-term colder and drier conditions may play a reverse role and cause the forest line to retreat in elevation. Recent human influence of the world climate may influence these long-term climatic patterns and indirectly alter "normal" timberline fluctuations. Climate models may allow predictions of possible climate change and thus concomitant changes in timberline elevations.

Short-term warm/cold cycles, sometimes only 24 hours long, may cause disruption of wet alpine soils, resulting in churning of soil particles and instability of the substrate. These disturbance can form small, fine soil "frost boils", extensive "rock nets", and solifluction terraces

(Johnson and Billings 1962). Climatic changes that might prevent short-term freeze/thaw cycles, or extend the period between a thaw and freeze period, may alter the extent of frost action soils and greatly change the types of alpine vegetation establishing in these areas.

High elevations have thin air, consequently, the partial pressure of photosynthetic gases (i.e., CO₂) is low resulting in the need for photosynthetically efficient plants. Reduced CO₂ may not be considered a stressor as it is normal in the alpine zone, however, human caused increases of atmospheric CO₂ may result in reduced need for photosynthetic efficient plants and possible changes in alpine plant communities. Also, timberline trees may produce more growth under an increased CO₂ environment and better withstand the extreme environmental gradient at the alpine/timberline ecotone.

Wind also is a normal part of the alpine/timberline environment (Hadley and Smith 1986). Climate models do not predict local wind patterns or velocities, but it is probable that with climate change, including changes in temperature gradients, wind patterns and velocities could change.

High elevations are known for high levels of radiation and the magnitude of UV is discussed above. However, human caused reduction in stratospheric ozone has increased the amount of UV entering the earth's atmosphere. Consequently, elevations that already receive high levels of UV can be expected to have increasing UV levels which will directly affect most biotic functions and survival of high elevation organisms. Eventual UV resistant adaptations may develop but this type of evolutionary process is long-term and plant community changes may take place before UV resistant adaptation does.

Fire has been mentioned as a normal part of forest dynamics directly influencing the timberline forest stands. However, fire suppression has modified the occurrence and extent of fires in the GRYN area directly changing an important timberline environmental factor. Reduced fires or possibly more extensive wildfires resulting from long-term fire suppression and fuel build up must be considered an environmental stressor of timberline forests even if fires are a normal part of forest dynamics.

Topography, that is, slope aspect and angle, is a relatively stable part of the alpine environment. Some changes occur under frost action solifluction (soil surface movement), but stability is the norm. It is included here as a stressor because at high elevations small changes in topography alter the extremes of the environment. Thus, plants growing in the shelter of an organic mound, or behind a rock in the alpine zone cannot grow out in an exposed location. The very

limitations created by topography can be stressful to alpine plants.

Alpine vegetation is one of the most sensitive vegetation types in the Rocky Mountains (Billings 1973). It grows only in sheltered areas or on deeper soils that have existed for some time. Its sensitivity to external physical stress is illustrated recently by the loss of alpine communities in areas where there is high human use (Cole and Monz 2002). Human trampling loosens the plant surface, especially cushions or mats, making it susceptible to wind scour (Hartley 1976, Jackson 1998). National parks have put in trails with off-trail foot traffic excluded with the hope of protecting alpine plant communities in heavy human use areas. Increasing human use can only exacerbate human impacts.

Grazing (wild and domestic) alters composition of alpine areas through plant consumption and trampling. In the GRYN parks, grazing is limited to wild animals, but adjacent alpine areas (e.g., Beartooth Plateau) shows evidence of long-term erosion and trail development where domestic livestock have grazed. Although this is not as significant a stressor as some of the climatic factors, it works synergistically with other factors in the alteration of the alpine vegetation community.

Introduction of exotic plants in the alpine/timberline zone does not play as important a role in vegetation community modification as found in lower elevation zones. However, care should be taken to avoid introduction of exotic species, especially where trails and roads have been established in these high-elevations.

Disease is evident in all biotic communities of the GRYN. In alpine/timberline areas disease can be found in timberline forests, and in high elevation ungulate populations. White pine blister rust has become a disease of concern in the high elevation forests of the GRYN. Whitebark pine, a timberline species, has become infected over the past several decades (Kendall and Keane 2001). Although the magnitude of the disease is less in the GRYN than in areas like Glacier National Park, it still has potential of eliminating or greatly reducing the whitebark pine community, thus eliminating whitebark pine seeds, a primary food source for grizzly bear. Disease in the alpine community, although probably present, does not have the potential yet of greatly altering that community.

Processes, Outcomes and Indicators

Interaction of several stressors influence alpine and timberline processes (Figures 3 and 7). These interactions can be represented in several process submodels which explain in greater detail how factors influence each other.

A. ALPINE ZONE PROCESSES, OUTCOMES, AND INDICATORS

1. Soil frost dynamics.

Interaction of temperature changes and soil moisture greatly modifies areas of the alpine zone through cryopedogenic processes (Johnson and Billings 1962). Cryopedogenic or soil frost action causes water to shrink and expand thus moving soil particles around. In some cases these processes are limited to small areas called "frost boils" where larger soil particles are pushed outward. These frost churned soils create instable locations that often prevent establishment of vegetation and long-term stability of the alpine vegetation community. Soil frost action can also sort larger rocks creating what are called "rock nets" or "rock polygons" in the alpine zone. In this case, sod may develop between the rocks and dense alpine plant communities establish. Alpine soils on steeper slopes may form "solifluction terraces" when the soil frost action expands the wet soils and gradually moves them down slope. These terraces are usually covered with alpine vegetation.

2. Scree slope dynamics.

Many alpine and subalpine slopes are steep and relatively unstable. These scree and fellfield slopes often cannot support vegetation, although in some cases pockets of alpine herbs or shrubs may find sufficiently stable sites to establish (Griggs 1956). Again, thaw-freeze action can maintain instability of these slopes.

3. Alpine vegetation dynamics.

Alpine plant communities are a product of all of the factors (and stressors) that influence the mountain plant communities found above timberline. Winds, high UV, wide temperature fluctuations, human and animal use, disease and introduced species all play a role, but the magnitude of that role varies. If future climatic changes reduce the potential for thaw-freeze actions, then those plants dependent on disturbed soils may decline. Increased human and animal activities in the alpine zone will also alter the vegetation composition of alpine communities. Consequently, plant species composition of in the alpine zone becomes a measure of the synergistic effects of all of the stressors.

The primary outcome of the several process models is vegetation composition and cover and shows the importance of environmental stress on plant communities (Kammer and Mohl 2002). Scree slopes and greatly altered frost action areas will have little vegetation cover, while alpine areas with well developed soils may have a continuous,

dense plant cover. Changes in these vegetation characteristics in response to environmental stresses thus becomes indicators of the influence of these stressors on the alpine zone.

B. TIMBERLINE PROCESSES, OUTCOMES AND INDICATORS

1. Timberline elevation dynamics.

Timberline, that is the elevation location of the ecotone between forest and alpine vegetation, has fluctuated over the past millennia (Carrera et al. 1991). The fluctuation is mostly driven by climatic factors, warmer or cooler climates, and/or wetter or drier climates (Hessl and Baker 1997). Human induced climate change may cause a rise in the elevation of timberline, if warmer is expected. Although this change is slow, evidence of past location of timberline can be found in presence of remnants of trees well up in the alpine zone. Dating of these trees can establish the time when forests occurred at higher elevations (Graumlich 1991, 1994). Establishment of a long-term record of timberline fluctuations may be a useful indicator of natural and human-induced influence on timberline forests.

2. Timberline woody plant dynamics.

Composition of timberline forests varies according to the combined influence of those factors that limit forest species from advancing upwards on a mountain. For example, protective structures such as rocks and coarse stable soils may allow forest species to establish at high elevations. Lack of these conditions may prevent forests from establishing higher, unless climatic factors ameliorate. Fire and disease have recently become more important factors in modifying timberline forest location and composition. If white pine blister rust mostly eliminates whitebark pine, then timberline forests will be primarily spruce and fir, or may be reduced to dead and dying trees above the subalpine forest. Extensive fires, a result of forest fire suppression, may also reach into the timberline forest destroying the existing trees. Recovery from fires then will be a result of ability of timberline tree species to regain their normal elevation location, a process that is difficult because of the extreme environments at these elevations. Consequently, the composition of the timberline forest, a product of natural and human activities, may be a good indicator of changes occurring within the GRYN regions parks.

3. Alpine/Treeline Potential Indicators

The ecosystems that compose alpine and timberline areas have developed in extreme environments. Wind, cold and thin air char-

acterize the extremes that control these ecosystems, and yet, human activities also have influenced their present state. Changing environments, both natural and human caused, may alter the future conditions of alpine and timberline zones. Consequently, the indicators selected for the vital signs program will give a warning of the gradual changes these ecosystems may have as a changing local and global environment alters the drivers that form these sensitive, high elevation ecosystems.

a. *Timberline forest densities and health*

Resource Monitored: Timberline forest, including large trees such as whitebark pine, and krummholz stands in exposed and protected areas.

Justification: Timberline in the Rocky Mountains, as in most temperate-zone mountains, has fluctuated in elevation over the past millennia. Changes in the elevation of timberline occur slowly; however, the actual elevation should be monitored (see another indicator). The forest trees and woody plants near timberline begin to show new recruitment at higher elevations, or decline in forest stature long before the actual timberline change stables for some time. Timberline is dynamic, and yet there are periods when it appears to be stable allowing long-term monitoring of forest conditions at or near timberline to show possible precursor forest modification prior to solid evidence of timberline change. Recently, introduced diseases (e.g., white pine blister rust) have initiated more rapid changes in timberline forest health. For this reason alone, timberline forests should be part of a long-term monitoring program.

Comment: The long-term dynamic nature of timberline and the variation of forest types require that any sampling of forest condition at or near timberline must include the variability of forest structure. Measurement of health of krummholz stands is quite different than measurement of health of high elevation whitebark pine stands.

Example of specific measurements for indicator: In randomly selected, representative timberline zones in the GRYN area, sampling transects within and just above the forest, and randomly selected krummholz patches should be monitored on a regular basis (e.g., 2-5 years). Forest transects will measure the density of living and dead trees and the condition (e.g., percent canopy dead). The cover and ratio of dead to living canopy should be measured in the krummholz patches.

b. Timberline elevation boundaries

Resource Monitored: Elevation where the forest ends and alpine tundra begins, and the highest elevation of krummholz patches.

Justification: The justification for monitoring timberline elevation is essentially the same as that for monitoring the timberline forests. Timberline is dynamic and has fluctuated in the past in response to long-term climate changes (i.e., warming and cooling, and/or wetter or drier periods). More recently, disease may be accelerating the rate of forest change which justifies monitoring not only the effects of the disease on the forest but how it may be altering the elevational dynamics of the ecotone between forest and alpine zones.

Comment: Monitoring changes in timberline elevation is obviously a long-term procedure. However, with more rapid changes in climate expected, elevational changes may occur more rapidly, especially upward encroachment of forest species. Thus, monitoring techniques should be established to address the upward encroachment expected from a warming climate without forgetting to monitor potential downward changes or forest withdrawal which may result from other factors such as disease or other human induced influences.

Example of specific measurements for indicator: Monitoring elevational limits of forest species is easily done by establishing markers (stakes and GPS) at representative timberline locations. Aspect (compass direction) plays an important role in elevation of timberline, thus markers should be at all aspects. Markers should be placed at the extent of any upward forest reproduction, edge of mature forest, and highest elevation of krummholz patches. The long-term aspect of timberline change does not require frequent measurement, but annual (or 2-3 year) reconnaissance of timberline edge relative to the markers is necessary.

c. Alpine plant community characteristics

Resource Monitored: Alpine vegetation on different substrates in the alpine zone.

Justification: The extreme environments of the alpine zone limit the types of plants that can survive. In most cases alpine plants are low in stature, often in cushions, or isolated in microhabitats where environmental extremes are attenuated. Different alpine plant communities occur on stable and unstable soils, the latter being scree slopes and frost altered ground. Human activity, especially recreation, but also livestock use of alpine vegetation and

introduction of exotic plants, has modified alpine plant communities. These pressures will unlikely decrease and thus the alpine plant community can be expected to decline in cover and vigor. Once lost, alpine vegetation takes decades or more to reestablish. Monitoring of select alpine plant communities may offer shorter notice of change than casual observation of the alpine zone.

Comment: Monitoring alpine plant communities will require establishment of sampling locations in a variety of habitats. Some habitats appear to be more stressed by human use and these might have priority over others that continue to be unaltered. However, assuming that some plant communities are more resistant or resilient to human use and changes in other driving variables such as changing climate should not cause these communities to be omitted from a monitoring program. The interval between monitoring for these plant communities might be longer than the more sensitive, less resistant communities.

Example of specific measurements for indicator: Establish randomly selected quadrats (plots) on different alpine plant community types: meadow, scree slope, wind blown semi-barren coarse soils, solifluction terraces, and high-organic wet soils, and frost-boil areas. Set priorities on sensitivity of each type based on literature and early monitoring. Monitor plant composition and cover (including density of patches where dispersed, a form of frequency measurement). Monitoring should be done annually until evidence of sensitivity is established and then longer-term monitoring can be established for more resistant and/or resilient plant community types.

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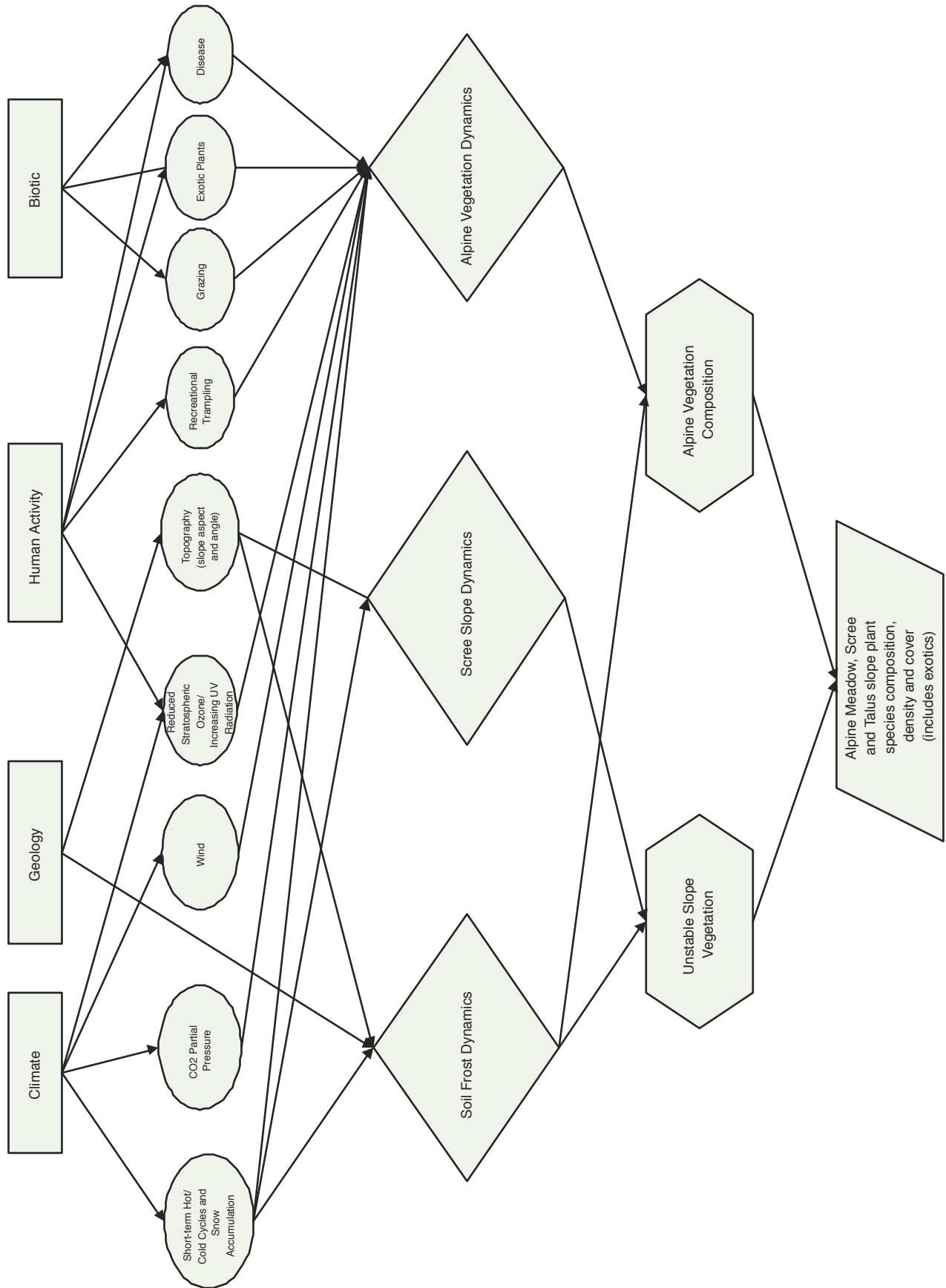


FIGURE 3 General alpine model.

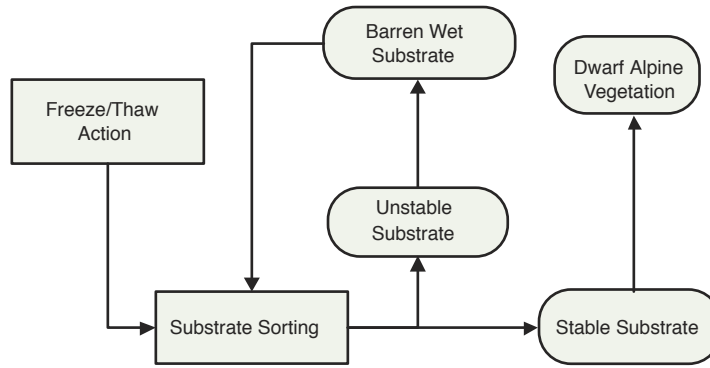


FIGURE 4 Alpine soil frost dynamics submoel.

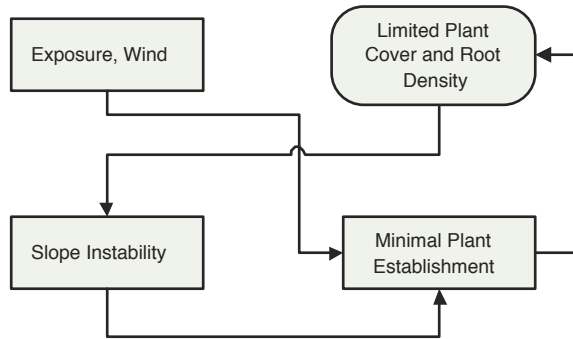


FIGURE 5 Alpine scree slope dynamics submoel.

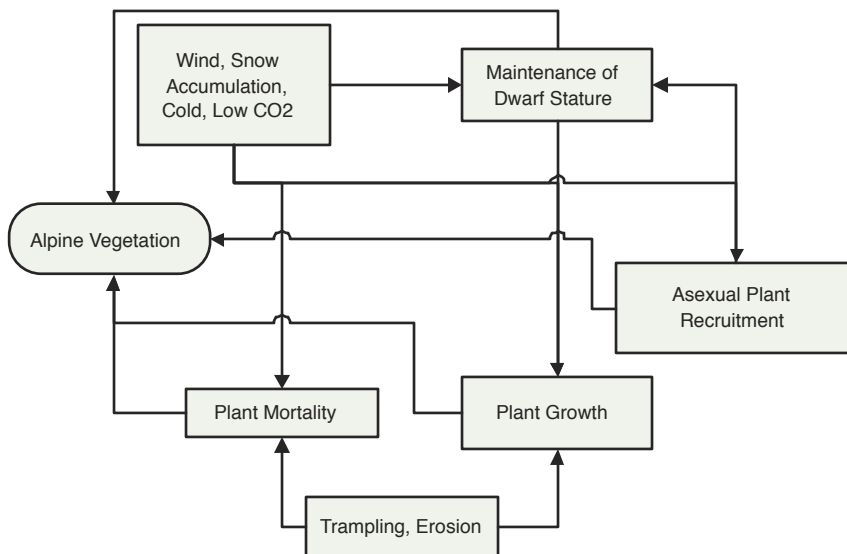


FIGURE 6 Alpine vegetation submodel.

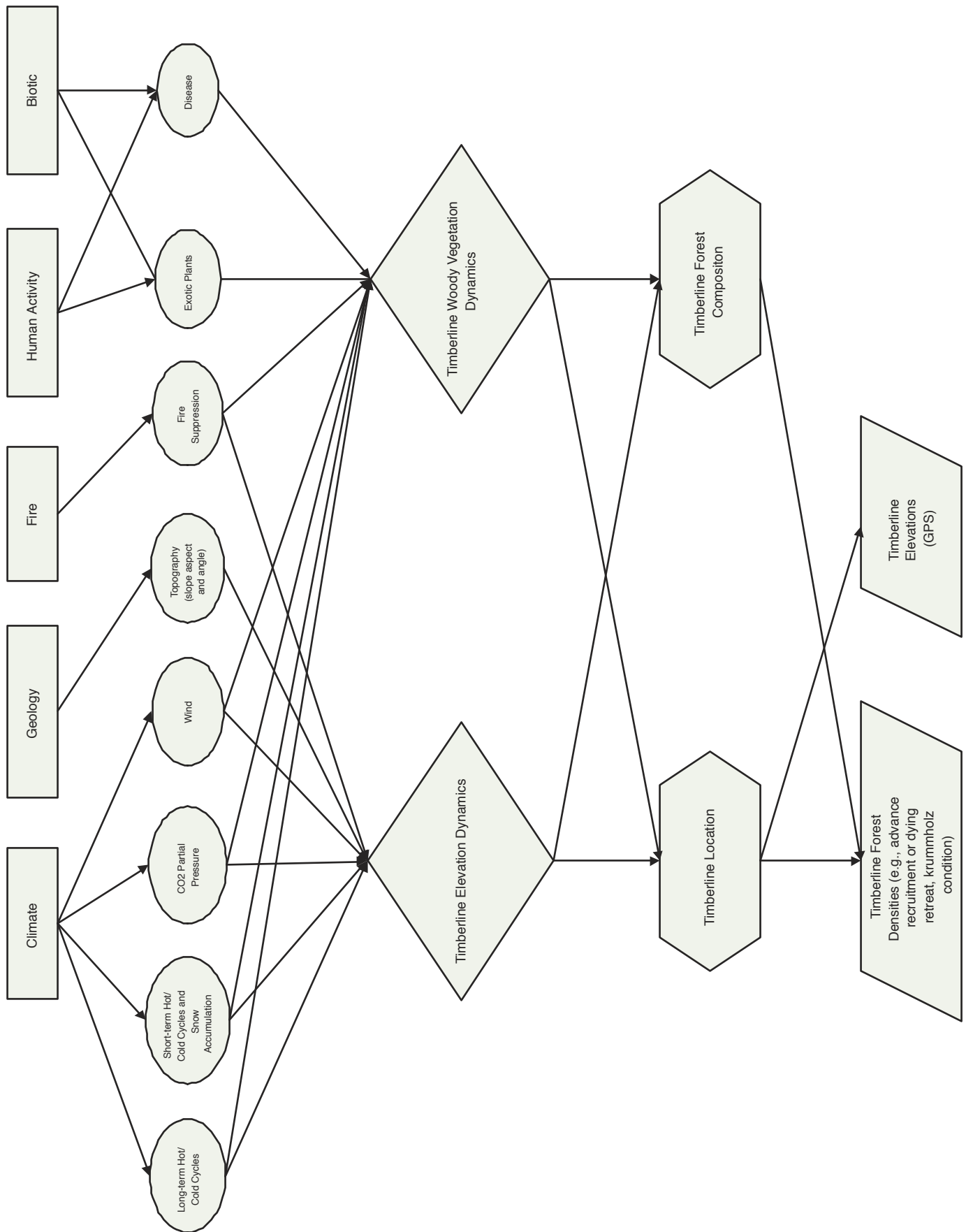


FIGURE 7 General alpine timberline model.

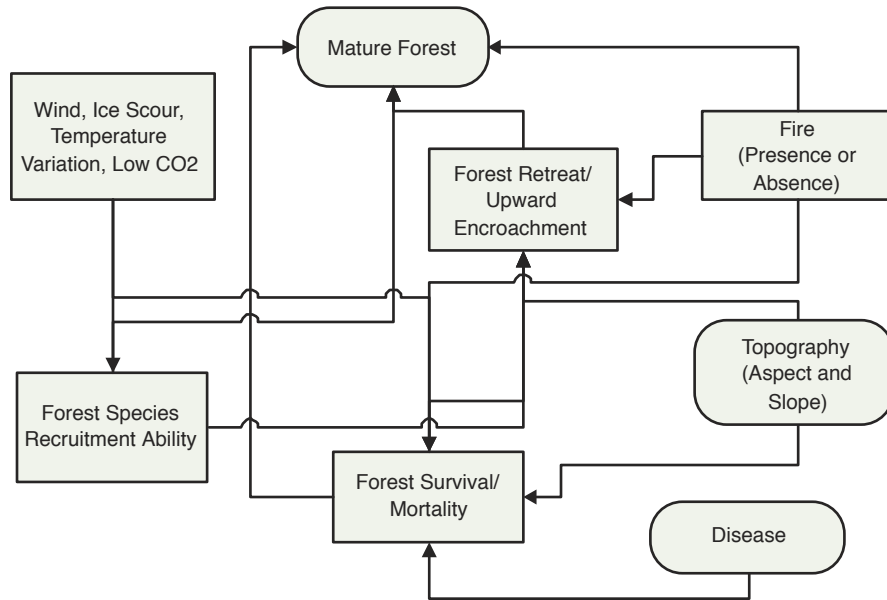


FIGURE 8 Alpine timberline elevation submodel.

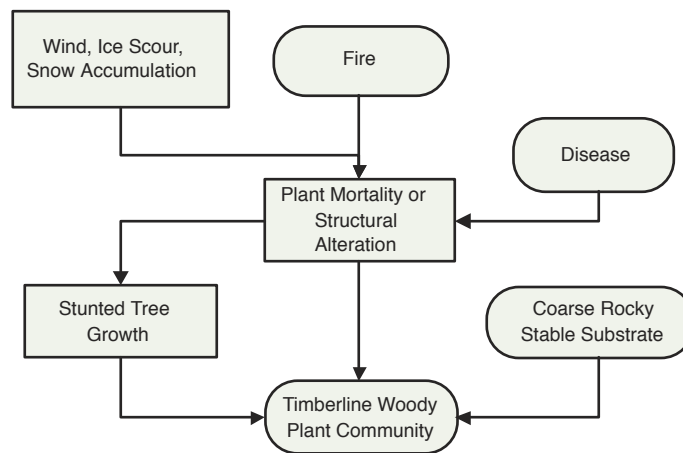


FIGURE 9 Alpine woody vegetation dynamics model.

ASPEN ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(authors: Duncan Patten and Dan Tinker)

Overview of Aspen Ecosystems

A. GENERAL CHARACTERISTICS OF ASPEN ECOSYSTEMS

Aspen (*Populus tremuloides*) is an important component of landscapes in the Greater Yellowstone Ecosystem (GYE), but is absent or rare in the Bighorn Canyon region (Knight et al. 1987). Notably, aspen is the only native upland deciduous tree found in Yellowstone National Park (YNP). Aspen stands play important ecological roles, supporting high numbers and diversity of breeding birds (DeByle 1985) and providing critical habitat and an important source of forage for summer and winter browsing ungulates (Olmsted 1979). Aspen stands throughout the GYE appear to have been declining through the 20th century and the causes and consequences of this apparent decline have caused considerable discussion (Schier 1975, Olmstead 1979, Bartos and Hinds 1985, Boyce 1989, Kay 1990, Bartos et al. 1994, Romme et al. 1995, Baker et al. 1997). In the northern range of YNP, aspen occurs in relatively small stands and is associated with more mesic conditions. However, aspen stands in the GYE are often not as complex or robust as stands in the mid-intermountain regions of Utah and Colorado (Mueggler 1988).

In the Rocky Mountain region and in the GYE, aspen is primarily a clonal species which reproduces almost exclusively via root sprouting and produces stands composed of stems from only one or a few genetic individuals (Barnes 1966, McDonough 1985, Tuskan et al. 1996). Aspen most commonly regenerates by means of vegetative sprouting from the root system following disturbances such as fire that kills the mature trees (See also Aspen-Fire Dynamics Submodel). These shoots grow rapidly and rely upon the root system of the parental tree for growth for the first 25 years (Zahner and DeByle 1965). However, rare episodes of seedling recruitment sometimes occur (Jelinski and Cheliak 1992), including widespread establishment of aspen seedlings in the GYE following the 1988 fires (Kay 1993, Romme et al. 1997, Stevens et al. 1999).

Aspen, like most *Populus* species, is recognized as a preferential browse species for ungulates during the growing season and even in winter (Olmsted 1979). In fact, in many parts of the GYE, elk commonly browse nearly all root sprouts present in aspen stands

(Romme et al. 1995, Larsen and Ripple 1999). Several studies have suggested that elk browsing is the primary cause for the lack of aspen regeneration in the GYE (Beetle 1974, 1979, Krebill 1972, Kay 1990, Bartos et al. 1994).

B. FIRE EFFECTS IN ASPEN ECOSYSTEMS

Fire is the primary disturbance agent in aspen forests of the GRYE, where large, infrequent, stand-replacing fires dominate the fire regime, and human efforts at fire suppression have historically had little effect (Romme and Despain 1989). Because of its ability to resprout following disturbance (See Aspen-Fire Dynamics Submodel), fire often facilitates secondary succession and the reestablishment of aspen. However, these stands are often eventually dominated by lodgepole pine, Engelmann spruce, or subalpine fir after several decades. Fire suppression in the GRYE may lead to a reduction in the abundance and vigor of many of the aspen stands (Knight 1994).

Conceptual Model Development

A. DRIVERS

Climate, working with soils and topography, creates appropriate site conditions for establishment and/or maintenance of aspen communities. Aspen communities are found in mesic sites and may be in riparian locations. Climate of the GRYE is characterized by long, cold winters, and cool, dry summers. Much of the precipitation falls in the form of snow and summers may be dry. Winter snowpack melts rapidly in May and June, wetting low areas and recharging groundwater which provides much of the water available for growth of aspen. Seasonal drought, such as were experienced during the summer of 1988, may exert considerable influence on soil and fuel moisture, as well as fire regimes which influence the presence of aspen.

Soils across GRYN area are diverse, a product of highly variable parent materials. For example, soils across much of YNP are mostly volcanic in origin, while glacial outwash and older Precambrian material dominates the Grand Teton landscape (Knight 1994). In Yellowstone, two different parent materials, derived from underlying bedrock, determine the soil characteristics. Differences in these parent materials lead to variation in soil texture, and therefore, water holding capacity, as well as nutrient supply and availability (see Soil and Ground Water Processes Submodel).

Fire is also an important driver in aspen ecosystems, and the management of prescribed fires and wildfires may greatly influence many natural ecosystem processes. Aspen reproduction may be closely aligned with fire dynamics (see Aspen-Fire Dynamics Submodel).

Aspen is susceptible to several biotic drivers. The Browse Dynamics Submodel illustrates how large ungulate herds, as well as domestic animals in surrounding national forests, may utilize aspen shoots and suckers for forage. Management policies of the ungulates may influence the magnitude of impacts of herbivory. Other biotic drivers include such phenomena as beaver dams, competition from vegetation (See Aspen/Vegetation Submodel), and insect herbivory. These drivers may directly and indirectly affect many ecological processes in aspen ecosystems as described below.

B. STRESSORS AND ECOLOGICAL RESPONSES

Beaver dams may affect aspen growth and establishment through herbivory and tree removal, as well as influencing availability of soil and ground water, important components of mesic sites selected by aspen. Herbivory of aspen sprouts and bark stripping by ungulates, often the result of limited forage during severe winters, may greatly reduce long-term establishment of mature aspen stands (Kay 1997). Similarly, reduction in vigor of adult and sprout aspen is possible as a result plant competition and of other forms of herbivory.

Wildfire affects many aspects of these ecosystems, including both the volatilization and creation of essential nutrients from the organic materials combusted or consumed by fire (Knight et al. 1991). Fires managed for fuel reduction or wildfires that are allowed to burn will alter availability of aspen for forage, but also stimulate aspen reproduction, both sexual and asexual.

Droughts, and other forms of wet and dry climatic cycles, affect aspen systems directly through alteration of surface and ground water processes, and the concomitant effects on plant growth and reproduction (See Aspen Growth and Reproduction Submodel). Indirectly, such climatic events may alter the establishment and survival of aspen through impacts on natural fire dynamics.

C. INDICATORS

Many non-vegetative components of aspen communities are important indicators of community structure and function. The presence, or relative abundance of some of the associated populations of faunal assemblages such as songbirds, amphibians, or ungulates, may serve as indicators of community integrity by their use of aspen stands. The absence of some of these assemblages may represent a decline in community health. Population estimates of selected major taxa such as birds or ungulates, as well as measures of stand use through behavioral studies, are useful measures for monitoring these assemblages.

The structure and function of aspen communities is important for understanding the condition of many aspen stands. For example, aspen may function as riparian species when elevated groundwater levels create moist soil conditions. In drier areas, the size and abundance of aspen sprouts and seedlings, which are rare, may serve as indicators of future stand development. Given the abundance and impact of large herbivores, and the rarity of establishment by seed, aspen seedlings or sprouts that survive to heights greater than browsing abilities of ungulates could signify significant recruitment into new or mature stands.

Measuring browsing effects by both large and small herbivores within mature aspen stands, as well as on new seedlings, provides a quantitative assessment of impacts on aspen such as truncated growth. These measures may also indicate the likelihood that root sprouts and suckers or new seedlings will be recruited into an adult growth form. Other browsing effects such as gnarling of mature trees may quantify browsing pressure within specific stands.

Landscape-scale parameters such as the spatial pattern of aspen stands across the GRYE, helps quantify and characterize heterogeneity in landscape structure, which influences many important ecosystem functions. In addition, topographic and elevational analyses may identify potential sites for future aspen recruitment by delineating more potentially moist sites from drier sites.

1. *Associated Animal Populations*

Resource Monitored: Faunal community structure

Justification: Many non-vegetative components of aspen communities are important indicators of community structure and function. These components intimately occupy niches within the aspen community and thus may change as the aspen community changes. The presence, or relative abundance of some of the associated populations or faunal assemblages such as songbirds, amphibians, or insects, may serve as indicators of community integrity by their use of aspen stands. The absence of some of these assemblages may represent a change or decline in aspen community health.

Example of Specific Measurements of this Indicator: Population estimates of selected major taxa such as birds, as well as measures of their use of particular stand structural niches.

2. *Aspen community parameters*

Resource Monitored: Ecosystem structure and function.

Justification: Aspen may function as riparian species when elevat-

ed groundwater levels create moist soil conditions. In addition, the size and abundance of aspen sprouts and seedlings, which are rare, may serve as indicators of future stand development. Given the abundance and impact of large herbivores, and the rarity of establishment by seed, aspen seedlings or sprouts that survive to heights greater than browsing abilities of ungulates could signify significant recruitment into new or mature stands.

Example of Specific Measurements of this Indicator: Belt transect or quadrat estimates of sprout or seedling presence and size. Associated measurements should include, soil moisture measurements and community descriptions through plant surveys.

3. *Browsing Effects*

Resource Monitored: Ecosystem structure

Justification: Measuring browsing effects by both large and small herbivores within mature aspen stands, as well as on new seedlings, provides a quantitative assessment of impacts on aspen such as truncated growth. These measures may also indicate the likelihood that root sprouts and suckers or new seedlings will be recruited into an adult growth form. Other browsing effects such as gnarling of mature trees may quantify browsing pressure within specific stands.

Example of Specific Measurements of this Indicator: Repeated measures of sprout and seedling heights within a given stand or plot. An alternative metric would be repeated measurements of percent browsing on representatively selected sprouts and seedlings.

4. *Landscape parameters*

Resource Monitored: Ecosystem structure and function.

Justification: The spatial pattern of aspen stands across the Greater Yellowstone landscape influences many important ecosystem functions. In addition, topographic and elevational analyses may identify potential sites for future aspen recruitment by delineating moist sites from drier sites.

Example of Specific Measurements of this Indicator: Metrics commonly quantified using landscape description software (FRAGSTATS) and GIS. Vegetative cover most common base map used.

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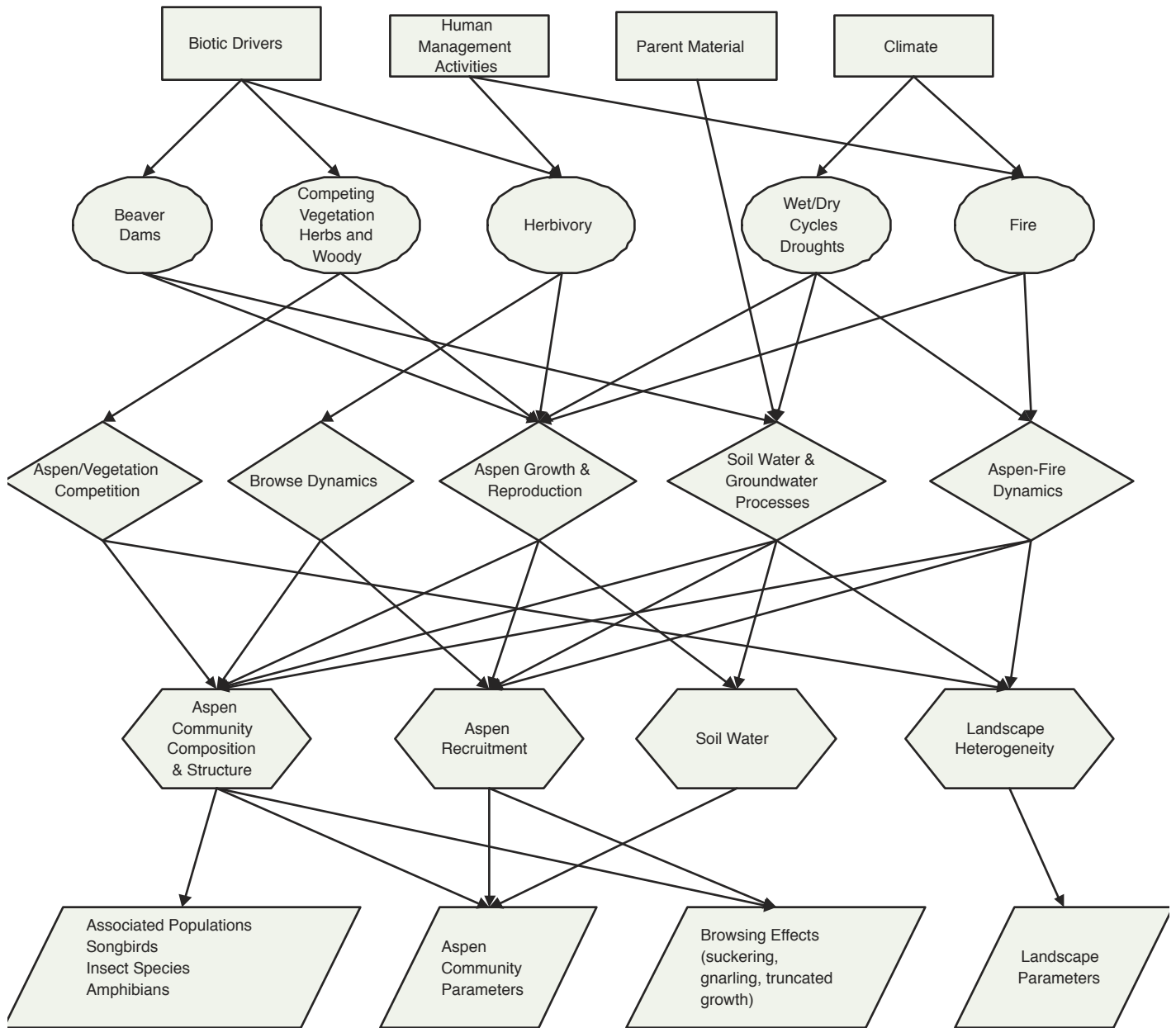


FIGURE 10 General aspen model.

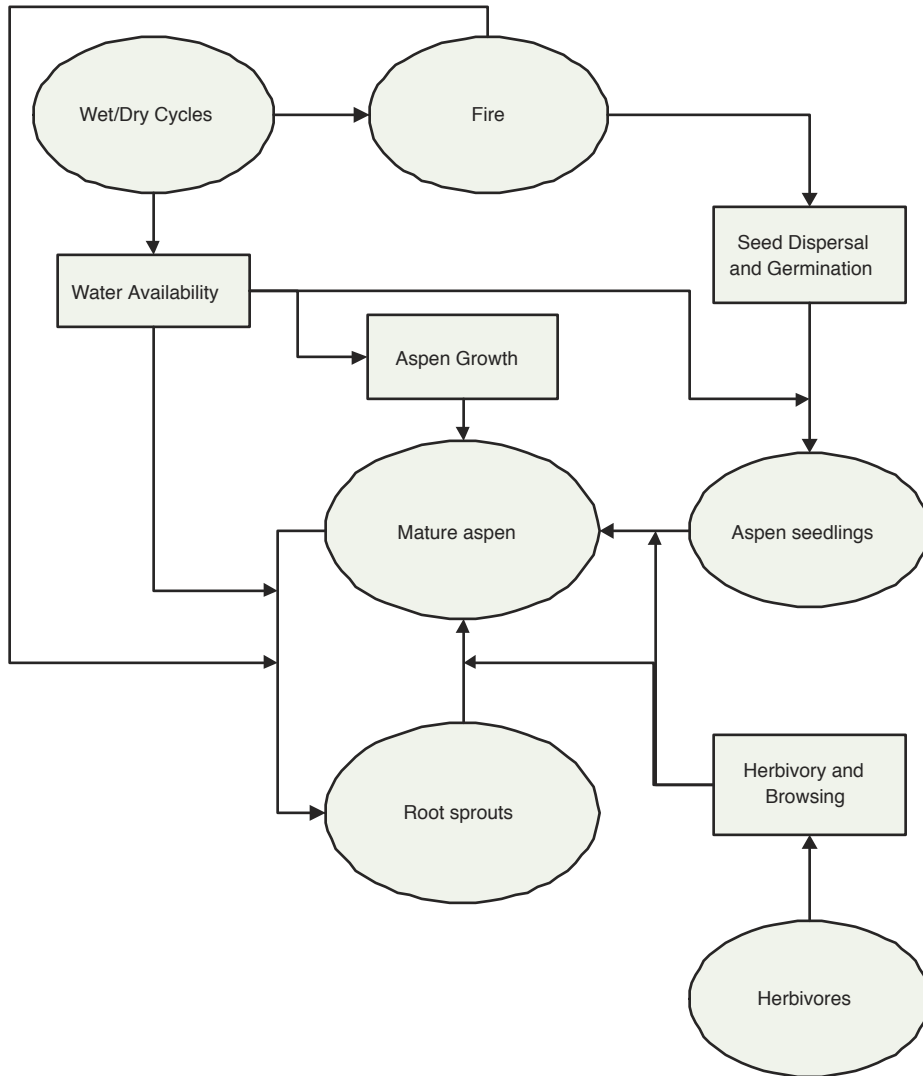


FIGURE 11 Aspen growth and reproduction submodel.

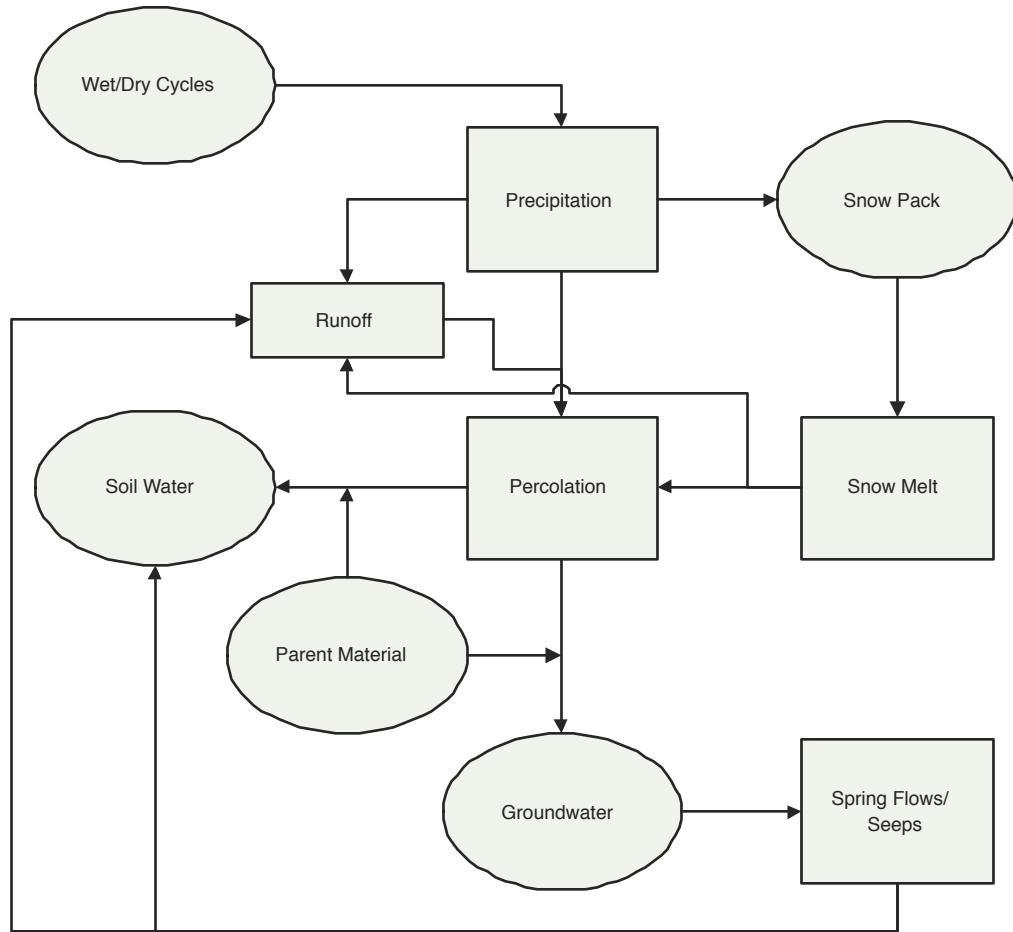


FIGURE I 2 Aspen soil and groundwater processes submodel.

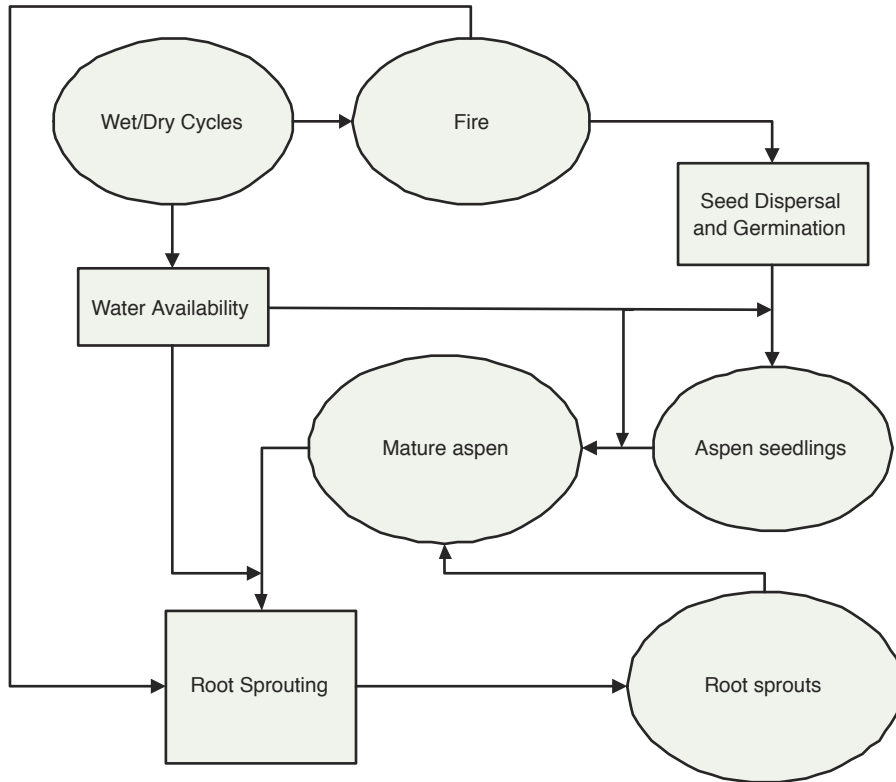


FIGURE I3 Aspen fire dynamics submoel.

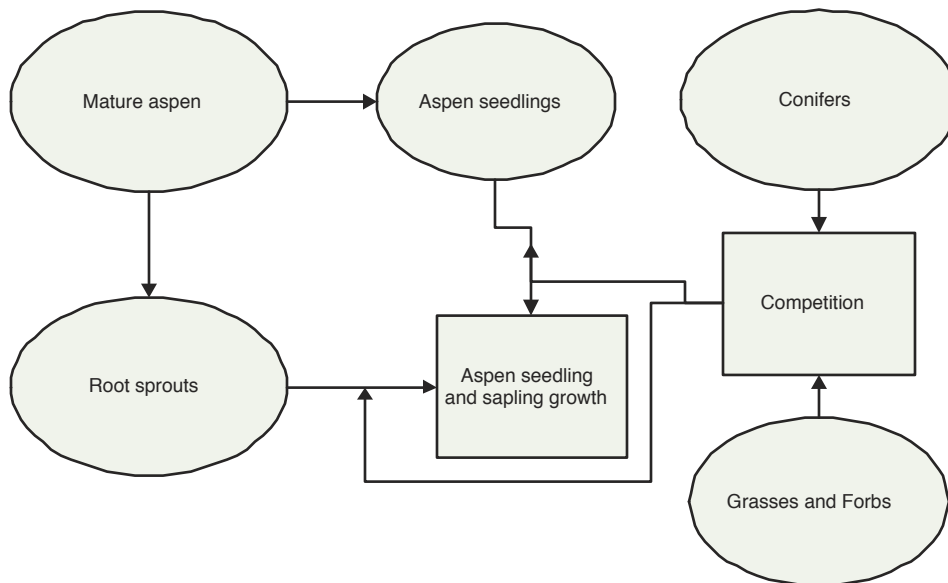


FIGURE I4 Aspen vegetarian composition submoel.

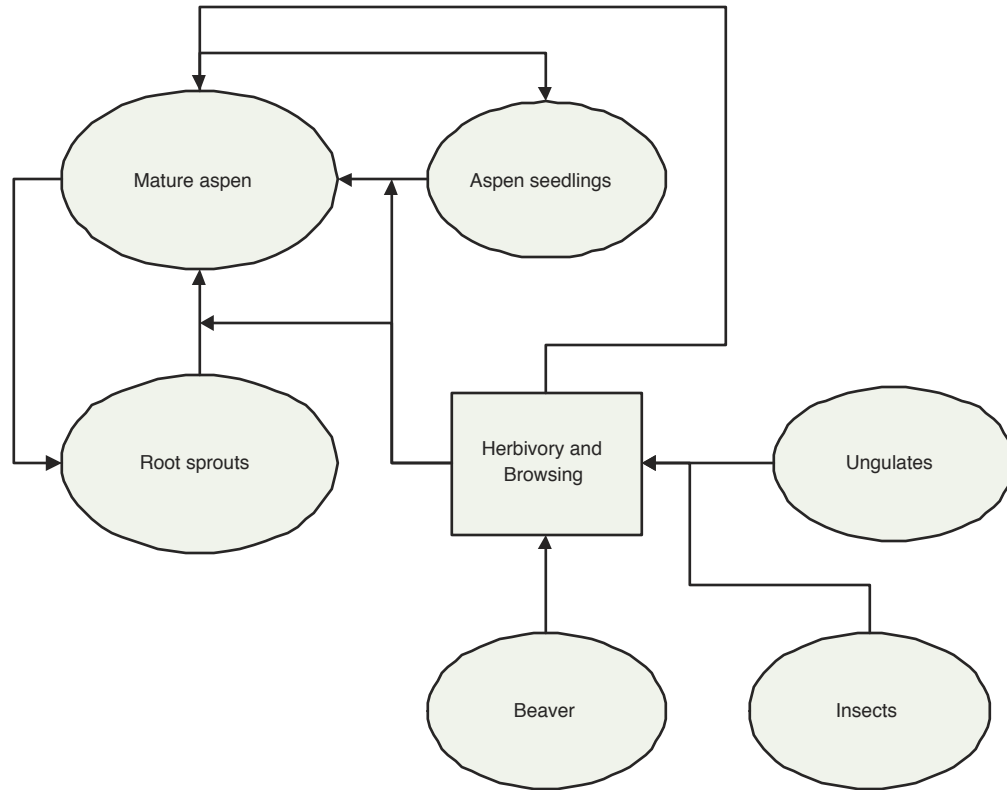


FIGURE 15 Aspen browse dynamics submodel.

DRY WOODLAND ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Cathie Jean)

Dry Woodlands are a characteristic feature of Bighorn Canyon National Recreation Area (BICA), occupying 40% of the land area (Knight et al. 1987) between 1127–1545m elevation. Dry woodlands in the Wyoming Basin are found on shallow, coarse-textured rocky sites on fractured bedrock (Wight and Fisser 1968). This environment has an inverse texture effect; roots penetrate deep in the fractured bedrock to underground water sources.

Knight et al. (1987) divide the dry woodlands into three types, mountain mahogany shrublands (*Cercocarpus ledifolius*), juniper woodlands (*Juniperus osteosperma*) and juniper / mountain mahogany woodlands based solely on the abundance of dominant species. Although the authors were unable to determine any environment differences that could distinguish a juniper site from a mountain mahogany site, the latter is more usually found on steeper, more barren sites. All three types of woodlands are present on a variety of geologic substrates (Knight et al. 1987). The dry woodland ecosystem as described here also includes stands of limber pine (*Pinus flexilis*) and Rocky Mountain juniper (*Juniperus scopulorum*).

The juniper zone is often considered low value but, nevertheless, it is an important component of the range complex by providing forage and shelter for wild game. The dry woodland ecosystem is important wildlife habitat for bighorn sheep (*Ovis canadensis*) mule deer (*Odocoileus hemionus*) and feral horses (*Equus caballus*). Dry woodlands provide thermal cover for wildlife, although a dense woodland cover is a barrier to bighorn sheep as sheep are more secure in open habitats where they can see predators.

Bighorn sheep reintroduction efforts in the Bighorn and Pryor Mountains and surrounding areas by the Wyoming Department of Game and Fish and subsequent dispersal from translocations have resulted in the Bighorn Canyon bighorn sheep population (Sloan 1995 as cited in Gudorf et al. 1996). These sheep occupy areas adjacent and within the dry woodland ecosystem.

Drivers

Dry woodlands were formally restricted to rocky – fire free settings – largely controlled by geology and topographic position. Modern distribution of juniper species is traditionally attributed to overgrazing and fire suppression, however historic invasions could also mark the

current progress of continued migration resulting from climate fluctuation (Betancourt 1987).

Drought in combination of fire suppression and grazing favor an increase in juniper cover and invasion into new sites. Grass and shrublands are vulnerable to juniper invasion, especially where herbivory results in a decrease of palatable plants which can lead to an increase of woody species or where herbivory results in the redistribution of fine fuels (Waugh 1986 as cited in Knight et al 1987) and a subsequent change in burn patterns. Fire suppression can accelerate succession grassland or shrublands to woodlands in two ways: directly preventing mortality in young, more easily burned juniper stands and indirectly by favoring the development of shrublands that serve as nurse plants for juniper seedling survival (Wright et al 1979). Once juniper is established, it is self-perpetuating as it competes well for available light, water and nutrients.

Stressors and Ecological Responses

A. FIRE SUPPRESSION AND GRAZING:

Fire suppression and grazing of palatable plants can lead to an increase in juniper cover and invasion of juniper into grassland and shrublands. This phenomenon is documented throughout the western states (see Burkhardt and Tisdale 1976). Furthermore, grasses are reduced due to juniper invasion (Jameson 66, 70 as cited in Knight et al 1987) and quality forage habitat for Bighorn Sheep and other wildlife is diminished. Low forage availability creates a need for Bighorn Sheep to forage further from escape terrain, thus increasing susceptibility to predators. Juniper leaf litter is high in phytotoxic chemicals (Jameson, 66, 70 as cited in Knight et al 1987) and this may further restrict available forage.

B. HUMAN ACTIVITIES AND LAND MANAGEMENT:

The decline and elimination of bighorn sheep from most of their historical range (Buechner 1960 as cited in Gudorf et al 1996), during the past century is believed to be attributed to human activities and land management practices that alter bighorn sheep habitat (Gudorf et al 1996). The steep, rugged escape terrain in Bighorn Canyon and its tributaries are a critical feature of bighorn sheep habitat. The openness of plant communities, or horizontal visibility, is fundamental determinant of bighorn sheep habitat quality (Gudorf et al 1996). Natural succession of dry woodlands into these habitats will make them increasingly less suitable for bighorn sheep as the thicker vegetation will obscure visibility and reduce forage availability.

C. HORSE GRAZING:

Wild horse herbivory in the Pryor Mountain Wild Horse Range and its effect on range and forage condition is a concern to wildlife and park managers. Fahnestock and Detling (2000) investigating the effects of short- and long-term ungulate grazing on plant species cover and composition found that long-term ungulate herbivory has significantly reduced grass cover and increased plant species diversity at some sites, especially lowlands in the Pryor Mountain Wild Horse Range.

3. Potential Indicators:

a. Extent and distribution of woodlands

Resource Monitored: Juniper and mountain mahogany woodlands in BICA

Justification: The spatial distribution and density of juniper and mountain mahogany woodlands influence habitat quality for Bighorn Sheep in Bighorn Canyon NRA. As forage grasses are reduced due to juniper invasion (Knight et al. 1987), quality forage habitat is diminished. Low forage availability creates a need for sheep to forage further from escape terrain and increases the chance of predation. Dry woodlands have the capability to both increase thermal cover, a valuable asset during the winter months, and the decrease security for bighorn sheep.

b. Ungulate population abundance, distribution, productivity

Resource Monitored: Demographic parameters (survivorship and population structure) of Bighorn Sheep.

Justification: The decline and elimination of bighorn sheep from most of their historical range (Buechner 1960 as cited in Gudorf et al 1996), during the past century is believed to be attributed to human activities and land management practices that alter bighorn sheep habitat (Gudorf et al 1996). Environmental stressors and management actions affect vital rates directly. Concerns persist regarding habitat quality, predation and disease and the effect on population viability in BICA.

c. Dry woodland community structure and composition

Resource Monitored: Abundance of potential forage for bighorn sheep and other wildlife species

Justification: Forage for wild and native ungulates is a management concern in BICA because of increased cover and density of juniper woodlands, increased pressure on available forage due to competition with feral horses and the spread of exotic species.

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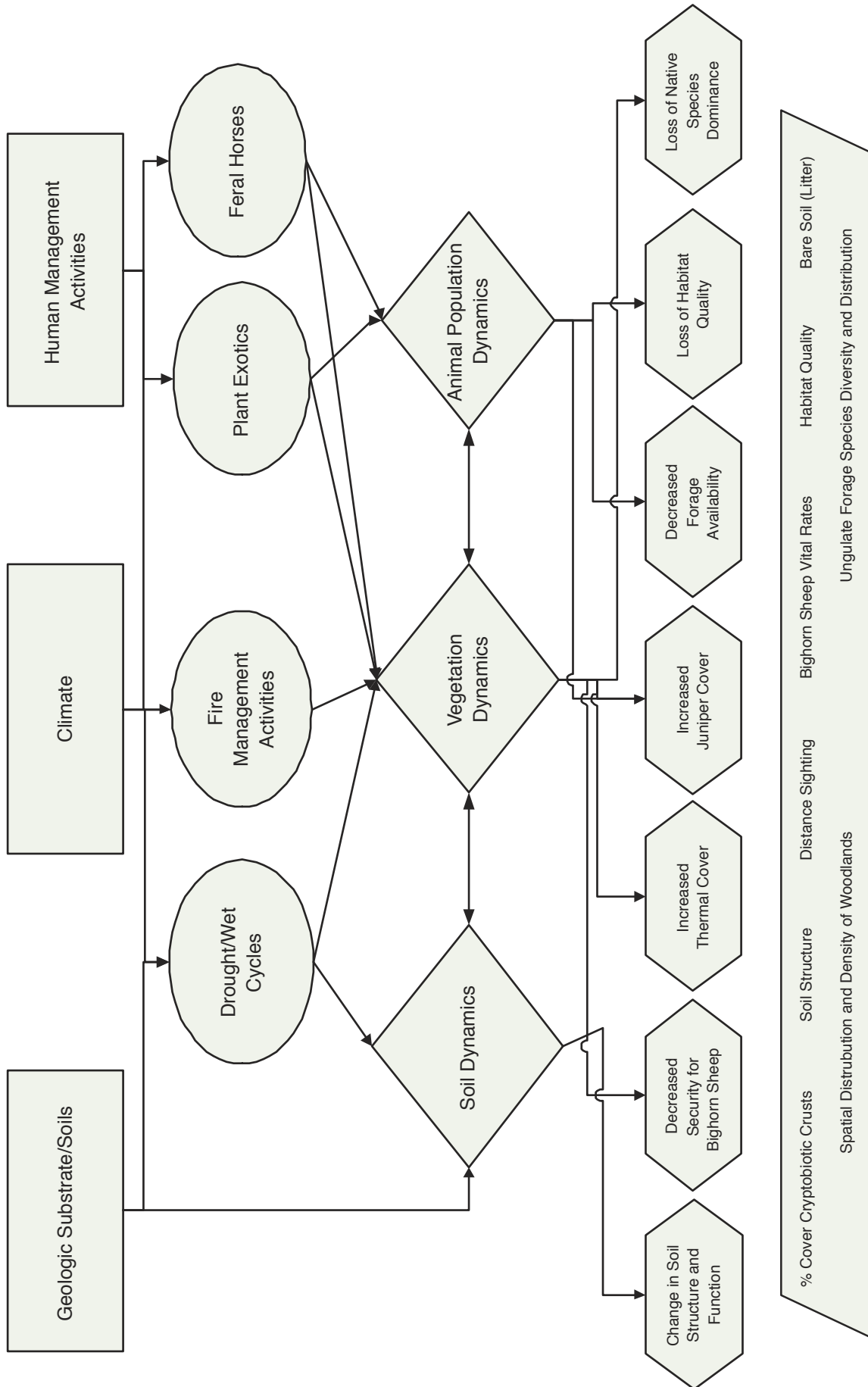


FIGURE 16 Dry woodland model.

GEOTHERMAL ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(authors: Hank Heasler and Cheryl Jaworowski)

In this paper, we present two conceptual models: a geologic conceptual model and a vital signs conceptual model. The geologic conceptual model of Yellowstone's geothermal system and processes is well understood. Among geologists, it is standard practice to draw schematic or geologic cross sections of the Earth that summarize geologic knowledge and earth processes. In geologic cross sections or schematic diagrams, the bottom of the diagram shows the deepest portion of the Earth and the top of the diagram represents the Earth's surface. In contrast, the vital signs conceptual model places Yellowstone's magma chamber (deepest portion of the Earth) at the top of the diagram as the driver for the model. We inverted the well-accepted geologic conceptual model of Yellowstone and generated a vital signs conceptual model that integrates with ecological conceptual models of Yellowstone.

Geological Conceptual Model

The geologic conceptual model of Yellowstone's geothermal system is well documented (Fournier and others, 1994; Smith and Siegel, 2000; White and others 1975). A partially molten (10-30% molten) magma chamber (45 by 30 miles wide and 3-8 miles deep) exists beneath Yellowstone National Park (Smith and Siegal, 2000). The magma chamber beneath Yellowstone National Park is in contact with a self-sealing high temperature and high concentration brine (See Figure 17). The brine exits in a porous rock layer between 1.5 to 3 miles deep. This tectonically sensitive brine may leak geothermal fluids to a high temperature reservoir. Geothermal fluids from the high temperature (~350°C) reservoir may discharge directly to the surface as hydrothermal features with unusual chemistry such as Beryl Springs. Or fluids from the high temperature reservoir may first discharge to medium temperature reservoirs (~250°C) and subsequently to the Earth's surface as neutral chloride springs. Medium temperature reservoirs may discharge fluids (water or gases) to low temperature (~150°C) reservoirs. Low temperature reservoirs may discharge fluids (water or gases) to the Earth's surface and form acid sulfate springs. Precipitation of silica and zeolites along fractures provides a self-sealing mechanism. The competing effects of a self-sealing mechanism and earthquakes control the upflow of geothermal fluids to reservoirs.

Acid sulfate thermal springs, neutral chloride thermal springs, mud pots, paint pots geysers, or fumaroles exist where there is an appropriate combination of water chemistry, plumbing, heat, and hydrology. Neutral chloride springs represent unrestricted discharge of thermal waters from reservoirs. Above the local water table where there is more heat than water, steam vents to the surface forming fumaroles. At the Earth's surface, oxidation of H₂S will form acid sulfate springs. Additionally, acidic waters will cause chemical decomposition of the bedrock, generate clay minerals and form mud pots or paint pots (with ferric-oxides). A key to understanding the geochemistry of thermal waters in the Upper Geyser Basin is knowledge of dissolved gases such as CO₂ (Fournier and others, 1994). In the Upper Geyser Basin, the amount of boiling (no boiling to maximum boiling) in the intermediate reservoirs determines the chemical composition of thermal waters in the shallow, low temperature reservoirs and ultimately the geochemistry of thermal springs at the Earth's surface. Annual, generally widespread changes in thermal features in the Norris Geyser Basin are the result of changes in the potentiometric surface of cold water adjacent to or interconnected with the hydrothermal system (Fournier and others, 2002). Thus, to understand short-term cyclical and catastrophic changes as well as long-term changes that may be natural or anthropogenic to the Yellowstone hydrothermal system both cold ground water and hydrothermal systems the must be monitored and assessed.

Rainfall and snowmelt (meteoric waters) from the Earth's surface may recharge fluids in the low temperature, medium temperature or high temperature reservoirs. The amount of meteoric waters entering the various subsurface reservoirs depends upon the amount of precipitation falling over the Yellowstone National Park. During times of glaciation, the balance between meteoric waters entering subsurface reservoirs and fluids from the magma chamber changes. During the last glacial maximum (Pinedale), geochemical evidence indicates that cold-water recharge entered the hydrothermal system (Fournier and others, 1994). As the glaciers melted, fluid flow reversed and became a hydrothermal system dominated by discharge. Changes in the magma chamber itself also affect the release of geothermal waters and gases. Thus, monitoring hydrothermal waters in Yellowstone's geyser basins will yield information about the mixing of fluids and the health of the geothermal system.

Vital Signs Conceptual Model

A. THE DRIVER: YELLOWSTONE'S MAGMA CHAMBER

Yellowstone's magma chamber is the ultimate geophysical driver of the vital signs conceptual model (See Figure 27). Geothermal fluids convect towards the surface via fracture systems that are self-sealing and tectonically sensitive. Geothermal fluids from deep, intermediate and shallow depths mix and interact with meteoric waters and eventually are discharged as hydrothermal features in Yellowstone's geyser basins.

B. STRESSORS

Precipitation, climate change, volcanic activity, earthquakes and human activity affect thermal feature chemistry, thermal feature extent, hydrothermal fluids, and thermal feature temperature. Yellowstone National Park has two distinct climates within YNP (Despain, 1987) and YNP is located near the boundary between regional atmospheric flow patterns. Depending upon where this boundary is located the annual climate and precipitation may be above or below normal precipitation in different areas of the park. Climate and weather (precipitation) directly influence the amount of "cold" meteoric waters in thermal areas. Earthquakes and volcanic activity can rejuvenate thermal features by opening new pathways for fluids or close existing thermal pathways. Human activities such as geothermal development, oil & gas exploration, the drilling and production of water wells or vandalism may affect the fluid flow of thermal features.

C. EFFECTS

Stressors affect changes in the chemistry of thermal features, extent of thermal features, fluid flow, and temperature of thermal features.

D. OUTCOMES

Acid sulfate thermal springs, neutral chloride thermal springs, mud pots, geysers, fumaroles and heated ground are consequences of Yellowstone's magma chamber and its stressors.

Measures or Vital Signs

The following vital signs are measures of Yellowstone's geothermal systems: chloride flux, the temperature of well waters, water levels in wells, the spatial extent of features, and the heat flux.

E. VITAL SIGNS

1. Chloride Flux

Over 94% of the chloride in waters originating in Yellowstone is of magmatic origin (Norton and Friedman, 1985). A study of variations in chloride flux can be used to establish a baseline for measuring the

interaction of the deep geothermal waters with the surficial geothermal system. In addition, chloride flux baseline information may be used to assess any future adverse impacts on the Park's thermal features that may be caused by commercial development of geothermal energy, gas, oil and groundwater adjacent to the Park.

Resource Monitored: Thermal Features (mud pots, geysers, fumaroles, neutral chloride thermal springs and acid sulfate thermal springs)

Justification: The chloride flux method for estimating geothermal activity in YNP has been extensively peer reviewed, accepted, and published (Fournier and others, 1976, Norton and Friedman, 1985; Friedman and Norton, 1990; Norton and Friedman, 1991; and Friedman and others, 1993). In addition, 19 years of chloride flux data exists for Yellowstone's major rivers-the Fall, Madison, Snake, and Yellowstone.

2. Heat Flux

Yellowstone's heat flux has been estimated using the chloride flux method, airborne sensors and satellite images. Increased heat flux in an area may indicate changes in subsurface hydrothermal activity. Additionally, warm ground affects the health of vegetation, migration of animals, and safety of park visitors.

Resource Monitored: Heated Ground

Justification: The chloride flux method for estimating heat flux in YNP has been extensively peer reviewed, accepted, and published (Fournier and others, 1976, Norton and Friedman, 1985; Friedman and Norton, 1990; Norton and Friedman, 1991; and Friedman and others, 1993). Remote sensing is a cost-efficient method to map and monitor heated ground. In the early days of remote sensing, Haze (1971) estimated heat flow and geothermal resources. In 2002, Watson and others used Landsat 7 sensors to estimate ground that was snow-free or minimal snow cover due to thermal activity. In the winter and spring, animals make use of thermal areas with minimal snow cover. In 2002, thermal airborne sensors were flown over the Mammoth-Norris corridor. Mapping new areas of heated ground and yearly changes in the heated ground can assist with maintenance of roads and visitor safety.

3. Temperature of Water in Wells

In Yellowstone National Park, water can come from several sources: a high temperature, deep reservoir (~350°C), medium temperature, intermediate depth reservoirs (~250°C), or low temperature, shallow reservoirs (~150°C). Water from the high temperature reservoir di-

rectly connected to the magma chamber may be discharged as the unique thermal feature known as Beryl Springs. Water from medium temperature reservoirs may be directly discharged to the surface and form neutral chloride thermal features or flow to low temperature reservoirs. Water from the low temperature reservoirs may be directly discharged to the surface and form acid sulfate springs.

Resource Monitored: Groundwater system associated with thermal features

Justification: In Yellowstone, human activities such as road construction can adversely impact unique thermal features such as Beryl Springs or the many neutral chloride and acid sulfate springs. Potential threats outside of Yellowstone (geothermal development, oil and gas development, groundwater development) may also affect Yellowstone's thermal features.

4. *Water Level in Wells*

Water levels in wells respond to variations in climate, precipitation, geothermal development or development of petroleum resources adjacent to the Yellowstone National Park. Monitoring of water levels in wells will capture changes in the groundwater system. Comparison of water levels with meteorological data, seismic data, ground deformation or recent earthquakes will aid in distinguishing natural changes in thermal features from climatic change or human causes (geothermal, oil or gas wells outside of Yellowstone).

Resource Monitored: Groundwater system associated with thermal features

Justification: Comparison of water levels in wells will aid in distinguishing natural changes in thermal features from climatic change or human causes (geothermal development, oil or gas wells, groundwater development).

5. *Spatial Extent of Thermal Features*

Geologists use various visible, infrared, and microwave sensors to map surficial deposits, flow structures in lava flows, faults, fractures, ash flows, basalts, rhyolites, andesites, and allow lithologic discrimination of sedimentary rocks. Additionally, visible, infrared, thermal and microwave sensors (AVIRIS, TIMS, LANDSAT and RADAR) can detect subsidence, predict movements of animals, discriminate between healthy versus stressed vegetation, map active hot springs, map hydrothermal mineralization, and generate detailed mineral maps of specific areas (Dzurisin and others, Evans, 1988; 1990; Kokaly and others 1998; Kokaly and others 1999; Kruse, 1997, Shafer, 1998; Wicks and others, 1998).

Resource Monitored: Thermal features (mud pots, geysers, fumaroles, neutral chloride thermal springs and acid sulfate thermal springs)

Justification: Remote sensing technologies are a cost-efficient method of mapping and monitoring the spatial extent of thermal features. Change detection maps of thermal features can aid the assessment of natural changes versus human-caused changes of thermal areas. Maps derived from remote sensing technologies have applications to geology, hydrology, geobiology, archeology, and ecology. Additionally, these colorful images can be used by park interpreters to educate visitors and by park managers to inform politicians or other resource managers.

F. SUMMARY

We propose to monitor the following vital signs as indicators of the thermal activity and integrity of Yellowstone's geothermal areas: (1) chloride flux, (2) the temperature of water wells, (3) water levels in wells, (4) the spatial extent of thermal features, and (5) heat flux.

A more complete discussion of methodology proposed for monitoring Yellowstone National Park's geothermal resources can be found in the draft version of "A Geothermal Monitoring Plan for Yellowstone National Park", March 2003 by H. Heasler, C. Jaworowski, and D. Susong.

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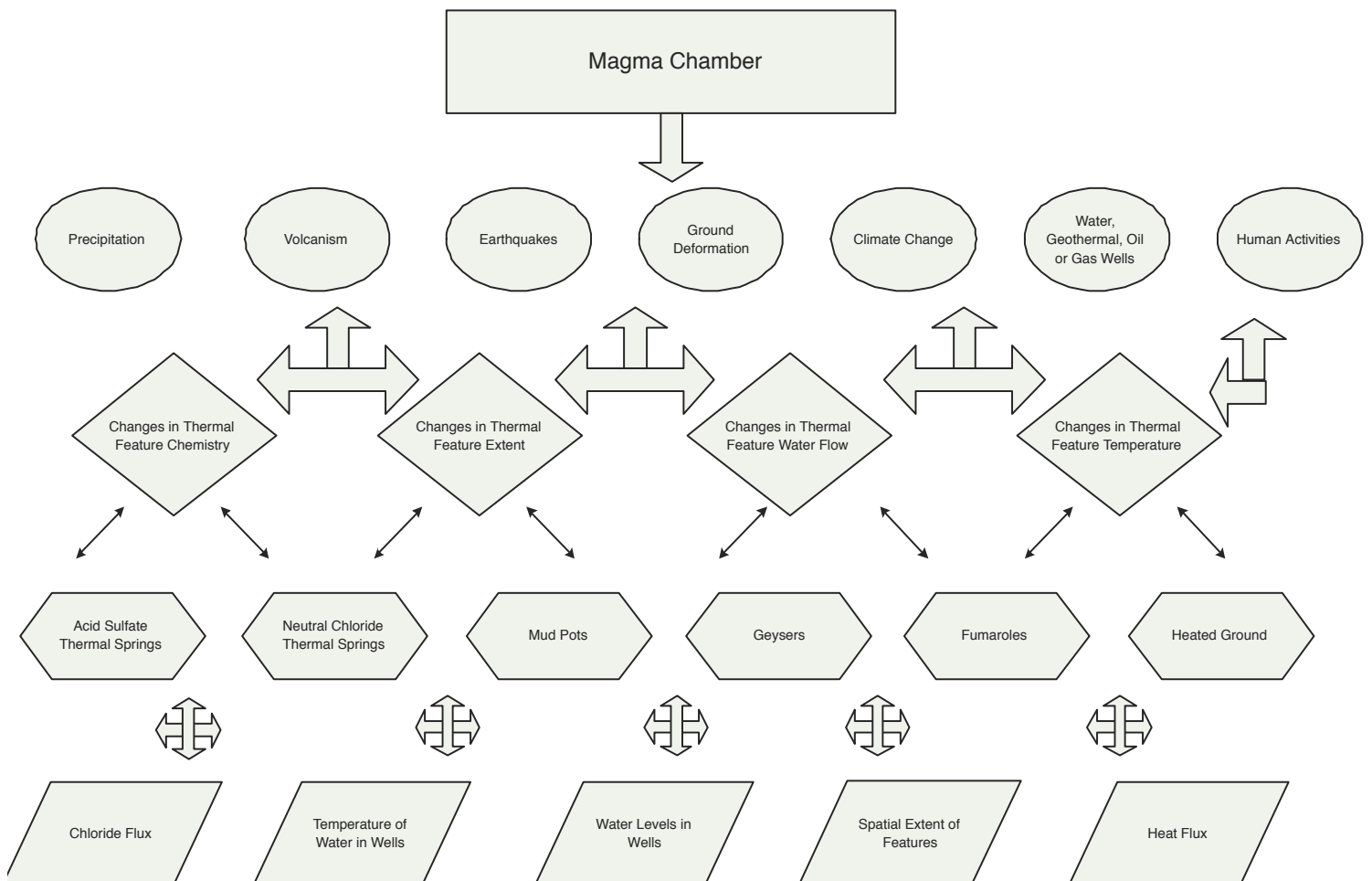


FIGURE 17 Geothermal model.

GRASSLAND ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Glenn Plumb)

Grass plants evolved between seventy to eighty million years ago with adaptations that allow them to survive under intense and frequent disturbances including tremendous removal of living phytomass (e.g. fire and herbivory) and drought. Grasses often grow in vast concentrations, most often in semi-arid climates (Brown 1985) with a fairly uniform and continuous cover. Grasslands are the largest of the four major natural vegetation formations covering the planet (Gould 1968) and have certain characteristics in common, including a rolling to flat topography with precipitation between ten and 40 inches per year distributed unevenly with seasonal peaks followed by extended periods of drought (Sims 1988). Historically, grasslands covered up to 800 million ha in North America (Kuchler 1964) and still remain the largest native biome covering approximately 125 million ha (USFS 1980). Although most grasslands were historically located on extensive plains, relatively small pockets of mountain grasslands and grassland-forest combinations occur in the western coniferous forests (Sims 1988). Grasslands are dominated by grasses and grass-like plants (e.g. Cyperaceae) with particular grassland's biomass dominated by fewer than 6 species (Coupland 1974). Yet, typically grasses contribute less than 20% of the total vegetative species richness to a grassland community. Forbs (non-grass-like herbs) are seasonally important along with dwarf shrubs and occasional trees (Coupland 1979). Grassland plants invest carbohydrates in structural development early in the growing season when moisture is adequate and thus during successive drought, grassland plants can utilize stored labile carbohydrates, decrease dark respiration and maintain gas-exchange process under stressed water potentials. Nutrient uptake is rapid when moisture is available and at these times, plants are most palatable and tolerant of herbivory with removal of phytomass often stimulating increased rates of photosynthesis by the remaining tissues and intercalary meristems of grasses permitting growth after herbivory (Risser 1985). Under periodic drought stress grassland plants close stomata with extensive leaf curling to reduce water loss (Risser 1985).

Conceptual Model Development

I. DRIVERS

The climate of the GRYN parks is characterized by long, cold winters and cool, dry summers with much precipitation occurring as snow-

pack that melts rapidly April – June, depending on elevation providing much of the water available for annual growth in mountain grasslands. Snowpack generally begins to accumulate in October and November, reaches maximum in early to mid-April. Due to late-winter rates of accumulation, the annual snowpack can become isothermic before peak accumulation and thus melts rapidly beginning in May to July depending on elevation. Despain (1990) describes two major local climatic types as a valley type with peak precipitation coming in the spring and a mountain type with peak precipitation in the winter. Merrill and Boyce (1996) evidenced that mountain grassland seasonal biomass production was more correlated with climate and snowpack controls that the total number of herbivores occupying the grassland.

Soils of grasslands often differ markedly from those soils found under forest canopy due to variation in underlying depositional origins and the differences in soil formation processes unique to vegetation types (Coupland 1979). In grasslands, leaching is often limited due to general aridity and so grassland soils are often more basic with organic matter distributed throughout the soil profile. While many grassland soils are derived from glacial and associated outwash sand and gravel parent materials, the GRYN mountain grasslands are also heavily influenced by volcanic rhyolitic and andecitic parent materials (Despain 1990). The GRYN parks are also influenced by glacial depositional/windblown loess that was strongly influenced by the distribution and duration of glacial icecaps (Despain 1990).

2. STRESSORS AND ECOLOGICAL RESPONSES

Frank and McNaughton (1992) examined the interactive roles of large animal herbivory and drought on mountain grasslands and found that although the process of aboveground net primary productivity, large herbivore consumption and dung deposition varied widely among different grassland sites, grassland production and consumption, and consumption and dung deposition were positively correlated across sites. Despite the evidenced role of herbivory and dung deposition in controlling site-level production, they also concluded that climate is the principal driving variable of ecosystem processes and that direct and indirect effects of single-season drought will persist for several years after the event. Frank and McNaughton (1993) concluded that in the absence of drought, herbivory at the site level can result in a compensatory growth response and hence stimulate mountain grassland productivity due in part that the migratory behavior of native ungulates tracks young, high quality forage as it varies temporally

and spatial along an elevational gradient across these ecosystems. The nutrient dynamics of mountain grasslands that support abundant migratory large-body sized wildlife are generally poorly understood (Frank et al. 1994), but evidence from Yellowstone National Park suggests that grazers are important component of mountain grassland N budgets with 1) landscape position and soil water affecting nutrient dynamics, 2) annual mineralization positively associated with soil N content, 3) the proportion of soil N mineralized negatively correlated to soil C/N, and 4) rates of nitrogen mineralization higher in mountain grasslands than in other temperate grassland ecosystems, possibly due to grazers promoting N cycling.

Detling (1998) reviewed the effects of mammalian herbivores on GRYN park grassland plant species composition, biomass, productivity and nitrogen cycling and concluded that patch dynamics controlled by local small mammal soil disturbances, fire, grazing, and urine/dung deposition underpinned temporal and spatial variability in grazing intensity and facilitated N mineralization and persistence of grassland communities. The role of fire in mountain grasslands was also examined by Norland et al. (1996) who concluded that forage biomass decreased where moderate soil heating occurred, forage quality (N and digestibility) increased, herbivore diets and habitat use patterns did not change, but that large herbivore use of riparian shrubs did increase. Simulation model experiments by Turner et al. (1994) explored the effects of fire size, fire pattern and winter severity on large herbivore foraging and population dynamics on a mountain grassland. Although, fire pattern (clumped vs fragmented) and winter severity seemed to control temporal and spatial variation in grassland foraging and habitat use patterns, the interactions between fire scale and grassland spatial patterns suggest that fire size along is not sufficient to predict grassland response and ungulate survival. A review of ecological stressors and responses in a mountain grassland in northern Yellowstone National Park (YNP 1997) concluded that 1) large ungulate herds and intensive grazing did not appear to be affecting native or Alpha diversity (Singer 1996), 2) there is no consistent effects of large animal grazing on forbs (Coughenour et al. 1995, Reardon 1996), 3) soil bulk densities were higher on grazed areas (Lane 1990, Lane and Montagne 1996) and soil moisture levels were unaffected by grazing (Lane 1990, Coughenour 1991, Singer and Harter 1996), 4) accumulated organic litter was greater in ungrazed sites and exposed bare ground was higher in grazed areas (Frank 1990, Singer 1996), and 5) mountain grassland root biomass and nitrogen exhibited no responses to grazing (Merrill et al. 1994).

3. INDICATORS

Grasslands of the GRYN are characterized generally by montane communities dominated by varying levels of perennial C4 graminoids, C3 graminoids, forbs and dwarf or small shrubs with local sites often dominated by either C4 or C3 graminoids. There are few if any sites that would be characterized as true short or mixed grass prairie. Aboveground vegetative biomass production is a cumulative process within a single growing season, with peak biomass roughly equivalent to Annual Net Primary Production (Briggs and Knapp 1995). In these montane systems, peak vegetative biomass production occurs dependent on elevation and aspect controls on soil temperature and precipitation regimes. Grassland annual aboveground vegetative biomass production responds directly to a suite of intra- and inter-annual primary stressors including grazing (e.g. herbivory), fire, drought, snowpack, and in some circumstances trampling by hoofed medium and large herbivores, and directly reflects the primary photosynthetic capacity that can be quantified across multiple spatial and temporal scales. Although climate has been described as the primary driving variable of montane grassland processes (McNaughton and Frank 1992), each park has qualitative and quantitative models to partition the interactive effects of these multiple primary stressors. Extra-normal variation in grassland vegetative biomass capacity will be a direct response indicator of both short and long term stressor effects. Multiple factors can control and limit ANPP at larger scales in grasslands including fire, climatic variability, and various activities by herbivores, with soil nitrogen and water limitations often operating at local scales. Knapp et al. (1998) suggest that these scale-dependent controls on ANPP underpin patterns of temporal switching among limiting resources that results in non-equilibrium behaviors in which transient periods occur where no resources are limiting. Thus, ANPP becomes a reliable predictive ecological indicator only with long-term records and a non-equilibrium perspective.

In GRYN montane grassland communities, vegetative biomass production is underpinned by temperature and soil moisture availability that are generally controlled temporally by delayed onset of the growing season according to increasing elevation. Onset and timing of herbivory of the annual increment of primary vegetative production by large and medium sized herbivores is generally synchronized with onset of seasonal "growth pulse" of green-up as it moves from winter ranges to higher elevation summer ranges. Migratory native GRYN herbivores (e.g. elk, bison) often utilize the initial green-up phase but move to higher elevations prior to onset of plant

reproduction. Non-migratory GRYN herbivores (e.g. wild horses) will sustain utilization of montane grasslands until current annual growth or residual cover is depleted. Frank (1990) showed that seasonal utilization of montane grasslands could stimulate total annual productions beyond levels of ungrazed sites. Thus, offtake as a measure of the amount of annual vegetative growth increment that is removed by these native large and medium sized herbivores can serve as a variably important stressor on the resiliency of montane grasslands. Although, short-term interannual variation in vegetation offtake can be explained by inherent variability of climate and herbivory interactions, long-term trends and patterns of montane grassland resiliency can be inferred from measures of offtake as an integrative indicator of whether there are immediate or long-term concerns for residual effects of overgrazing of these systems. Unlike fire or climatic influences that can generate some levels of uniform grassland vegetation responses, seasonal grazing of montane grasslands can generate patchy heterogeneity. Overlaid on these patterns of heterogeneity are heterogeneous patterns of trampling, urine and dung deposition and the issues of patchy compensation and even overcompensation by grazed plants. Thus, although annual temporal and spatial patterns of offtake can be variable, long-term measurements of offtake can be an important integrative ecological indicator of grassland non-equilibrium dynamics.

The availability and cycling of nutrients, especially N, is a primary controlling stressor on grassland community structure and function, and in turn are directly affected by variation in ecosystem processes such as vegetation production and decomposition (Blair et al. 1998). Variation in N availability can determine and limit productivity, species composition, and plant physiological responses to disturbances and rates of litter decomposition. Additionally, N cycling processes can be directly altered by human activities such as prescribed fire and external influences such as climate and topography (Turner 1997). Thus, long-term measurements of N cycling processes and outcomes can provide the basis for evaluating the role of natural or anthropogenic stressors on ecosystem function, small and large scale redistribution or transport of N between summer and winter ranges, grassland plant and animal communities, and abiotic ecosystem characteristics such as soil chemistry. In GRYN parks there are important and sizeable large and medium body-sized herbivore populations that are very important components of nitrogen cycle processes and outcomes. In addition to local defoliation processes and outcomes, redistribution of N through urine and feces, these

herbivores play an important role in stimulating patterns of aboveground and belowground production. They also contribute to nutrient cycling through the return of carcasses to these systems. Despite these important processes, N limitation is not a universal feature of montane grasslands and that its relative importance can vary with influences of fire, grazing, elevation, topography and precipitation regimes. This loose coupling of relationships is due to the potential for the direct influences of these same variables under variable environmental and management regimes. Thus N cycling process and outcomes reinforce the viewpoint that montane grasslands operate as a nonequilibrium system in which the relative importance of N varies in space and time (Knapp and Seastadt 1998).

The native species richness of montane grasslands are often characterized by a matrix of widely distributed, temporally stable, and abundant "core" species, a second tier of localized, less abundant, and temporally dynamic and somewhat unpredictable "satellite" species (subdominant graminoids and forbs). The exotic species richness of montane grasslands often follows a two-tiered similar pattern with species such as timothy, smooth brome, bluegrass and annual bromes dominating some landscapes while other montane grassland landscapes include only few subdominant exotic forbs. These "satellite" species suggest a subdominant role for non-equilibrium dynamics in the persistence of native montane grassland community abundance and distribution. By contrast, the spatial and temporal stability of the "core" species richness suggests a certain dominant equilibrium dynamic to native montane grassland community abundance and distribution. Still, although there can be a dominant equilibrium matrix of montane grassland species, these systems are far from static and can be disrupted severely by the emergence of dominant exotic species described above. Indeed, the increasing presence of exotic species, described above, has greatly altered some GRYN grassland communities. Thus, long-term measures of native and exotic species abundance and distribution can serve as an important integrative ecological indicator to assess the interplay between equilibrium and nonequilibrium processes that regulate montane grassland plant species persistence and coexistence. For this vital sign to be useful, GRYN parks will need robust models of the relationship between montane grassland condition and exotic species presence and resultant effects on broader ecological processes and outcomes.

Research from a variety of grassland types indicates that there are important mechanisms by which the dominant disturbance regimes

(e.g. fire, grazing, drought, trampling, wallowing) can have important interactive effects on the emergent spatial and temporal patterns of populations and communities of grassland small mammals, birds and insects. Variation in scale-dependent effects on abundance and distribution of taxon can be attributed to variation in food and/or habitat requirements (generalist versus specialist), differences in vagility (e.g. flying versus walking), differences in life span (annual vs. perennial) and combinations of these factors. Additionally, population-level mechanisms that underpin fire- or grazing- induced dynamics on animal populations or communities are taxon- and species-specific. For example, many species of grasshoppers overwinter as eggs in soil and are mobile as adults and spring conditions may be independent of grasshopper abundance, whereas sedentary insect species that are above ground during fires can suffer catastrophic mortality (Fay and Samenus 1993). Thus there exists opportunity to identify taxon that are relatively tightly coupled to key ecosystem stressors and that when coupled to measures of grassland production and offtake could serve as key integrative ecological indicators. There is some evidence that grassland small mammals, birds and insects conform to Hanski's (1982) core-satellite hypothesis wherein these communities are characterized by several abundant, widely distributed, and relatively stable species, accompanied by a larger number of rare, localized, and dynamically variable species. Thus, the temporally variable patterns in species abundance, distribution and diversity are influenced strongly by changes in the distribution and abundance of rare species. Climate and topographic influences can also control spatial and temporal heterogeneity in montane grassland animal populations and communities. Hence, the spatial and temporal variation in population abundance and community structure require multifactoral explanations (Kaufmann et al. 1998) and may make single-limitation explanations for population and community dynamics unrealistic (Belovsky and Joern 1995).

a. Grassland Annual Net Primary Productivity – ANPP (e.g. Aboveground Vegetation Production, Photosynthetic Capacity)

Justification: Grasslands of the GRYN are characterized generally by montane communities dominated by varying levels of perennial C4 graminoids, C3 graminoids, forbs and dwarf or small shrubs with local sites often dominated by either C4 or C3 graminoids. There are few if any sites that would be characterized as true short or mixed grass prairie. Aboveground vegetative biomass

production is a cumulative process within a single growing season, with peak biomass roughly equivalent to Annual Net Primary Production (Briggs and Knapp 1995). In these montane systems, peak vegetative biomass production occurs dependent on elevation and aspect controls on soil temperature and precipitation regimes. Grassland annual aboveground vegetative biomass production responds directly to a suite of intra- and inter-annual primary stressors including grazing (e.g. herbivory), fire, drought, snowpack, and in some circumstances trampling by hoofed medium and large herbivores, and directly reflects the primary photosynthetic capacity that can be quantified across multiple spatial and temporal scales. Although climate has been described as the primary driving variable of montane grassland processes (McNaughton and Frank 1992), each park has qualitative and quantitative models to partition the interactive effects of these multiple primary stressors. Extra-normal variation in grassland vegetative biomass capacity will be a direct response indicator of both short and long term stressor effects.

Comment: Multiple factors can control and limit ANPP at larger scales in grasslands including fire, climatic variability, and various activities by herbivores, with soil nitrogen and water limitations often operating at local scales. Knapp et al. (1998) suggest that these scale-dependent controls on ANPP underpin patterns of temporal switching among limiting resources that results in non-equilibrium behaviors in which transient periods occur where no resources are limiting. Thus, ANPP becomes a reliable predictive ecological indicator only with long-term records and a non-equilibrium perspective.

b. Grassland Vegetation Annual Offtake (e.g. Current year growth utilization by primary consumers)

Justification: In GRYN montane grassland communities, vegetative biomass production is underpinned by temperature and soil moisture availability that are generally controlled temporally by delayed onset of the growing season according to increasing elevation. Onset and timing of herbivory of the annual increment of primary vegetative production by large and medium sized herbivores is generally synchronized with onset of seasonal "growth pulse" of green-up as it moves from winter ranges to higher elevation summer ranges. Migratory native GRYN herbivores (e.g. elk, bison) often utilize the initial green-up phase but move to higher elevations prior to onset of plant reproduction.

Non-migratory GRYN herbivores (e.g. wild horses) will sustain utilization of montane grasslands until current annual growth or residual cover is depleted. Frank (1990) showed that seasonal utilization of montane grasslands could stimulate total annual productions beyond levels of ungrazed sites. Thus, offtake as a measure of the amount of annual vegetative growth increment that is removed by these native large and medium sized herbivores can serve as a variably important stressor on the resiliency of montane grasslands. Although, short-term interannual variation in vegetation offtake can be explained by inherent variability of climate and herbivory interactions, long-term trends and patterns of montane grassland resiliency can be inferred from measures of offtake as an integrative indicator of whether there are immediate or long-term concerns for residual effects of overgrazing of these systems.

Comment: Unlike fire or climatic influences that can generate some levels of uniform grassland vegetation responses, seasonal grazing of montane grasslands can generate patchy heterogeneity. Overlaid on these patterns of heterogeneity are heterogeneous patterns of trampling, urine and dung deposition and the issues of patchy compensation and even overcompensation by grazed plants. Thus, although annual temporal and spatial patterns of offtake can be variable, long-term measurements of offtake can be an important integrative ecological indicator of grassland non-equilibrium dynamics.

c. Grassland Nitrogen (e.g. availability, inputs, loss and associated processes)

Justification: The availability and cycling of nutrients, especially N, is a primary controlling stressor on grassland community structure and function, and in turn are directly affected by variation in ecosystem processes such as vegetation production and decomposition (Blair et al. 1998). Variation in N availability can determine and limit productivity, species composition, and plant physiological responses to disturbances and rates of litter decomposition. Additionally, N cycling processes can be directly altered by human activities such as prescribed fire and external influences such as climate and topography (Turner 1997). Thus, long-term measurements of N cycling processes and outcomes can provide the basis for evaluating the role of natural or anthropogenic stressors on ecosystem function, small and large scale redistribution or transport of N between summer and

winter ranges, grassland plant and animal communities, and abiotic ecosystem characteristics such as soil chemistry.

Comment: In GRYN parks there are important and sizeable large and medium body-sized herbivore populations that are very important components of nitrogen cycle processes and outcomes. In addition to local defoliation processes and outcomes, redistribution of N through urine and feces, these herbivores play an important role in stimulating patterns of aboveground and belowground production. They also contribute to nutrient cycling through the return of carcasses to these systems. Despite these important processes, N limitation is not a universal feature of montane grasslands and that its relative importance can vary with influences of fire, grazing, elevation, topography and precipitation regimes. This loose coupling of relationships is due to the potential for the direct influences of these same variables under variable environmental and management regimes. Thus N cycling process and outcomes reinforce the viewpoint that montane grasslands operate as a nonequilibrium system in which the relative importance of N varies in space and time (Knapp and Seastadt 1998).

d. Grassland Vegetation Community Structure (Patterns of abundance and distribution)

Justification: The native species richness of montane grasslands are often characterized by a matrix of widely distributed, temporally stable, and abundant "core" species, a second tier of localized, less abundant, and temporally dynamic and somewhat unpredictable "satellite" species (subdominant graminoids and forbs). The exotic species richness of montane grasslands often follows a two-tiered similar pattern with species such as timothy, smooth brome, bluegrass and annual bromes dominating some landscapes while other montane grassland landscapes include only few subdominant exotic forbs. These "satellite" species suggest a subdominant role for non-equilibrium dynamics in the persistence of native montane grassland community abundance and distribution. By contrast, the spatial and temporal stability of the "core" species richness suggests a certain dominant equilibrium dynamic to native montane grassland community abundance and distribution. Still, although there can be a dominant equilibrium matrix of montane grassland species, these systems are far from static and can be disrupted severely by the emergence of dominant exotic species described above.

Indeed, the increasing presence of exotic species, described above, has greatly altered some GRYN grassland communities. Thus, long-term measures of native and exotic species abundance and distribution can serve as an important integrative ecological indicator to assess the interplay between equilibrium and nonequilibrium processes that regulate montane grassland plant species persistence and coexistence.

Comment: For this vital sign to be useful, GRYN parks will need robust models of the relationship between montane grassland condition and exotic species presence and resultant effects on broader ecological processes and outcomes.

e. Grassland Insect and Vertebrate Community Structure

Justification: Research from a variety of grassland types indicates that there are important mechanisms by which the dominant disturbance regimes (e.g. fire, grazing, drought, trampling, wallowing) can have important interactive effects on the emergent spatial and temporal patterns of populations and communities of grassland small mammals, birds and insects. Variation in scale-dependent effects on abundance and distribution of taxon can be attributed to variation in food and/or habitat requirements (generalist versus specialist), differences in vagility (e.g. flying versus walking), differences in life span (annual vs. perennial) and combinations of these factors. Additionally, population-level mechanisms that underpin fire- or grazing- induced dynamics on animal populations or communities are taxon- and species-specific. For example, many species of grasshoppers overwinter as eggs in soil and are mobile as adults and spring conditions may be independent of grasshopper abundance. Sedentary insect species that are above ground during fires can suffer catastrophic mortality (Fay and Samenus 1993). Thus there exists opportunity to identify taxon that are relatively tightly coupled to key ecosystem stressors and that when coupled to measures of grassland production and offtake could serve as key integrative ecological indicators.

Comment: There is some evidence that grassland small mammals, birds and insects conform to Hanski's (1982) core-satellite hypothesis wherein these communities are characterized by several abundant, widely distributed, and relatively stable species, accompanied by a larger number of rare, localized, and dynamically variable species. Thus, the temporally variable patterns in species abundance, distribution and diversity are influenced strongly by changes in the distribution and abundance of rare

species. Climate and topographic influences can also control spatial and temporal heterogeneity in montane grassland animal populations and communities. Hence, the spatial and temporal variation in population abundance and community structure require multifactoral explanations (Kaufmann et al. 1998) and may make single-limitation explanations for population and community dynamics unrealistic (Belovsky and Joern 1995).

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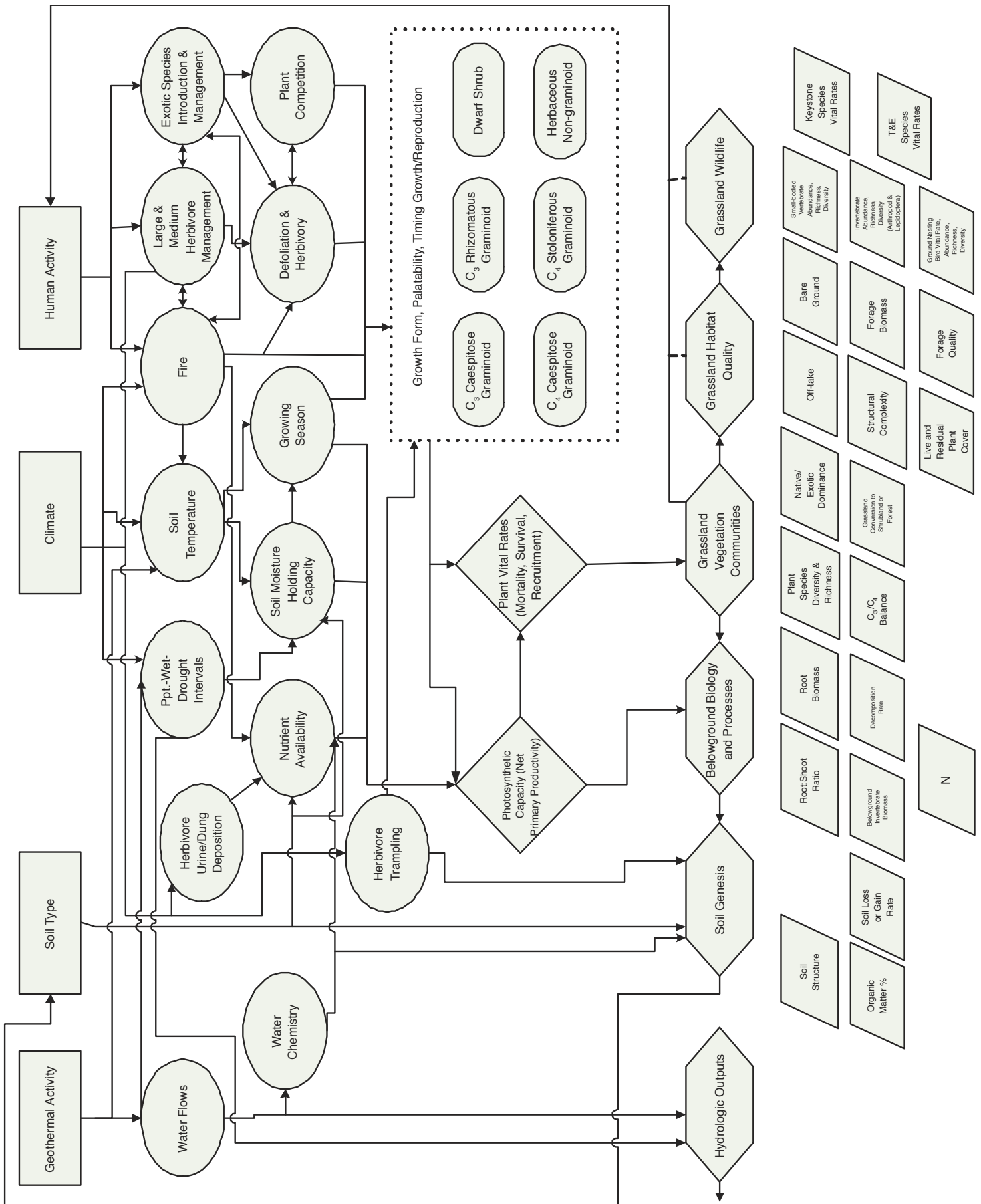


FIGURE 18 Grassland model.

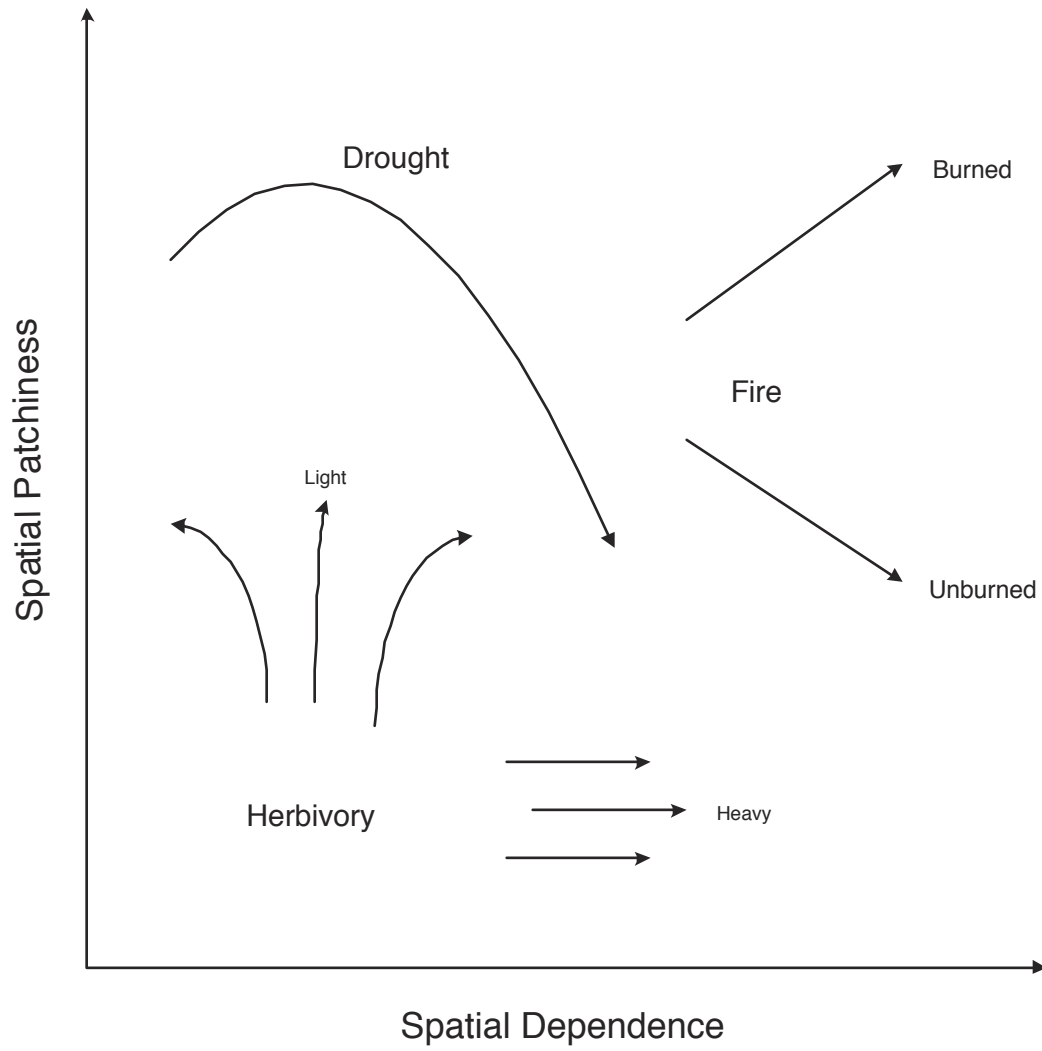


FIGURE 19 Grassland net primary productivity submodel (adapted from Briggs 1998).

SHRUBLAND ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Glenn Plumb)

Many shrubland communities are characterized by a matrix of shrub growth forms and interspaces that may be occupied by variable levels of native graminoids and herbaceous non-graminoid cover. The floristic composition of shrubland interspace communities can be heavily controlled by moisture competition and allelopathy. The natural evolutionary resilience of shrubland communities can be altered under severe disturbance regimes such as fire in fire-intolerant communities or excessive grazing/trampling by large herbivores. The natural resilience of shrubland communities can be further stressed by the introduction of aggressive exotic plant species into these interspaces. Foremost among these aggressive exotics is *Bromus tectorum* that can, by virtue of completing its annual growth cycle by early summer, outcompete native C3 or C4 graminoids through moisture competition. This continuous fine fuel layer can then facilitate increased fire frequency and intensity, reducing fire-intolerant shrub species, resulting in reduced soil organic matter and nutrient pools and a spiral of downward ecosystem degradation. Shrubland interspaces are often characterized by either a microcryptic crust dominated by mosses, lichens, and algae between the perennials or abundant exposed mineral soil surface between the perennials. Excessive grazing or trampling of microcryptic crusts can predispose shrubland communities to invasion by aggressive exotic species. Thus, for shrubland exotic species to serve as a meaningful ecological indicator, there needs to be relatively strong models that predict the interactive relationships between natural system resilience, excessive disturbance, and the ecology of exotic species.

Woody, lignified or partially lignified shrubs provide food or feeding sites, security, and breeding areas for aboveground and belowground small vertebrates and insects in montane shrubland communities. Research from a variety of shrubland types indicates that there are important mechanisms by which the dominant disturbance regimes (e.g. fire, grazing, drought, trampling, wallowing) can have important interactive effects on the emergent spatial and temporal patterns of populations and communities of small mammals, birds and insects. Variation in scale-dependent effects on abundance and distribution of taxon can be attributed to variation in food and/or habitat requirements (generalist versus specialist), differences in vagility (e.g. flying versus walking), differences in life span (annual vs.

perennial) and combinations of these factors. Additionally, population-level mechanisms that underpin fire- or grazing- induced dynamics on animal populations or communities are often taxon- and species-specific. For example, many species of grasshoppers overwinter as eggs in soil and are mobile as adults and spring conditions may be independent of grasshopper abundance, whereas sedentary insect species that are above ground during fires can suffer catastrophic mortality (Fay and Samenus 1993). Thus there exists opportunity to identify taxon that are relatively tightly coupled to key ecosystem stressors and serve as key integrative ecological indicators. There is some evidence that shrubland small mammals, birds and insects conform to Hanski's (1982) core-satellite hypothesis wherein these communities are characterized by several abundant, widely distributed, and relatively stable species, accompanied by a larger number of rare, localized, and dynamically variable species. Thus, the temporally variable patterns in species abundance, distribution and diversity are influenced strongly by changes in the distribution and abundance of rare species. Climate and topographic influences can also control spatial and temporal heterogeneity in montane shrubland animal populations and communities. Hence, the spatial and temporal variation in population abundance and community structure require multifactoral explanations (Kaufmann et al. 1998) and may make single-limitation explanations for population and community dynamics unrealistic (Belovsky and Joern 1995).

In montane shrublands primary production is segregated into patches of relatively high (undershrub) and low (interspace) long-term response and it follows that nutrient cycling will be anisotropic. As shrubs or shrub patches accumulate under-canopy litter, nutrient pools will also collect there. These spatial patterns occur because of absorption of nutrients that extend beyond plant crown area, N fixation by the plant or associate symbiotic organisms and net import of N by fauna using shrubs for nesting, resting, roosting, feeding or burrowing, and deposition of litter and soil by wind and water. Thus, long-term measurements of N cycling processes and outcomes can provide the basis for evaluating the role of natural or anthropogenic stressors on ecosystem function, small and large scale redistribution or transport of N between summer and winter ranges, shrubland plant and animal communities, and abiotic ecosystem characteristics such as soil chemistry. In GRYN parks there are important and sizeable large and medium body-sized herbivore populations that are very important components of nitrogen cycle processes and outcomes. In addition to local defoliation processes

and outcomes, redistribution of N through urine and feces, these herbivores play an important role in stimulating patterns of aboveground and belowground production. They also contribute to nutrient cycling through the return of carcasses to these systems. Despite these important processes, N limitation is not a universal feature of montane shrublands and that its relative importance can vary with influences of fire, grazing, elevation, topography and precipitation regimes. This loose coupling of relationships is due to the potential for the direct influences of these same variables under variable environmental and management regimes. Thus N cycling process and outcomes reinforce the viewpoint that montane shrublands might operate as a nonequilibrium system in which the relative importance of N varies in space and time.

Adequate vegetation cover is one of the most critical aspects of any watershed ecosystem in terms of upland water infiltration and sediment yields. The natural evolutionary vegetal cover resilience of shrubland communities can be altered under severe disturbance regimes such as fire in fire-intolerant communities or excessive grazing/trampling by large herbivores. The natural resilience of shrubland community vegetal cover can be further stressed by the introduction of aggressive exotic plant species. Alteration and loss of shrubland understory vegetal cover will increase overall soil erosion processes and outcomes. Montane shrubland communities with moderate to steep slopes will be most stable where shrub roots permeate soils to the geologic parent material. A diverse cover of both deep-rooted shrubs and shallow-rooted shrubs will serve to minimize soil erosion processes and outcomes. Thus, measures of soil erosion processes and outcomes can be strongly indicative of important declines in vegetal cover and the interactive processes that underpin such declines. Not all shrubs provide a positive feedback to erosional processes. Some shrubs have chemicals in their foliage or litter that can lead to hydrophobic soil surfaces resulting in less infiltration and xerification of microsites. Indeed, not all erosional processes and outcomes should be seen as outside the natural range of variability for montane shrubland communities. Cupped interspace depressions arising from differential erosion (aggregation, infiltration, growth and soil genesis) have been occurring at the microsite level for extended intervals in shrubland communities.

Some structural characteristics of montane shrublands can be coupled closely with spatial organization of growth forms and the interplay of ecosystem functional attributes that center around energy flow and nutrient and water cycles. The primary character in-

involved in shrublands is that of dispersion (West 1989) that underpins the aggregation and deviation from random spatial arrangement. The vertical and horizontal structures of a variety of shrublands are remarkably similar across relatively undisturbed examples. In sagebrush steppe, shrubs have a cover of 10%-80%, depending on site and successional status (West 1988) with a herbaceous stratum that can reach 30-40 cm during the growing season. On many sagebrush steppe sites, cover usually exceeds 80% and can exceed 200%. Measures of shrubland cover and vertical or horizontal structure can track the tendency for stable shrubland community structure and function. Thus, measurable deviation in these parameters could provide a relatively rapid integrative assessment of shrubland community stability. Shrub non-random aggregation can serve as the grit starting a pearl (Vasek and Lund 1980), the nucleus of successional change and ecosystem development (West 1989) that leads towards system stabilization.

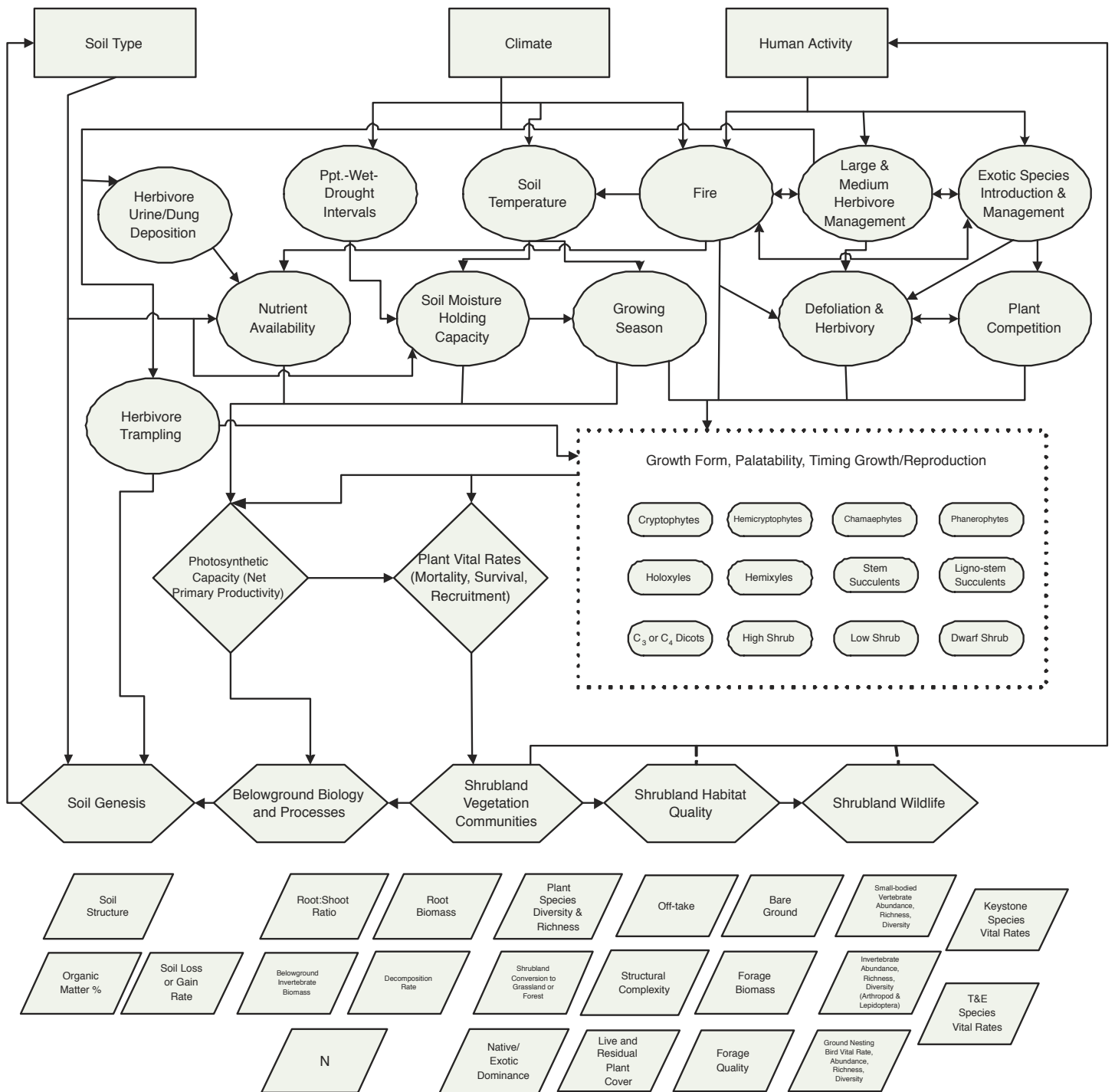


FIGURE 20 Shrubland model.

LOGEPOLE PINE ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Dan Tinker)

Lodgepole pine (*Pinus contorta* var. *latifolia*) is the most common tree in the northern Rockies, especially in northern Wyoming. These montane forests range from 1,800-3,200 m in elevation in the GRYE. Although commonly described as a seral, or pioneer species that often gives way to Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) during later stages of succession, climax stands of lodgepole pine may be found on very dry and nutrient-poor sites, where other tree species are unable to survive (Moir 1969; Despain 1983; Lotan and Perry 1983). Lodgepole pine usually forms relatively young, even-aged stands as a result of regeneration following severe fires (see below), but older, uneven-aged stands may exist at higher elevations where fire frequency is low (Despain 1990).

Fire is the primary disturbance agent in lodgepole pine forests of the GRYE. Large, infrequent, stand-replacing fires dominate the fire regime, and human efforts at fire suppression have historically had little effect (Romme and Despain 1989). Lodgepole is a fire-adapted species, rather than fire-resistant, due to its relatively thin bark and the production of serotinous cones. These serotinous cones remain closed at maturity, and only open to release their seeds when exposed to very high temperatures, such as fires will create (Lotan 1975). Following stand-replacing fires, seedlings establish quickly, usually within two years, creating new stands where post-fire seedling density may vary by six orders of magnitude (Turner et al. In review).

Conceptual Model Development

A. DRIVERS

The parent materials for soils across the subalpine plateaus of YNP, where lodgepole pine dominates the vegetation, are mostly volcanic in origin. Two different parent materials, derived from underlying bedrock, determine the soil characteristics in Yellowstone. Rhyolitic soils are found most often on drier sites, and are typically very nutrient limited. Andesitic soils are relatively more fertile, and often occur at higher elevations (Despain 1990). Differences in these parent materials is responsible for soil texture, and therefore, water holding capacity, as well as nutrient supply and availability. Rhyolitic soils are more sandy while andesitic soils contain much more clay (Despain 1990). Calcium is ten times more abundant in soils derived from andesite (Despain 1990).

Yellowstone's climate is characterized by long, cold winters, and cool, dry summers. Most of the precipitation falls in the form of snow. Winter Snowpack melts rapidly in May and June, providing much of the water available for growth in lodgepole pine forests. In addition, periods of seasonal drought, such as were experienced during the summer of 1988, may exert considerable influence on soil and fuel moisture, as well as fire regimes.

Topography on the subalpine plateaus in Yellowstone is quite varied. Much of the landscape is dominated by gently rolling hills, however, steep canyons and mountains may break up the continuous nature of the plateaus. Topographic effects on snow accumulation and on the spread of natural disturbances such as fire or exotic species may be significant.

Biotic drivers such as insects, plant pathogens and disease, and herbivory by both ungulates and insects may directly and indirectly affect many ecological processes in lodgepole pine ecosystems. As more fully described below in the section on Stressors, these biotic drivers can lead to extensive episodes of tree mortality, which can affect critical processes such as coarse woody debris accumulation and net primary productivity.

Given the importance of fire in lodgepole pine ecosystems, the management of prescribed fires and wildfires may greatly influence many natural ecosystem processes. For example, large, intense crown fires may help control episodic outbreaks of Mountain Pine Beetle by burning entire stands where significant outbreaks have occurred. Many of the indirect effects of fire suppression will be discussed below in subsequent sections.

B. STRESSORS AND ECOLOGICAL RESPONSES

Drought, snowpack, and windstorms, all driven by weather and climate, affect many important ecosystem processes. Drought will affect soil moisture during the growing season, thereby affecting plant development and primary productivity, as well as forage abundance. Reduced soil moisture may also reduce nutrient supplies by a reduction in microbial activities such as decomposition and mineralization (Litton et al in press). Snowpack is the single largest contributor to soil moisture, and therefore water and nutrient availability during the growing season. Windstorms may cause large blowdowns, such as the 6,000-ha event that occurred in the Teton Wilderness in 1987. These events directly affect forest and landscape structure through widespread tree mortality and creation and accumulation of large quantities of coarse woody debris (CWD). Large areas of uprooted

trees may also allow for the invasion of new plant species, and may also affect the growth rates of the new and existing species.

Biotic stressors, primarily insects and plant pathogens, have important effects in lodgepole pine forest ecosystems (Romme et al. 1986; Veblen et al 1991). Openings may be created in the forest canopy through tree mortality, which can result in increases in understory vegetation production (Knight 1994). Plant parasites, such as dwarf mistletoe and comandra blister rust, are also common in these forests. Mistletoe may reduce tree growth or even result in tree death, and has been labeled the most important problem in lodgepole pine forests (Knight 1994). The native mountain pine beetle is present at low population levels most of the time (Brown 1975; Baker and Veblen 1990), but periodic outbreaks, such as occurred during the 1970s in YNP, resulting in the death of thousands of trees (Despain 1990). This, in turn, also leads to changes in CWD biomass and distribution, plant species composition and productivity, and fuel availability, as well as broad-scale changes in landscape patterns (Romme et al. 1986). Herbivory, both by insects and ungulates, may reduce plant cover and may result in the mortality of young seedlings and saplings (Houston 1982; Singer et al. 1989).

Abiotic stressors such as wildfire, and human-induced changes to the ecosystem via management impacts can also alter ecological characteristics of lodgepole systems. Wildfire affects many aspects of these ecosystems, including both the volatilization and creation of essential nutrients from the organic materials combusted or consumed by fire (Knight et al. 1991). Wildfire directly kills many trees during severe surface or crown fires, which results in significant additions to the CWD biomass of these forests (Tinker and Knight 2000). Notably, fire regimes seem to be the controlling mechanism for the production of serotinous cones (see section on fire regime), which is the most important predictor of postfire seedling density, and therefore productivity (Tinker et al. 1994; Turner et al. 1997; Turner et al. in review). Also, fire clearly can eliminate plant cover, but also provides new substrate for rapid reestablishment of residual plants (Turner et al. 1997). If fire suppression efforts are successful, this will obviously result in a reduction of tree mortality and CWD accumulation, and may allow for the build-up of high levels of woody fuels.

C. INDICATORS

The vegetation dynamics of lodgepole pine ecosystems are fairly well-understood (Turner et al. 1997) and the composition of the forest plant community composition, as well as the proportions of exotic and na-

tive species, could provide an excellent index of ecosystem structure and function. Similarly, plant species diversity, and the historic range of variability in this measure, will also allow for relatively straightforward assessment of ecosystem stability. The amount and distribution of forest floor litter and coarse woody debris are critical for key forest floor ecosystem processes such as decomposition and mineralization (Tinker and Knight 2000), and are directly linked to the availability and loss of essential nutrients from the soil (Knight 1994). All of these indicators are easily measured, and reflect the potential for the ecosystem to maintain long-term site productivity. Similarly, an excellent measure of potential ecosystem productivity is leaf area index, or LAI, which is the square meters of leaf area per square meter of forest floor). LAI is highly correlated with aboveground net primary productivity (ANPP) as well as evapotranspiration, and is routinely estimated through the use of remotely sensed data. Finally, landscape structure and forest stand age structure are also easily quantified through the use of geographic information systems and software designed to characterize landscape structure (McGarigal and Marks 1995). The historic range of variability in landscape structure has been recently described for portions of the Greater Yellowstone Ecosystem (Tinker et al, in press) and monitoring landscape heterogeneity may provide a much needed broad-scale assessment with which to compliment the finer, stand-level metrics.

1. *Plant community composition*

Resource Monitored: Flora – plant species presence and abundance

Justification: Lodgepole pine communities are relatively uniform systems (Knight 1994). Departures from the natural range of variability in community composition may indicate structural and functional changes in the ecosystem resulting from natural perturbations such as drought, fire, or windstorm, or human-caused disturbances or alterations such as non-prescribed fire or fire management (Pickett 1976). Vegetative reproduction following disturbance is the most common mechanism for plant reestablishment (Anderson and Romme 1991) and departures from this contribution may indicate considerable degradation of the seed bank.

Comment: This indicator is relatively well-understood and may therefore be most useful when attempting to evaluate current ecosystem conditions.

Example of Specific Measurements of this Indicator: Total species present and estimate of percent cover of each in relation to expected species present within the community. Common measures include quadrat and relevé methods.

2. *Plant species diversity*

Resource Monitored: Flora - Biodiversity

Justification: High species diversity may maintain ecosystem stability through redundancy of the ecological roles of different species.

Comment: This is a very easy indicator to measure and has much public appeal, and is likely a priority of many agencies.

Example of Specific Measurements of this Indicator: Common measures include quadrat and relevé methods.

3. *Forest floor litter and coarse woody debris (CWD)*

Resource Monitored: Ecosystem structure - forest floor structure; ecosystem processes

Justification: Forest floor litter and coarse woody debris play important ecological roles in lodgepole pine systems (Tinker and Knight 2000). CWD may provide habitat for many organisms (Harmon et al. 1986), and many decomposers such as bacteria and fungi derive energy and nutrients from decaying forest floor materials (Frankland et al. 1982). CWD and litter are also important inputs to soil organic matter (Edmonds 1991).

Comment: Lodgepole pine systems are often nitrogen- and nutrient-limited. Forest floor litter and CWD provide critical raw organic material for decomposition and mineralization processes.

Example of Specific Measurements of this Indicator: Litter depth and biomass; CWD biomass and percent cover. Common measures include line intercept method for CWD percent cover, planar intercept for CWD biomass, and randomly placed measures of litter depth, with subsamples for dry weight.

4. *Landscape structure and heterogeneity*

Resource Monitored: Landscape structure – patchiness, fragmentation, core habitat, patch edge density

Justification: The spatial pattern of lodgepole pine landscapes influences many important ecosystem functions such as habitat use and foraging patterns (Pearson 1993; Turner et al. 1994), nutrient movement (Peterjohn and Corell 1984), and disturbance dynamics (Turner 1987).

Comment: Disturbance is now considered an integral part of lodgepole pine ecosystems. Various disturbance types such as fire, insect outbreaks, windstorms, and earthquakes may significantly alter landscape structure in these ecosystems. This, in turn, will likely influence future processes such as net primary productivity, animal movement, forage availability, and habitat.

Example of Specific Measurements of this Indicator: Metrics

commonly quantified using landscape description software and GIS, such as FRAGSTATS (McGarigal and Marks 1995) or r.le (Baker and Cai 1992) programs; vegetative cover most common base map used.

5. *Leaf area index (LAI)*

Resource Monitored: Ecosystem structure and function - primary productivity

Justification: Leaf area index is highly correlated with net primary productivity, a critical ecosystem process that describes the accumulation of biomass over some time period. Productivity reflects many current conditions within ecosystems such as climatic trends. Leaf area index is relatively easy to measure with today's remote sensing technology and, given its strong relationship to primary productivity

Comment: Because of its relationship with aboveground net primary productivity, estimates of LAI provide maximum information about the productivity of the ecosystem with a single measure. Leaf area index is also a good surrogate for photosynthetic capacity (greenness)

Example of Specific Measurements of this Indicator: Remotely sensed data such as NDVI (Normalized Difference Vegetation Index) may be used. These data are inexpensive and are published on a regular basis.

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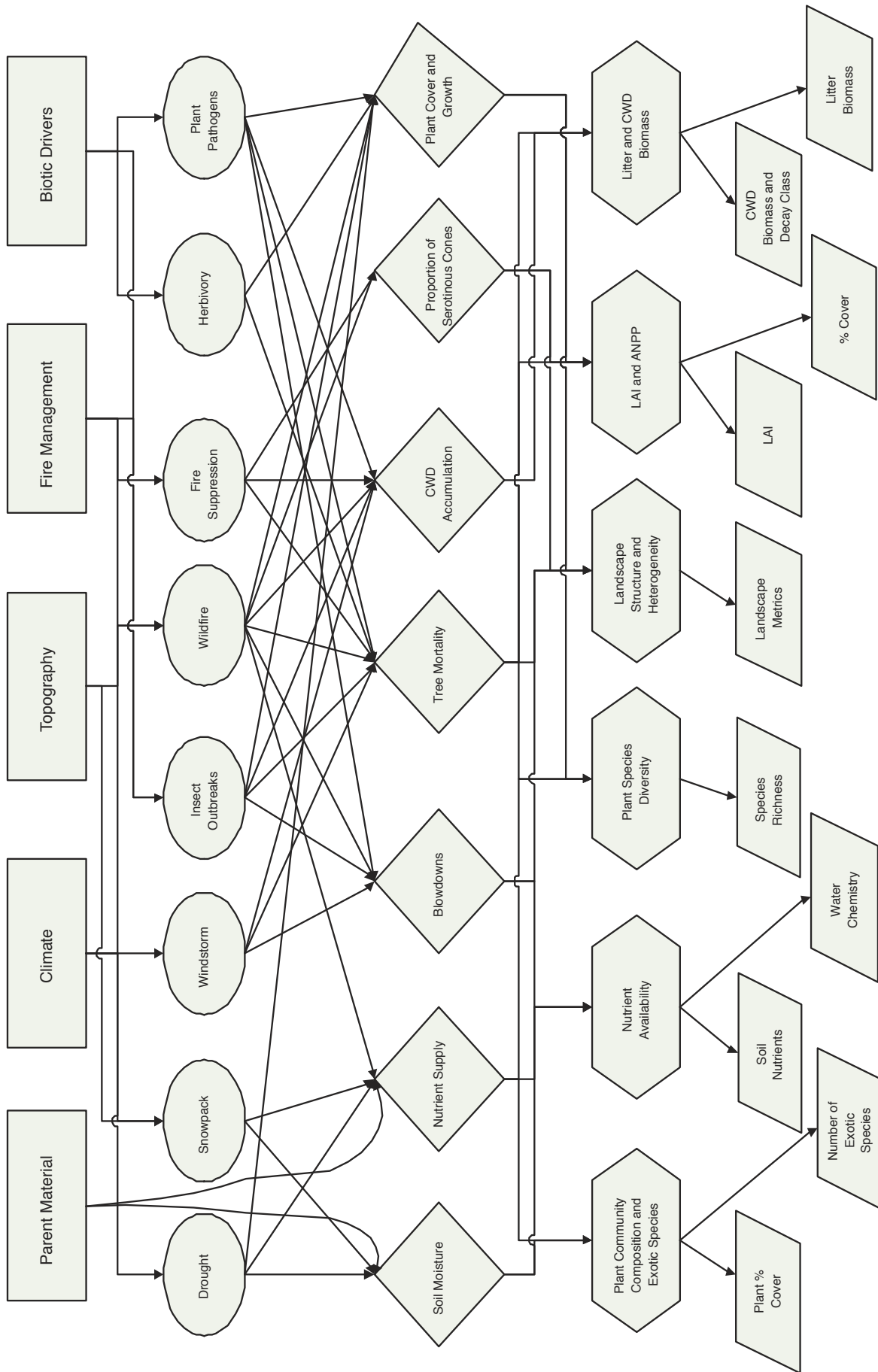


FIGURE 21 Lodgepole model.

MIXED CONIFER ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Dan Tinker)

For the purposes of this document, mixed conifer forests are considered to be forest types that are dominated by species other than lodgepole pine (*Pinus contorta* var. *latifolia*) or aspen (*Populus tremuloides*). This would include primarily Douglas-fir (*Pseudotsuga menziesii*) forests and spruce-fir (*Engelmann spruce* (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests. Notably, all of these forest types may contain some component of the other, and may also contain individuals of limber pine (*Pinus flexilis*) lodgepole pine or aspen; however, in many areas, Douglas-fir forests occur at lower elevations than lodgepole pine forests, and spruce-fir forests are typically found to occur at higher elevations than lodgepole pine (Peet 2000). These montane forests are relatively ubiquitous in the GRYE, and range from 1,800-3,200 m in elevation. In BICA, mixed conifer forests are found primarily on the eastern slopes of East Pryor Mountain, in the western portion of the Bighorn Canyon Recreation Area.

Fire regimes are quite different between Douglas-fir forests and spruce-fir forests, and are addressed separately here. Douglas-fir trees produce very thick bark, enabling individual trees to survive many surface fires (Veblen and Lorenz 1986). Crown fires also occur periodically in Douglas-fir forests, and fire return intervals have been estimated from 20-25 years in northern areas of Yellowstone National Park (Houston 1973) up to 60 years in northwest Montana (Arno and Gruell 1986). Because spruce-fir forests are often the climax condition of stands that began as lodgepole pine, fire return intervals for spruce-fir forests are more similar to lodgepole pine, and may be even longer than 100-300 years at higher elevations where spruce and fir dominate the forest composition (Knight 1994).

Conceptual Model Development

Many of the drivers, stressors, and ecological responses in mixed conifer forests are similar to those in lodgepole pine forests, because of the coexistence of many of the species.

A. DRIVERS

Yellowstone's climate is characterized by long, cold winters, and cool, dry summers. Most of the precipitation falls in the form of snow. Winter snowpack melts rapidly in May and June, providing much of the water available for growth in lodgepole pine forests. In addition, periods of seasonal drought, such as were experienced during the summer of 1988,

may exert considerable influence on soil and fuel moisture, as well as fire regimes. Precipitation in BICA is quite variable, with the northern end of the Area receiving over 19 inches of precipitation per year, while the drier southern end receives, on average, only slightly more than seven inches per year (Knight et al. 1987). The climate is relatively more cool and moist at higher elevations, where mixed conifer forests occur. Because of its effects on precipitation, growing season, and tree mortality in both the GRYE and the BICA, elevation is also an important factor in determining the occurrence of wildfires.

Given the importance of fire in mixed conifer ecosystems, the management of prescribed fires and wildfires may greatly influence many natural ecosystem processes. For example, large, intense crown fires may help control episodic outbreaks of Mountain Pine Beetle by burning entire stands where significant outbreaks have occurred. Many of the indirect effects of fire suppression will be discussed below in subsequent sections.

Biotic drivers such as insects, plant pathogens and disease, and herbivory by both ungulates and insects may directly and indirectly affect many ecological processes in mixed conifer ecosystems. As more fully described below in the section on Stressors, these biotic drivers can lead to extensive episodes of tree mortality, which can affect critical processes such as coarse woody debris accumulation, changes in plant species composition, and net primary productivity.

The parent materials for soils across much of the Greater Yellowstone Area are largely volcanic in origin. Two different parent materials, derived from underlying bedrock, determine the soil characteristics in Yellowstone. Rhyolitic soils are found most often on drier sites, and are typically very nutrient limited. Andesitic soils are relatively more fertile, and often occur at higher elevations (Despain 1990). Differences in these parent materials is responsible for soil texture, and therefore, water holding capacity, as well as nutrient supply and availability. Rhyolitic soils are more sandy while andesitic soils contain much more clay (Despain 1990). Calcium is ten times more abundant in soils derived from andesite (Despain 1990).

In the BICA, mixed conifer forests on East Pryor Mountain occur primarily on shallow soils, where fractured bedrock reservoirs may serve as water sources during an otherwise dry growing season (Knight et al. 1987).

B. STRESSORS AND ECOLOGICAL RESPONSES

Drought, snowpack, and windstorms, all driven by weather and climate, affect many important ecosystem processes. Drought will affect soil moisture during the growing season, thereby affecting plant development and primary productivity, as well as forage abundance. Reduced

soil moisture may also reduce nutrient supplies by a reduction in microbial activities such as decomposition and mineralization (Litton et al. 2003). Snowpack is the single largest contributor to soil moisture, and therefore water and nutrient availability during the growing season. Windstorms may cause large blowdowns, such as the 6,000-ha event that occurred in the Teton Wilderness in 1987. These events directly affect forest and landscape structure through widespread tree mortality and creation and accumulation of large quantities of coarse woody debris (CWD) and standing dead trees. Large areas of uprooted trees may also allow for the invasion of new plant species, and may also affect the growth rates of the new and existing species.

Abiotic stressors such as wildfire and human-induced changes to the ecosystem via management impacts can also alter ecological characteristics of mixed conifer forest systems. Wildfire affects many aspects of these ecosystems, including both the volatilization and creation of essential nutrients from the organic materials combusted or consumed by fire (Knight et al. 1991). Wildfire directly kills many trees during severe surface or crown fires, which results in significant additions to the CWD biomass of these forests (Tinker and Knight 2000). Also, fire clearly can eliminate existing plant cover, but also provides new substrate for rapid reestablishment of residual plants, as well as the establishment of seral species such as aspen and lodgepole pine (Turner et al. 1997). If fire suppression efforts are successful, this will obviously result in a reduction of tree mortality and CWD accumulation, and may allow for the build-up of high levels of woody fuels.

Biotic stressors, primarily insects and plant pathogens, have important effects in mixed conifer forest ecosystems (Romme et al. 1986; Veblen et al. 1991). Openings may be created in the forest canopy through tree mortality, which can result in increases in understory vegetation production (Knight 1994). Plant parasites, such as dwarf mistletoe and comandra blister rust, are also common in many of these forests. The native mountain pine beetle is present at low population levels most of the time (Brown 1975; Baker and Veblen 1990), but periodic outbreaks, such as occurred during the 1970s in YNP, resulting in the death of thousands of trees (Despain 1990). This, in turn, also leads to changes in CWD biomass and distribution, plant species composition and productivity, and fuel availability, as well as broad-scale changes in landscape patterns (Romme et al. 1986). Herbivory, both by insects and ungulates, may reduce plant cover and may result in the mortality of young seedlings and saplings (Houston 1982; Singer et al. 1989).

Nutrient availability can be important for determining the proportions of spruce and fir in many mixed conifer forests. On sites where

nutrients are limiting, as is common on many of the drier sites at lower elevations in the GRYE, lodgepole pine may be the only coniferous tree that is able to survive; on more nutrient rich sites, spruce and fir will generally be more abundant in mature forests (Peet 2000).

C. INDICATORS

Departures from the natural range of variability in plant community composition in mixed conifer ecosystems may indicate structural and functional changes in the ecosystem resulting from natural perturbations such as drought, fire, or windstorm, or human-caused disturbances or alterations such as non-prescribed fire or fire management (Pickett 1976). Vegetative reproduction following disturbance is the most common mechanism for herbaceous and shrubby plant reestablishment, as well as invasion by exotic species (Anderson and Romme 1991) and departures from this contribution may indicate considerable degradation of the seed bank. High population levels of spruce beetle or budworms within a stand may indicate that a stand has relatively low growth rates, which is often indicative of low vigor. Spruce beetles typically attack older stands that contain a high proportion of Engelmann spruce in the canopy. If stand-replacing fires are reduced through fire suppression, these older, senescent stands may facilitate increases in beetle population numbers. The density of standing dead trees, or snags, is an indicator of the amount of chronic, baseline mortality occurring within a stand, or across the landscape, and can help predict areas where beetle infestations may increase. Forest floor litter and coarse woody debris play important ecological roles in mixed conifer systems (Tinker and Knight 2000). CWD may provide habitat for many organisms (Harmon et al. 1986), and many decomposers such as bacteria and fungi derive energy and nutrients from decaying forest floor materials (Frankland et al. 1982). CWD and litter are also important inputs to soil organic matter (Edmonds 1991). Mixed conifer systems in the Greater Yellowstone Ecosystem and in BICA are often nitrogen- and nutrient-limited. Forest floor litter and CWD provide critical raw organic material for decomposition and mineralization processes. The heterogeneity of mixed conifer landscapes influences many important ecosystem functions such as habitat use and foraging patterns (Pearson 1993; Turner et al. 1994), nutrient movement (Peterjohn and Corell 1984), and disturbance dynamics (Turner 1987). Disturbance is now considered an integral part of mixed conifer ecosystems. Various disturbance types such as fire, insect outbreaks, windstorms, and earthquakes may significantly alter landscape structure in these ecosystems. This, in turn, will likely influence future processes such

as net primary productivity, animal movement, forage availability, and habitat. Along with landscape metrics, an understanding of the age structures of the mixed conifer forests provides insights into the long-term effects of fire suppression, grazing, and other human influences within the ecosystem.

1. *Plant community composition and exotic species*

Resource Monitored: Flora – plant species presence and abundance

Justification: Departures from the natural range of variability in community composition in mixed conifer ecosystems may indicate structural and functional changes in the ecosystem resulting from natural perturbations such as drought, fire, or windstorm, or human-caused disturbances or alterations such as non-prescribed fire or fire management (Pickett 1976). Vegetative reproduction following disturbance is the most common mechanism for herbaceous and shrubby plant reestablishment (Anderson and Romme 1991) and departures from this contribution may indicate considerable degradation of the seed bank.

Comment: This indicator is relatively well-understood and may therefore be most useful when attempting to evaluate current ecosystem conditions.

Example of Specific Measurements of this Indicator: Total species present and estimate of percent cover of each in relation to expected species present within the community. Common measures include quadrat and relevé methods.

2. *Beetle and budworm population levels*

Resource Monitored: Insect fauna

Justification: High population levels of spruce beetle within a stand may indicate that a stand has relatively low growth rates, which is often indicative of low vigor.

Comment: Spruce beetles typically attack older stands that contain a high proportion of Engelmann spruce in the canopy. If stand-replacing fires are reduced through fire suppression, these older, senescent stands may facilitate increases in beetle population numbers.

Example of Specific Measurements of this Indicator: Surveys of actual numbers through the use of insect traps, or surveys of beetle evidence within a stand, which may serve as a proxy of beetle populations.

3. *Understory Plant species diversity*

Resource Monitored: Flora – Biodiversity

Justification: High species diversity may maintain ecosystem stability through redundancy of the ecological roles of different species.

Comment: This is a very easy indicator to measure and has much public appeal, and is likely a priority of many agencies.

Example of Specific Measurements of this Indicator: Common measures include quadrat and relevé methods.

4. *Snag Density*

Resource Monitored: Ecosystem Structure

Justification: This measure is an indicator of the amount of chronic, baseline mortality occurring within a stand, or across the landscape, and can help predict areas where beetle infestations may increase.

Example of Specific Measurements of this Indicator: Common measures include belt transect, quadrat, and relevé methods.

5. *Forest floor litter and coarse woody debris (CWD)*

Resource Monitored: Ecosystem structure - forest floor structure; ecosystem processes

Justification: Forest floor litter and coarse woody debris play important ecological roles in mixed conifer systems (Tinker and Knight 2000). CWD may provide habitat for many organisms (Harmon et al. 1986), and many decomposers such as bacteria and fungi derive energy and nutrients from decaying forest floor materials (Frankland et al. 1982). CWD and litter are also important inputs to soil organic matter (Edmonds 1991).

Comment: Mixed conifer systems in the Greater Yellowstone Ecosystem are often nitrogen- and nutrient-limited. Forest floor litter and CWD provide critical raw organic material for decomposition and mineralization processes.

Example of Specific Measurements of this Indicator: Litter depth and biomass; CWD biomass and percent cover. Common measures include line intercept method for CWD percent cover, planar intercept for CWD biomass, and randomly placed measures of litter depth, with subsamples for dry weight.

6. *Landscape structure and heterogeneity*

Resource Monitored: Landscape structure – patchiness, fragmentation, core habitat, patch edge density

Justification: The spatial pattern of mixed conifer landscapes influences many important ecosystem functions such as habitat use and foraging patterns (Pearson 1993; Turner et al. 1994), nutrient movement (Peterjohn and Corell 1984), and disturbance dynamics (Turner 1987).

Comment: Disturbance is now considered an integral part of mixed conifer ecosystems. Various disturbance types such as fire, insect outbreaks, windstorms, and earthquakes may significantly alter landscape structure in these ecosystems. This, in turn, will likely influence future processes such as net primary productivity, animal movement, forage availability, and habitat.

Example of Specific Measurements of this Indicator: Metrics commonly quantified using landscape description software and GIS, such as FRAGSTATS (McGarigal and Marks 1995) or r.le (Baker and Cai 1992) programs; vegetative cover most common base map used.

7. *Age structure of forest*

Resource Monitored: Ecosystem structure

Justification: Along with landscape metrics, an understanding of the age structures of the mixed conifer forests provides insights into the long-term effects of fire suppression, grazing, and other human influences within the ecosystem.

Example of Specific Measurements of this Indicator: Age determination using tree increment borers to estimate the age of dominant trees within a stand.

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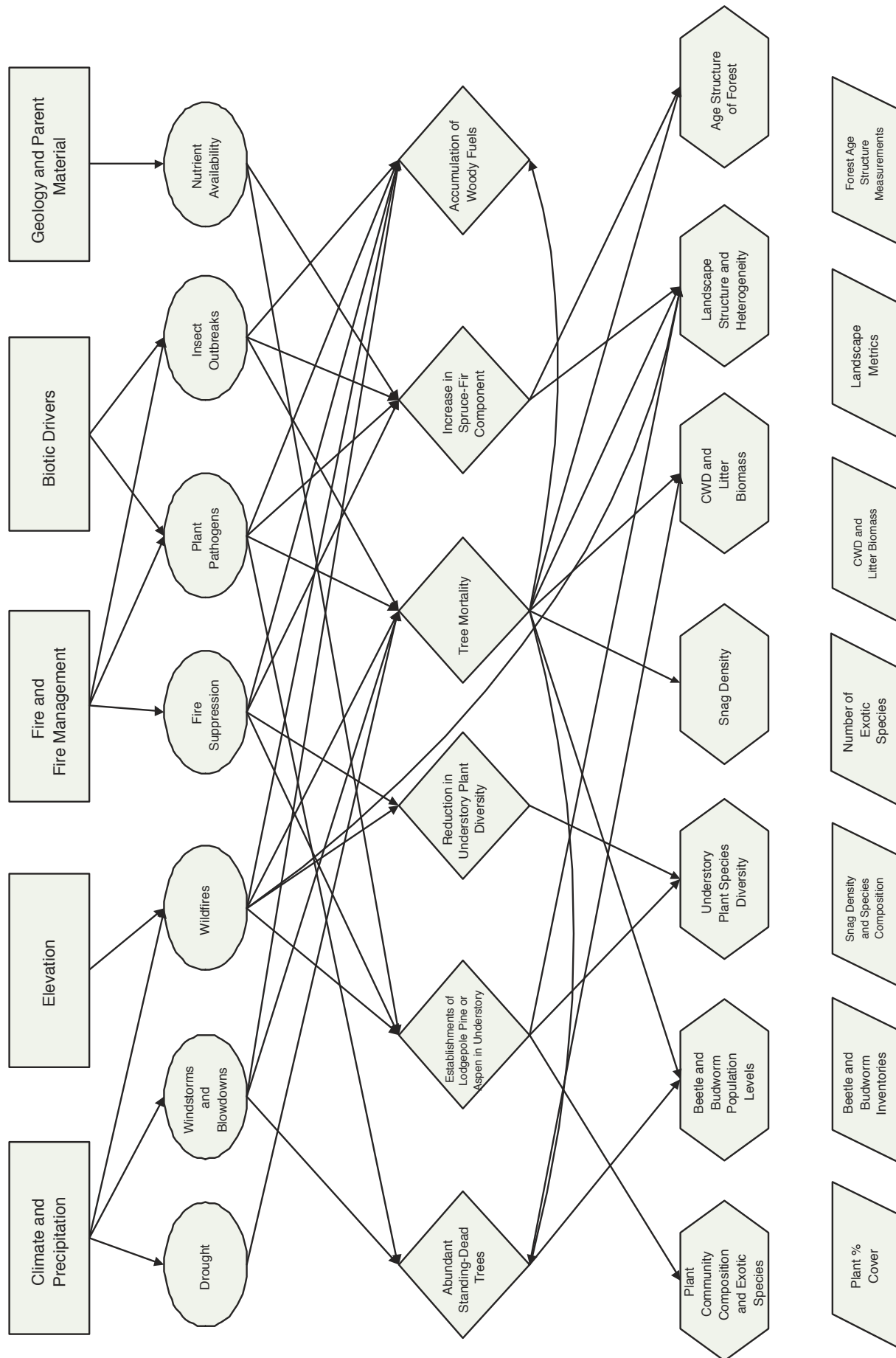


FIGURE 22 Mixed conifer model.

PONDEROSA PINE ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Dan Tinker)

Ponderosa pine woodlands occur only along the fringes of the eastern Rocky Mountains (Peet 2000) and, specifically within the GRYE, only in the Bighorn Canyon Recreation Area. These relatively open community types do not occur in the mountains of western Wyoming in GTNP or YNP, but exist on lower elevation sites where summer precipitation is higher and the growing season is longer (Knight 1994). The importance of ample summer precipitation for the establishment and maintenance of Ponderosa pine woodlands is illustrated by its absence in the southern portion of the BICA, where summer precipitation is ~30% of that of the more mesic northern portions of the Area, where it is currently found. Many Ponderosa pine woodlands in the Western U.S. have undergone dramatic transformation as a result of successful fire suppression and the introduction of grazing by domestic cattle (Peet 2000). This often results in a change to more of a true forest condition, rather than a woodland, or savannah physiognomy. Mechanisms for this shift are thought to be either a reduction in the density of grasses (Savage and Swetnam 1990) or increased establishment of seedlings following fires (Marr 1961).

While many Ponderosa pine communities of the southwestern U.S. have experienced frequent, low-intensity fires that often limit regeneration, pine woodlands in more northerly latitudes such as in BICA may have evolved with longer fire-return intervals, on the order of 25-40 years (Rowdabaugh 1978; Laven et al 1980).

Conceptual Model Development

A. DRIVERS

The climate of the BICA area is often described as temperate and semi-arid. As noted earlier, the occurrence of critical summer precipitation limits the distribution of ponderosa pine to the more northern areas of the Area, where annual precipitation averages 49 cm; approximately two-thirds of this falls during spring and early summer, and the rest as snow (Knight et al. 1987).

Given the importance of fire in ponderosa pine ecosystems, the management of prescribed fires and wildfires can dramatically influence tree regeneration, as well as many other natural ecosystem processes. Some of the indirect effects of fire suppression will be discussed below in subsequent sections.

The biotic drivers may, in the case of BICA, be among the most

important in the development, maintenance, or loss of ponderosa pine woodlands. Biotic drivers such as insects, plant pathogens and disease, and cattle grazing may directly or indirectly affect many ecological processes in ponderosa pine ecosystems. As more fully described below in the section on Stressors, these biotic drivers can lead to extensive episodes of tree mortality or creation of dense doghair stands, both of which can affect critical processes such as coarse woody debris accumulation and stand density.

B. STRESSORS AND ECOLOGICAL RESPONSES

As previously mentioned, summer precipitation, and its effect on soil moisture, is very important for the establishment and growth of ponderosa pine (Knight 1994). Successive drought years may result in the mortality of mature trees and particularly seedlings, even though young trees are somewhat drought resistant (Wellner 1970). Many human activities, including fire suppression, introduction of exotic plant species, and grazing by domestic cattle currently affect many aspects of ponderosa pine woodlands in BICA. For example, because historic frequent fires normally reduce the number of new seedlings that establish, elimination of these fires during the last century allows for the development of dense, doghair stands of ponderosa pine, which creates additional woody fuels for more severe crown fires (Knight 1994). Livestock or wild horse grazing may also improve conditions for seedling establishment through the removal of plant competition. Further, as mature trees die or are killed by pine beetles or other plant pathogens, invasion by exotic plant species may inhibit the germination and establishment of replacement trees, causing a shift in plant community composition and tree density. The pine beetle outbreaks may occur during years of inadequate precipitation, when mature trees are unable to produce sufficient resins to defend against beetle infestation (Knight 1994).

C. INDICATORS

Ponderosa pine is very sensitive to soil moisture availability. As an example, it is conspicuously absent from the southern end of the Bighorn Canyon, where summer rainfall is quite low, but is relatively abundant at similar elevations in the northern end of the canyon, where summer precipitation is much higher (Knight 1994). Ponderosa pine is also sensitive to cold pockets, such as collect in some drainages. However, many drainages in Bighorn Canyon contain ponderosa pine, where soil moisture availability is higher than surrounding uplands. Many ponderosa pine forests have dramatically increased in stand density as a result of fire suppression (Covington and Moore

1994). This is thought to be a significant departure from more park-like stand structure characteristic of pre-European settlement. If fire suppression continues, stand densities may continue to increase, resulting in an increased susceptibility to intense, stand-replacing fires. Exotic species composition and abundance is a critical issue in these ecosystems. Many ponderosa pines, especially in riparian areas and in drainages, are being eliminated in Bighorn Canyon by the invasion of exotic species such as tamarisk and Russian olive (Laura Gianakos, personal communication; personal observation, 2003). The proportion of standing dead trees serves as an indicator of both the susceptibility to intense, stand-replacing fires, which is not the typical fire regime for most ponderosa pine stands, as well as a response variable to mountain pine beetle infestation. The suppression of fire may allow mortality from beetle outbreaks to increase, as well as increase the risk of severe fires.

1. Soil Moisture

Resource Monitored: Ecosystem structure and function.

Justification: Ponderosa pine is very sensitive to soil moisture availability. As an example, it is conspicuously absent from the southern end of the Bighorn Canyon, where summer rainfall is quite low, but is relatively abundant at similar elevations in the northern end of the canyon, where summer precipitation is much higher (Knight 1994).

Comment: Ponderosa pine is also sensitive to cold pockets, such as collect in some drainages. However, many drainages in Bighorn Canyon contain ponderosa pine, where soil moisture availability is higher than surrounding uplands.

Example of Specific Measurements of this Indicator: Seasonal soil moisture monitoring.

2. Stand Density

Resource Monitored: Ecosystem structure and function.

Justification: Many ponderosa pine forests have dramatically increased in density as a result of fire suppression (Covington and Moore 1994). This is thought to be a significant departure from more park-like stand structure characteristic of pre-European settlement.

Comment: If fire suppression continues, stand densities may continue to increase, resulting in an increased susceptibility to intense, stand-replacing fires.

Example of Specific Measurements of this Indicator: Belt transect measures of stand density, or other quadrat or plot measurements.

3. Exotic species composition and abundance

Resource Monitored: Flora – species composition and abundance.

Justification: Many ponderosa pines, especially in riparian areas and in drainages, are being eliminated in Bighorn Canyon by the invasion of exotic species such as tamarisk and Russian olive (personal observation, 2003).

Example of Specific Measurements of this Indicator: Plant species surveys and percent cover estimates using quadrats.

4. Proportion of standing dead trees

Resource Monitored: Ecosystem structure and function.

Justification: This serves as an indicator of both the susceptibility to intense, stand-replacing fires, which is not the typical fire regime for most ponderosa pine stands, as well as a response variable to mountain pine beetle infestation. The suppression of fire may allow mortality from beetle outbreaks to increase, as well as increase the risk of severe fires.

Example of Specific Measurements of this Indicator: Belt transects or other quadrat methods for quantifying density of live and dead trees.

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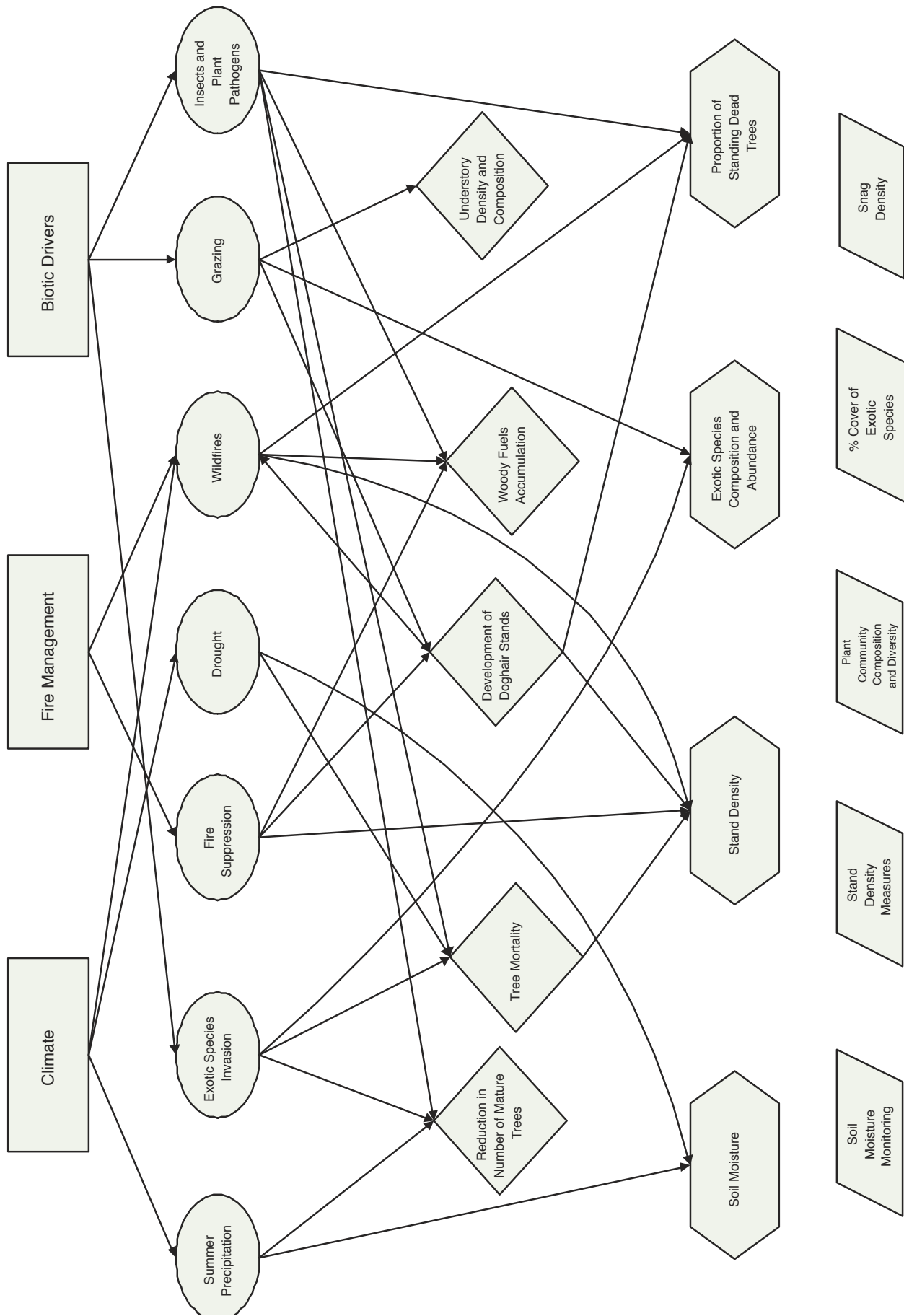


FIGURE 23 Ponderosa pine model.

WHITEBARK PINE ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Dan Tinker)

Whitebark pine (*Pinus albicaulis* Elgelm.) is a high-elevation tree of the Northern Rocky Mountains, forming open woodlands on relatively xeric slopes (Arno and Hammerly 1977). Whitebark pine is a member of the white pine group (*Pinus* subgenus *Haploxylon*), which also contains limber pine, and does not typically form continuous, closed stands characteristic of other montane forest species of the Northern Rockies (Peet 2000). Regeneration of whitebark pine occurs almost solely via seed dispersal by the Clark's Nutcracker (Hutchins and Lanner 1982). The birds will cache multiple seeds together in open areas, often in recently burned forests, and unclaimed caches will germinate and grow in the absence of shade and competition (Tomback et al. 1990). This form of avian dispersal of seeds often results in the germination and establishment of multi-stemmed trees (Furnier et al. 1987). The relatively large seeds serve as an important food source for at least 110 species of animals, including grizzly bears and red squirrels (Tomback 1989).

Following intense fires in lodgepole or spruce-fir stands, whitebark pine may act as a seral species, but is more typically found as a climax species, since seedling establishment often ceases with the establishment of more shade-tolerant species such as Engelmann spruce and subalpine fir (Schuster et al. 1995). It is relatively abundant across the subalpine plateaus of YNP, but only comprises about 2% of the vegetation in GTNP (Greater Yellowstone Coordinating Committee 1987).

Because of higher elevations, lower fuel accumulations, and much bare ground below the canopy, whitebark pine ecosystems burn less frequently than other Rocky Mountain conifers (Peet 2000). Depending on the location and site conditions, presettlement fire return intervals ranged from 30-300 years (Morgan et al. 1995).

Conceptual Model Development

A. DRIVERS

Moisture and temperature are the two factors that largely control the occurrence of different habitat types in the region (Despain 1990). The climate of the Greater Yellowstone Area is characterized by long, cold winters, and cool, dry summers. Most of the precipitation falls in the form of snow. Winter Snowpack melts rapidly in May and June, providing much of the water available for growth in high elevation whitebark pine forests. In addition, periods of seasonal drought, such as

were experienced during the summer of 1988, may exert considerable influence on soil and fuel moisture, as well as fire regimes.

Biotic drivers such as plant competition, insects, and plant pathogens and disease, particularly white pine blister rust may directly and indirectly affect many ecological processes in whitebark pine ecosystems. As more fully described below in the section on Stressors, these biotic drivers can lead to extensive episodes of tree mortality, which can affect critical processes such as coarse woody debris accumulation and net primary productivity.

Given the importance of fire in lodgepole pine ecosystems, the management of prescribed fires and wildfires may greatly influence many natural ecosystem processes. For example, large, intense crown fires may help control episodic outbreaks of Mountain Pine Beetle by burning entire stands where significant outbreaks have occurred. Many of the indirect effects of fire suppression will be discussed below in subsequent sections.

As mentioned earlier, the regeneration of whitebark pine occurs almost solely via seed dispersal by the Clark's Nutcracker (Hutchins and Lanner 1982). The birds will cache multiple seeds together in open areas, often in recently burned forests, and unclaimed caches will germinate and grow in the absence of shade and competition (Tomback et al. 1990).

B. STRESSORS AND ECOLOGICAL RESPONSES

Wildfire and management-related changes to the ecosystem such as fire suppression can also affect whitebark pine systems. Wildfire affects many aspects of these ecosystems, including both the volatilization and creation of essential nutrients from the organic materials combusted or consumed by fire (Knight et al. 1991). Wildfire directly kills many trees during severe surface or crown fires, which results in significant additions to the CWD biomass of these forests (Tinker and Knight 2000). Also, fire clearly can eliminate plant cover, but also provides new substrate for rapid reestablishment of residual plants (Turner et al. 1997). If fire suppression efforts are successful, this will obviously result in a reduction of tree mortality and CWD accumulation, and may allow for the build-up of high levels of woody fuels (Keane 2001). In addition, removing fire from these systems may result in increases in late successional forest and replacement of whitebark pine by more shade-tolerant species such as subalpine fir and Engelmann spruce (Arno and Hoff 1990, Keane et al. 1994).

Drought and wind, snow, and ice abrasion, all driven by weather and climate, affect many important ecosystem processes. Drought

will affect soil moisture during the growing season, thereby affecting plant development and primary productivity, as well as forage abundance. Reduced soil moisture may also reduce nutrient supplies by a reduction in microbial activities such as decomposition and mineralization (Litton et al. 2003). Snowpack is the single largest contributor to soil moisture, and therefore water and nutrient availability during the growing season. Because many whitebark pine communities occur at higher elevations, where growing conditions are often quite harsh, abrasion from wind, snow and ice can affect tree growth and vigor, or in extreme conditions, may result in the mortality of individual trees.

Biotic stressors have also accelerated the successional process in many whitebark pine forests, largely through epidemic outbreaks of the exotic white pine blister rust and native mountain pine beetles (Keane 2001). Other plant parasites, such as dwarf mistletoe is also common in these forests. The native mountain pine beetle is present at low population levels most of the time (Brown 1975; Baker and Veblen 1990), but periodic outbreaks, such as occurred during the 1970s in YNP, may result in the death of numerous trees (Despain 1990). This, in turn, can also lead to changes in runoff and erosion in high-elevation stands, along with an increase in establishment of other tree species such as Engelmann spruce and subalpine fir (Keane et al. 1994; Arno 1986).

C. ECOLOGICAL INDICATORS

Clark's Nutcracker abundance is critical for the regeneration of whitebark pine, which occurs almost solely via seed dispersal by the Clark's Nutcracker (Hutchins and Lanner 1982). The birds will cache multiple seeds together in open areas, often in recently burned forests, and unclaimed caches will germinate and grow in the absence of shade and competition (Tomback et al. 1990). Following intense fires in lodgepole or spruce-fir stands, whitebark pine may act as a seral species, establishing in the newly burned forest floor, where cached seeds distributed by Clark's Nutcrackers can germinate and establish in the absence of competition (Tomback et al. 1993). The burned forest seedbed availability is therefore very important for the germination and establishment of new whitebark pine seedlings. Whitebark pine is considered a "keystone" species for upper elevation areas in the Greater Yellowstone Ecosystem (Tomback et al. 2001), and the monitoring of the density of high-elevation whitebark pine trees is likely a good indicator of population trends. Further, because of fire suppression and recent outbreaks of Mountain Pine Beetle and

White Pine Blister Rust, whitebark pine is thought to be declining throughout the GYE (Tomback et al. 2001). Fire exclusion may have reduced fire frequency in many high elevation forests of the GYE, and consequently, the abundance of replacement tree species such as subalpine fir and Engelmann spruce may be another excellent indicator of population trends in whitebark pine (Arno 1986; Keane et al. 1994). The production of whitebark pine cones, and therefore seeds, is critical as forage for both Clark's Nutcrackers and Grizzly bears, as well as for the reestablishment of whitebark pine at both high and low elevations (Tomback et al. 2001). In addition, reduction of cone production can be an early indicator of infection by White Pine Blister Rust, which often kills cone-bearing branches prior to killing the entire tree (Tomback et al. 2001). Cone production in whitebark pine does not occur until trees reach the age of 20-30 years (Krugman and Jenkinson 1974). A significant reduction in cone – and therefore seed – production could represent a major shift in age classes at higher elevations. White pine blister rust is an exotic plant pathogen that only infects five-needle pines such as whitebark or limber pine (Tomback et al. 2001). In some areas of the Rocky Mountains, whitebark pine mortality has reached 90 percent (Keane et al. 1994). Monitoring of blister rust abundance and spread may help identify newly-developed strains of the organism, such as drought-tolerant strains that could accelerate the spread of the rust (Tomback et al. 2001). Finally, Whitebark pine in the Greater Yellowstone Ecosystem is a major food source for grizzly bears, which primarily forage on pine squirrel middens (Mattson et al. 1991) during the fall of the year. During years of low cone and seed production, grizzly bears will forage at lower elevations, searching for alternative sources of food. This low elevation foraging by grizzly bears in autumn can serve as a surrogate for estimates of annual cone and seed production. Grizzly bear foraging at lower elevations has historically resulted in increases in management actions, i.e., trapping and relocating, as well as increases in bear mortality (Mattson et al. 1992).

1. *Clark's Nutcracker Abundance*

Resource Monitored: Fauna – Seed disperser

Justification: Regeneration of whitebark pine occurs almost solely via seed dispersal by the Clark's Nutcracker (Hutchins and Lanner 1982). The birds will cache multiple seeds together in open areas, often in recently burned forests, and unclaimed caches will germinate and grow in the absence of shade and competition (Tomback et al. 1990).

Comment: This indicator is relatively well-understood and may therefore be most useful when attempting to evaluate future establishment of whitebark pine.

Example of Specific Measurements of this Indicator: Census measures of Clark's Nutcrackers could include simple counts or nesting successes.

2. *Burned forest seedbed availability*

Resource Monitored: Ecosystem structure and function.

Justification: Following intense fires in lodgepole or spruce-fir stands, whitebark pine may act as a seral species, establishing in the newly burned forest floor, where cached seeds distributed by Clark's Nutcrackers can germinate and establish in the absence of competition (Tomback et al. 1993).

Comment: Fire suppression may reduce the amount of available seedbed for whitebark pine establishment, especially at lower elevations, where it acts as a seral species.

Example of Specific Measurements of this Indicator: Landscape analysis using Geographic Information Systems to annually map the locations and extent of fires within the ecosystem.

3. *Low elevation foraging by grizzly bears in autumn*

Resource Monitored: Fauna – forage and behavior.

Justification: Whitebark pine in the Greater Yellowstone Ecosystem is a major food source for grizzly bears, which primarily forage on pine squirrel middens (Mattson et al. 1991) during the fall of the year. During years of low cone and seed production, grizzly bears will forage at lower elevations, searching for alternative sources of food. This presence at lower elevations can serve as a surrogate for estimates of annual cone and seed production.

Comment: Grizzly bear foraging at lower elevations has historically resulted in increases in management actions, i.e., trapping and relocating, as well as increases in bear mortality (Mattson et al. 1992).

Example of Specific Measurements of this Indicator: Monitoring grizzly bear movements and foraging habits during late summer and early fall using radio-collared bears and GIS.

4. *Density of high-elevation whitebark pine trees*

Resource Monitored: Flora – species abundance and density.

Justification: Whitebark pine is considered a "keystone" species for upper elevation areas in the Greater Yellowstone Ecosystem (Tomback et al. 2001).

Comment: Because of fire suppression and recent outbreaks of Mountain Pine Beetle and White Pine Blister Rust, whitebark pine is thought to be declining throughout the GYE (Tomback et al. 2001).

Example of Specific Measurements of this Indicator: Repeated measures of whitebark pine stand densities at high elevations using belt transects or remotely sensed data.

5. *Abundance of replacement tree species*

Resource Monitored: Ecosystem structure and function

Justification: Fire exclusion has reduced fire frequency in many high elevation forests of the GYE, and consequently, it is being replaced by shade-tolerant species such as subalpine fir and Engelmann spruce (Arno 1986; Keane et al. 1994).

Example of Specific Measurements of this Indicator: Repeated measures of high elevation community composition using belt transect surveys or remotely sensed data.

6. *Whitebark pine cone production*

Resource Monitored: Flora – regeneration and food source.

Justification: The production of whitebark pine cones, and therefore seeds, is critical as forage for both Clark's Nutcrackers and Grizzly bears, as well as for the reestablishment of whitebark pine at both high and low elevations (Tomback et al. 2001). In addition, reduction of cone production can be an early indicator of infection by White Pine Blister Rust, which often kills cone-bearing branches prior to killing the entire tree (Tomback et al. 2001).

Comment: Cone production in whitebark pine does not occur until trees reach the age of 20-30 years (Krugman and Jenkinson 1974). A significant reduction in cone – and therefore seed – production could represent a major shift in age classes at higher elevations.

Example of Specific Measurements of this Indicator: Repeated measures of stand-level cone production.

7. *Blister Rust abundance and spread*

Resource Monitored: Ecosystem structure and function – plant pathogens.

Justification: White pine blister rust is an exotic plant pathogen that only infects five-needle pines such as whitebark or limber pine (Tomback et al. 2001). In some areas of the Rocky Mountains, whitebark pine mortality has reached 90 percent (Keane et al. 1994).

Comment: Monitoring of blister rust abundance and spread may help identify newly-developed strains of the organism, such as drought-tolerant strains that could accelerate the spread of the rust (Tomback et al. 2001).

Example of Specific Measurements of this Indicator: Repeated collections and analysis of samples of infected branches or trees.

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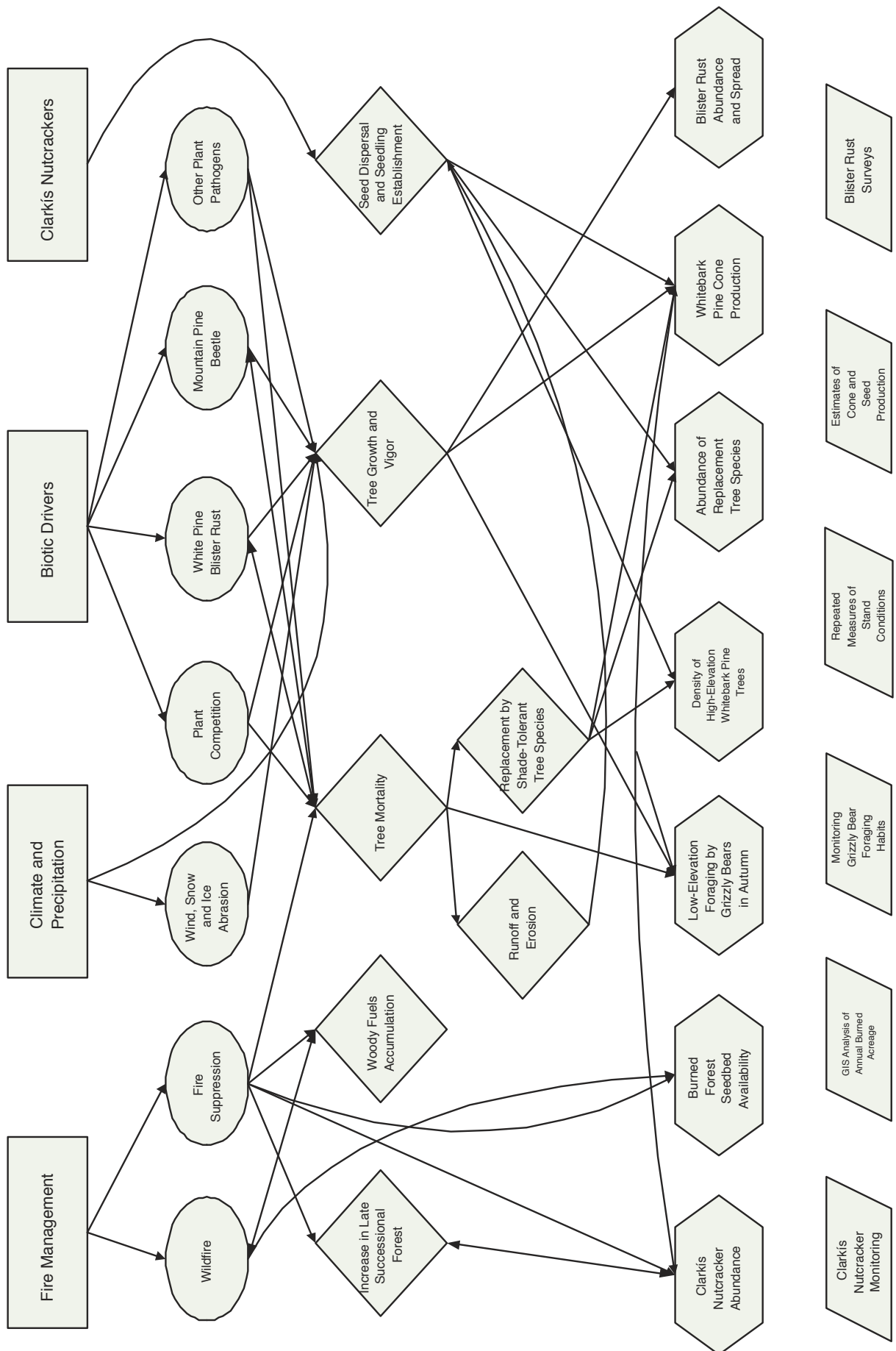


FIGURE 24 Whitebark pine model.

RIPARIAN/RIVERINE ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: *Duncan Patten*)

Introduction

Riverine systems often include terrestrial habitat: riparian ecosystems, stream-edge wetlands and nearly-barren sediment deposits; and aquatic habitats. This discussion of riverine systems is limited to the terrestrial ecosystems. Riparian and edge-wetlands are grouped as riparian ecosystems. Riparian ecosystems, the transition from stream to upland, occupy a very small part of the landscape, often less than 1 %, and yet play an important role in stream dynamics, wildlife ecology, and biodiversity. (Naiman et al., 1993; Naiman and Decamps, 1997; Patten, 1998). In most cases riparian ecosystems occur on alluvial sediment deposits where the hydrological connection between river and alluvial groundwater supplement water available from precipitation (Gregory et al., 1991). Riparian ecosystems offer many ecological services and functions. These services and functions are closely related to the structure, composition and abundance of the riparian vegetation and its location within the landscape. Riparian ecosystems not only influence hydrologic and geomorphic processes, but are driven by these processes as well. This synergistic relationship between riparian vegetation and hydrogeomorphic phenomena complicates the understanding of riparian response to human activities. One important function of riparian systems is that of habitat for a wide variety of organisms. In semi-arid regions over 75% of animals species use riparian ecosystems for all or part of their life cycle (Brinson et al. 1981; Kondolf et al. 1996). Because of close affinity with various characteristics of riparian ecosystems, avian community composition often is used as a surrogate for condition of riparian systems (Anderson et al. 1983; Hunter et al. 1987).

The occurrence of most riparian communities in the Greater Yellowstone Network (GRYN) parks results from recruitment and survival of obligate riparian plant species in response to seasonal hydrological events, variation in groundwater depth, and availability of favorable fluvial geomorphic surfaces. For example, most cottonwood species recruit along streams on bare moist surfaces during the declining limb of spring high flows (Friedman et al., 1995; Scott et al., 1997; Stromberg et al., 1997). Willow species may follow a similar pattern but tend to spread clonally. Survival of these woody riparian species is dependent on maintenance of a high alluvial water table and avoidance

of scour events such as floods and ice flows. Mortality, or inability to survive following recruitment, may result from a water table lowered below those tolerated by young or maturing plants (Rood and Mahoney, 1995). Other factors, especially those human controlled, also play a role in riparian decline throughout the West.

Landscape Diversity

The parks represented in the GRYN (i.e., Yellowstone, Grand Teton and Big Horn) have heterogeneous landscapes ranging from mountains to broad valleys and deep canyons. Consequently, streams and rivers flowing from the mountains transect a diverse geomorphology that creates steep gradients through shallow-bedrock narrow valleys as well as low-gradient, broad valleys with deep alluvial. Throughout this region, variability in valley morphology directly influences the extent and type of riparian communities (Patten, 1998). Streams flowing through broad valleys with low gradients may be lined by woody and/or herbaceous riparian vegetation. If the water table is shallow, wetland herbaceous plants (e.g., sedges and wetland grasses) may extend for some distance from the river creating fens in some areas. These wetland areas often are devoid of woody species because the herbaceous cover may prevent establishment of willows, cottonwoods or other woody plants. Willows (*Salix spp.*) and sometimes cottonwoods (*Populus spp.*) may occur near the stream where floods enhance their recruitment. Once established, these species may spread asexually and expand within the floodplain often occurring away from the stream as it migrates across the floodplain. Steep gradient mountain streams may have riparian communities of mixed willows and conifers but cottonwoods may occur on suitable sites at lower elevations. Other woody species such as dogwood (*Cornus spp.*) and alder (*Alnus spp.*) also occur along these higher gradient streams.

Elevational differences also may influence riparian composition and structure. High elevation streams may not support large woody species such as cottonwood for physiological reasons. Alpine streams only support wetland herbaceous species or, occasionally, dwarf willows. Shrub willows and alders may be common along upper elevation streams sometimes mixed with stream-side conifer communities. With decreasing elevation, low stature riparian woody vegetation gives way to, or mixes with deciduous tree species. The gradient in the northern Rockies and represented in some of the GRYN parks goes from cottonwood/willow forests at lower elevations through alder/willow communities to spruce/aspen communities into alpine wetlands.

Common Features

Structural similarities of riparian communities occur across the GRYN because they are related to successional dynamics which are driven by common fluvial-geomorphic processes. For example, point-bars, channel margin, and island deposits provide exposed sediment that supports young riparian plants along meandering and braided rivers throughout the region. Also, sediment accumulation on terraces accompanies aging of riparian vegetation and establishment of later successional species. Cottonwood species found along streams from different regions have been shown to have similar recruitment requirements (Bradley and Smith, 1986; Scott et al., 1996, 1997; Shafroth et al., 1995; Stromberg et al., 1997; Auble and Scott, 1998; Rood and Kalischuk, 1998; Shafroth et al., 1998). For example, recruitment of cottonwood and associated riparian species is most often tied to hydrological events (i.e., high flows) occurring during the period of seed dispersal. The timing and cause of these events may differ throughout the region, but early succession woody riparian species (e.g., cottonwood and willow) respond the same way to high flow, recruiting new seedlings on the receding limb of the high flow event. The year of recruitment may be delayed along GRYN Rivers because snow melt floods may extend beyond the seed dispersal period, and recruitment occurs during high flows in succeeding years. Other species, for example, shrubby cinquefoil (*Potentilla fruticosa*) and water birch (*Betula glandulosa*) are also found in the riparian zone responding to other factors such as very moist soil or snow bank accumulation.

Patterns of riparian communities along elevation gradients and geomorphic gradients are similar throughout most of the GRYN. This region is arid to semi-arid thus availability of water and similarity of riparian vegetation structure allow ready transfer of information developed in one area to another.

Drivers or Forcing Functions of Riparian Systems

Hydrological factors controlling riparian processes may be quite different between the mountainous, headwater parks of Yellowstone and Grand Teton, and Big Horn Canyon NRA. Snow and ice may play a predominant role in the Yellowstone and Grand Teton while storm events on the arid landscape of Big Horn may be the primary hydrological driver. Snowmelt in the headwater parks creates a reliable hydrographic peak while erratic storms and controlled mainstem flows produce uncertain hydrographs in Big Horn. Recruitment of many riparian species is triggered by or coincides with the spring snowmelt peak which occurs in May to June (Scott et al., 1993). However, the peak may extend beyond seed dispersal causing recruitment to

be delayed by a year if peak flows of the succeeding year are sufficiently high. If insufficient, recruitment may be delayed further.

Heavy local storms may have greater impacts on stream flows in Big Horn than Yellowstone or Grand Teton. Less vegetative cover at Big Horn may result in flash floods in mountainous low order streams. Recruitment of spring seed-dispersal species such as cottonwood and willow is usually most successful when high spring flows that trigger riparian recruitment are followed by a relatively dry summer, and/or absence of large floods during the next year or two (Stromberg et al., 1991). Predicting future stream flows might allow projection of changes in riparian vegetation (Auble et al. 1994 Non-native species such as tamarisk (*Tamarix ramosissima*), Russian olive (*Elaeagnus angustifolia*), and many noxious weeds disperse seeds over long periods and thus take advantage of summer storms (Stromberg, 1998).

Riparian ecosystems of GRYN region may occasionally be scoured by flash floods but some are regularly affected by ice formation. Ice forms on the surface of rivers in the northern Rockies during extreme cold periods. During ice drives, ice may be elevated and scours the bank often well above levels of spring floods (Smith, 1980). Ice scour damages existing trees, removes riparian vegetation, forms new channels and controls the elevation of successful riparian recruitment (Johnson, 1994; Scott et al., 1997).

Geomorphic influences in the GRYN region may effect how successful recruitment might be for riparian species. Many riparian species require bare moist soil for recruitment (Stromberg et al., 1991; Scott et al., 1996). Many rivers of the north Rockies have gravel- or cobble-lined channels; however, fine sediment in these rivers may be held in overbank ice in winter and deposited in spring where riparian recruitment may occur. Fine sediments also are deposited within the interstices on the cobble and gravel bars.

River geomorphology, especially on smaller streams, is often controlled or altered by beaver activity (Naiman et al. 1986). Relatively permanent beaver dam structures collect sediment, altering sediment delivery downstream, and elevate local groundwater, enhancing growth and survival of most riparian species (Johnston and Naiman 1987). When beaver dam sites are active, beavers may alter the surrounding woody vegetation, harvesting and felling stream-side trees and shrubs (Hall 1960). Eventual abandonment of beaver dam sites results in floodplains covered in fine sediments and a vegetational successional process that leads towards the vegetation that occurred prior to beaver arrival.

Environmental Stressors

A. HYDROLOGICAL STRESSORS.

Factors that have created and maintained riparian systems within the GRYN parks are changing. Most changes are tied to water and channel management, land use, ungulate management, and introduction of non-native species. Throughout the region, rivers have been managed to produce water for irrigation, generate hydroelectric power, and for flood control. This is especially true in Grand Teton and Big Horn parks. In Grand Teton NP the Snake River is dammed at Jackson Lake, retaining irrigation water to be used during the growing season downstream in Idaho. Short reaches of the Snake River channel are also stabilized within GTNP. In BICA, the Big Horn River is dammed both upstream of the park and within the park. Dams and their impoundments have greatly altered downstream ecosystems (Ligon et al., 1995; Dynesius and Nilsson 1994; Collier, et al., 1996; Shafroth, et al. 2002). They impound spring floods that normally would scour channels, deposit sediment, and produce riparian vegetation along the high water zone (e.g., Johnson, 1991). Dam releases to satisfy downstream water uses, exemplified by operation of Buffalo Bill and Boysen dams upstream of BICA and the Jackson Lake dam, often do not coincide with normal high flow periods for the river, eliminating recruitment enhancing high flows and often producing scouring summer flows (Fenner et al., 1985; Rood and Mahoney, 1990, 1995; Johnson, 1992; Dominick and O'Neill, 1998; Mahoney and Rood, 1998). Reduction of peak flows though may result in widespread narrowing of channels resulting in riparian vegetation establishment in areas that once were active channels (Johnson, 1994, 1998; Friedman et al., 1996, 1997, 1998; Shafroth et al., 1998). Even when dams allow normal flows for recruitment and maintenance of riparian species, the river below the dam may carry little sediment, material important for creation of recruitment sites (Scott et al., 1997).

Stream diversion for irrigated agriculture may reduce surface flows or effect local floodplain vegetation. Several irrigation take out channels on tributaries of the Snake River within Grand Teton NP may be modifying the adjacent riparian communities. Grand Teton NP still has remnants of past agricultural uses within those areas of the park added in the 1950s. Where agriculture existed near rivers, removal of floodplain vegetation may still be evident as the floodplains recover. Recreational use of riparian areas has been found to leave them vulnerable to over-use and degradation (Johnson and Carothers, 1982). Although limits on use of streamside areas may

occur in some of the GRYN parks, BICA is established as a recreation area and potential heavy use along the Big Horn Lake margins may have deleterious effects. Effects of campers and day hikers on riparian vegetation along small mountain streams often are locally evident in Yellowstone and Grand Teton NPs.

B. BIOLOGICAL STRESSORS.

Ungulate grazing in riparian areas may disrupt the reproductive cycle of riparian trees such as cottonwoods, whose broad-leaved seedlings and saplings are extremely desirable forage. Removal of reproductive shoots also diminishes reproductive potential of willows (Kay 1994). Heavy ungulate use, both wild and domestic, of floodplains and riparian areas may greatly reduce riparian ground cover, destabilize streambanks, and increase sediment loads to streams (Patten 1968, Armour et al., 1991; Elmore, 1992; NRC 2002). Wild ungulate use in areas of Yellowstone NP, for example, the northern range, and Grand Teton NP, has altered the cover and structure of the riparian community (Singer et al. 1994, Singer 1996, Keigley 1997).

Beaver activity, although a normal component of riverine ecosystems in the GRYN parks, under specific conditions may be considered an ecosystem stressor. While beavers usually alter streams when occupying dam sites, or modify riparian vegetation whether housed in ponds behind dams or in stream banks, their absence may result in water table declines and associated long-term alteration or loss of riparian vegetation. Conversely, over-population of beavers in any reach of a river may cause major alterations of riparian vegetation through excessive harvesting of riparian woody plants. Several areas of the GRYN, for example, streams in the northern range of YNP, once supported extensive beaver populations but these are now absent (Bailey 1930, Wright and Thompson 1935, Jonas 1955). Also, continued beaver trapping outside the parks maintained low populations. Recently, however, beaver populations have dramatically increased in several areas of the GRYN parks. This recovery may ultimately result in "over-population" of beavers in some areas because many areas that once were suitable for beaver habitat in the region are no longer suitable for beaver population expansion because of unacceptable consequences of beaver activities in most areas of human habitation.

C. NON-NATIVE SPECIES AS STRESSORS.

Introduction of non-native species has greatly altered the west's riparian ecosystems and has become a major management issue in all three GRYN parks. Grazing and altered hydrology often favor the survival of introduced species (e.g., tamarisk) and allows thriving non-natives to

displace native species. Russian-olive and tamarisk are two non-native species that have greatly altered western riparian communities (Brock, 1984; Shafroth et al., 1995). Not only have they altered the communities they have invaded, they are difficult to remove. For example, tamarisk can repeatedly resprout after fire, cutting, or browsing, and it survives in very wet, very dry, or very salty soils (Gladwin and Roelle, 1998; Smith et al., 1998). An example of major tamarisk invasion in these parks is the exposed lake bed in BICA where the Big Horn River enters the park. Here tamarisk has developed a dense cover of young invasive woody plants. Extended inundation may be the only way to eliminate this extensive stand of tamarisk. Herbaceous non-natives are also becoming prevalent in many riparian areas creating dense ground cover that competes with native species, increases fuel for fires, and may be enhanced by grazing (Stromberg and Chew, 1997). All the parks are now contending with increasing cover of non-native herbaceous plants. This has become a sufficiently important issue that the Biennial Science Conference in Yellowstone NP in 2001 (ref) emphasized this issue.

D. CLIMATE FLUCTUATION AS A STRESSOR.

Climatic fluctuations over the past century have resulted in changes in local watershed hydrology which directly affect the condition of riverine and riparian systems. Long-term droughts not only reduce stream flows but diminish groundwater supplies, lowering water tables which are critical sources of water for riparian phreatophytic plants (Stromberg et al. 1996, Shafroth et al. 2000). Human accelerated climate change may create more erratic climatic fluctuations and could potentially produce extended droughts, much longer than that of the 1930s and similar to the 30-50 year droughts of 300 years ago. Riparian communities within the GRYN parks will respond relatively quickly to extended drought periods, reducing cover to only those areas that can maintain a shallow water table. These areas will be immediately adjacent to shallow bedrock streams and along margins of larger rivers where low flows may support alluvial groundwater. Climatic change and drought in the northern Rockies region will affect all three GRYN parks. Vegetation that is dependent on supplemental water, such as riparian vegetation, may be more altered by these changing conditions than upland vegetation.

E. CUMULATIVE EFFECTS OF STRESSORS.

Riparian ecosystem condition reflects the cumulative effects of all activities that influence watershed hydrology and thus may be an important indicator of changing environmental conditions within the GRYN parks. Multiple resource uses on mountains and in valleys

have modified the quantity and quality of water entering rivers. This is true for BICA, as the headwaters of the Big Horn River are used for many forms of resource extraction, ranching and agriculture often with release of stream contaminants. Sometimes the results of land use can be subtle, while in other cases, downstream impacts on riparian ecosystems can be dramatic. Timber harvest may result in larger and flashier floods which carry increased sediment. Leaving a buffer zone may help reduce sedimentation rates and provide for continued ecological interactions between streams and riparian vegetation (Kauffman, 1988).

Application to Greater Yellowstone Network Parks

Riverine and riparian systems within the three GRYN parks are influenced by many of the same stressors. The conceptual models illustrate the linkages between the many stressors (Figures 25-28). Although there may be many stressors that influence riverine and riparian systems in the parks, the conceptual model applies only a few that are known to potentially significantly alter these systems. As discussed above, stressors that influence riparian systems and that should be addressed in any inventory and monitoring program include (1) altered hydrology, (2) altered channel morphology, (3) climatic changes, especially droughts, (4) ungulate utilization of the riparian zone, (5) exotic plants, and (6) recreation. The discussion illustrates the importance of these stressors to each park but does not apply them specifically to park units. The importance to a park depends on extent and magnitude of a particular stressor. For example, altered hydrology is not a primary stressor in Yellowstone NP, but it plays an important role along the mainstem of the Snake River in Grand Teton NP, and is the primary stressor for the main water course and lake in BICA. Ungulates, on the other hand, may not be important in BICA along the river and lake, but are important locally in YNP and GTNP. BICA, on the other hand, may have ungulate herbivory issues in the uplands.

The conceptual model(s) show linkages among stressor and how they relate to dynamics of components of the riverine/riparian ecosystem. Following the flow of connected processes, it is possible to end up with a limited set of potential indicators that, if monitored, will offer evidence of changing watershed and river conditions within each park.

Each park has been geographically divided into watershed units (HUC units) for the purpose of addressing variability across the landscape of the parks. Within the GRYN parks there are several

riparian vegetation community types, some may occur in all parks while others may be specific to one or two parks, a consequence of geographic and environmental diversity. Table 1 presents riparian community types that occur within GRYN parks and identifies within HUC unit for each park those environmental threats or stressors that potentially may have an impact on long-term survival and condition of the riparian community. Eight different riparian vegetation community types are presented. Some of these relate to seral stages in riparian vegetation development and maturation, for example, gravel bar/river edge riparian communities up to mature cottonwood communities. Some riparian communities also relate to geographic locations, such as large river margins, lake shores, small mountain streams, or broad valley wetted-sediment deposits. The list of riparian community types is simplified for application to the whole GRYN. If expanded based on diversity within community type, the variability would create hundreds of types. For example, twenty four species of willow are found in the northern range of YNP and these produce a diverse set of willow communities based upon diverse environmental drivers (YNP 1997).

To allow comparisons across community types, a brief description follows:

- A. Gravel bar/edge wetlands:** this community type is found on point bars and the edges of rivers where flood disturbance is frequent. In most cases the vegetation cover includes herbaceous pioneer species, but young woody riparian species like *Salix exigua* and *Populus spp.* may also be present. In most cases the vegetation cover is sparse.
- B. Herbaceous meadow:** the community type may occur in broad alluvial valleys where the river is downcut and few woody plants are present. Herbaceous species are predominantly wetland sedge and grass species. Wetland forbs also may be present.
- C. Willow/shrub:** this is a diverse community because of the potential number of willows that may be present throughout the GRYN. The community is dominated by shrub willows and occurs on the edge of streams, adjacent floodplains, and wet alluvial flats and along seeps where groundwater is shallow. Some may be short willows (e.g., wolf willow), while some willow/shrub communities have tall willows (e.g., xxx). Other shrubs may be present with willows such as alder (*Alnus spp.*) in moist areas or shrubby cinquefoil (*Potentilla fruticosa*) in drier areas. In most cases, except where heavy browsing has reduced cover,

aerial cover of this community is high.

- D. Cottonwood:** this community type, usually found in mid to lower elevations within the GRYN, is dominated by mature cottonwoods and may have some cottonwood recruitment under the canopy or in adjacent floodplain and point bar areas. There is little understory of other woody plants. This type of community may be found in areas with heavy browsing pressure, or in relatively sterile gravel or cobbled areas where cottonwood has established and has resisted scour when it occurs, but other woody plants either never established or were scoured away by high magnitude floods.
- E. Cottonwood/willow/shrub:** this community type found in mid to lower elevations in GRYN represents a mature cottonwood community with a well established understory of shrubs, often willows, and herbaceous ground cover. These usually are undisturbed sites with no deficiency of shallow groundwater.
- F. Conifer/willow/shrub:** this community type is more typically found along mid to higher elevation streams that have limited overbank scour. The conifer overstory represents mesic upland species growing near the stream, whereas willow and shrubs such as alder are more typically riparian and phreatophytic.
- G. Lake shore:** this community type could be represented by several of those above but also may include true wetlands where saturated sediment occurs along the lake margin. Willows may grow along stable lake shores whereas gravel bar type communities may be common along fluctuating lakes. Mid to higher elevation lakes may have conifer communities growing along the shoreline.
- H. Riparian exotics (dominant):** this community type occurs in highly disturbed areas or where hydrological controls are greatly altered from the norm. Nearly pure stands of tamarisk represent this type of community which often occurs in moist sediment upstream and at tributaries mouths of lakes with fluctuating levels. Altered downstream hydrology below dams also often creates riparian communities dominated by extensive stands of exotic species. Communities dominated by herbaceous exotic species (often noxious weeds) may occur on floodplain areas following a high magnitude, overbank, scouring flood.

Stressors that play an important part in each park differ, except perhaps for climate change and drought stress. Riparian communities in YNP, especially in the northern range, are greatly influenced by ungulate herbivory. GTNP has altered hydrology of the Snake River as a

major issue, but it also has herbivory problems along some streams within the park. Primary stressors of riparian condition in BICA are altered hydrology and invasion of non-native riparian species. Table 1 summarizes the similarities and differences among the parks and the HUC units within the parks. Because riverine/riparian systems are linear and cover only a small percentage of the landscape, comparisons by watershed units within each park may be difficult; however, different conditions within each watershed, especially if they are some distance apart, might allow identification of different responses of riparian communities to similar environmental stressors.

Potential Indicators

Several indicators related to riverine and riparian ecosystems can be identified from the conceptual model and the discussion above. Some indicators may be stressors or other non-“outcome” parameters, but the best may be an outcome parameter that functions as an integrator of several processes.

- a. Riparian condition is one indicator, in actuality an index, that includes several riparian community parameters and channel geomorphic parameters. Riparian ecosystems are integrators of hydrogeomorphic conditions as well as local land use processes. Riparian condition includes metrics of horizontal and vertical vegetation structure, vegetation diversity and channel stability. The U.S. Forest Service and BLM have developed an index, Proper Functioning Condition (PFC), that attempts to address these parameters but it is subjective and includes little biological information. A modified version of PFC may be an appropriate index to use for “riparian condition”.
- b. Channel geomorphological metrics may also be a useful indicator of the condition of riverine and riparian systems. The ratio of channel width to depth and channel sinuosity in relation to floodplain type can be combined to develop a channel index that would indicate whether the channel is being changed from the “expected” geomorphic conditions.
- c. Riparian avian community structure may be used as an indicator of riparian condition. Species diversity of riparian avian communities, including presence and/or absence of certain species that have been identified as species commonly found in “healthy” or “degraded” riparian vegetation, can be used as a surrogate of riparian condition, including linear connectivity of riparian patches along a river.
- d. A biological stressor, exotic plants, may also be a useful indica-

tor of riparian vegetation condition. Increasing presence of exotic plant species has greatly altered many riparian systems in the West. A degraded riparian community may be altered primarily because of the presence of exotic species. If a relationship between altered condition and abundance of exotic species can be established, cover and diversity of exotic plant species in the riparian zone may be a useful long-term indicator.

- e. Aquatic biota, that is macroinvertebrates and/or fish populations, often indicate the geomorphology of a channel, the bedload materials, flow velocities at various stages as well as water quality. For general riverine and riparian conditions, aquatic biota may not be the best indicator, but if a combination of physical and chemical qualities need to be evaluated, aquatic biota may be a useful indicator. This indicator applies more to the river or lake systems of the GRYN parks and is discussed in more detail in that section.

Measurement of any of the above indicators would be done at randomly selected locations along reaches of rivers of interest. For lakes shores, randomly selected locations along a shore would be used in place of reach locations along a river. For the various parks, rivers of different sizes (orders) would be identified and long-term monitoring stations would be established.

8. ADDITIONAL INFORMATION ON POSSIBLE INDICATORS

Riparian ecosystems occur as the result of several environmental factors, hydrology being primary. However, new stressors such as heavy browsing, changes in beaver populations, introduction of exotic plants and recreation have become important in the health of overall distribution and condition of riparian communities. Because some of the “new” stressors have played a significant role in altering riparian communities, they may be important indicators, offering evidence of potential changes in the riparian communities of the GRYN area.

a. Riparian Condition.

Resource Monitored: Riparian vegetation structure and channel stability.

Justification: Riparian ecosystems, although a small part of the GRYN area landscape, support some of the greatest biodiversity. Changes in the health or condition of riparian communities will directly influence the assemblage of animal species found in the parks of the GRYN. Consequently, it is imperative that riparian condition (health) be included in a long-term monitoring program. Riparian condition is an indicator, in actuality an index, that includes sev-

eral riparian community parameters and channel geomorphic parameters. Riparian ecosystems are integrators of hydrogeomorphic conditions as well as local land use processes. They respond to changes in the watershed as well as the floodplain. They are very sensitive to climatic shifts that influence stream flows and groundwater levels. The woody vegetation in riparian areas is often the primary food source for wild and domestic ungulates during periods with forage shortages such as severe winters with deep snow, or summer drought.

Comment: Riparian condition includes metrics of horizontal and vertical vegetation structure, vegetation diversity and channel stability. The U.S. Forest Service and BLM have developed an index, Proper Functioning Condition (PFC), that attempts to address these parameters but it is subjective and includes little biological information. Other metrics of riparian condition include HGM (hydrogeomorphic methodology). This, however, is very comprehensive and would be difficult to apply to a large number of riparian areas.

Example of specific measurements for indicator: A modified version of PFC may be an appropriate index to use for “riparian condition”.

b. Channel Dimensions

Resource Monitored: Variability and changes in channel cross section geometry and river length to floodplain length relationships.

Justification: Riparian vegetation not only responds to changing channel geomorphology but plays a role in its formation. Any change in channel geomorphology will consequently alter the amount and distribution of the riparian community. Thus, channel geomorphological metrics may be a useful indicator of the condition of riverine and riparian systems. Altered hydrological conditions and concomitant degraded riparian systems play a role in channel changes. For example, changing regional hydrology or influences of upstream flow regulators, e.g., dams will cause channels to adjust to new conditions and offer less or more habitat for riparian plant communities.

Comment: The ratio of channel width to depth and channel sinuosity in relation to floodplain type can be combined to develop a channel index that would indicate whether the channel is being altered from “expected” geomorphic conditions. Decreasing width/depth ratios tend to indicate a degraded, incised channel; however, a greatly increasing width/depth ratio may result

TABLE I Riverine/Riparian Ecosystems. Environmental threats for each ecosystem type by HUB unit.

| National Park | HUC Units | Gravel bar/ edge wetlands | Herbaceous meadow | Willow/shrub | Cottonwood | Cottonwood/ willow/shrub | Conifer/ willow/ shrub | Lake shore | Riparian exotics (dominant) |
|---------------|----------------|---------------------------|-------------------|--------------|-------------|--------------------------|------------------------|------------|-----------------------------|
| GRTE | Jackson Lake | 1,2,3,4,5,6 | 3,4,5,6 | 1,2,3,4,5,6 | 1,2,3,4,5,6 | 1,2,3,4,5,6 | | 1,4,5,6 | |
| | Moran | | | 3,4,5,6 | | ?? | 3,4,5 | 1,4,5 | |
| | Jenny Lake | 3,4,5,6 | | 3,4,5,6 | | 3,4,5,6 | 3,4,5 | 4,5,6 | |
| | Spread Creek | 1,2,3,4,5,6 | 3,4,5,6 | 1,2,3,4,5,6 | 1,2,3,4,5,6 | 1,2,3,4,5,6 | 3,4,5 | | |
| | Fall Creek | 3,4,5 | | 3,4,5 | | ?? | 3,4,5 | 4,5,6 | |
| BICA | Black Canyon | 1,2,4,5,6 | | 1,2,4,5,6 | | | | 1,2,4,5,6 | |
| | Layout | 1,2,4,5,6 | | | 1,2,4,5 | 3,4,5 | | 1,2,4,5,6 | |
| | Fire Springs | 1,2,3,4,5,6 | | 1,2,3,4,5,6 | 1,2,4,5,6 | 1,2,3,4,5,6 | | 1,2,4,5,6 | 1,2,3,4,5,6 |
| YELL | Gallatin | 4,5,6 | 5,6 | 3,5 | | | 3,5 | | |
| | Northern Range | 4,5,6 | 3,4,5,6 | 3,5,6 | 3,5,6 | 3,5,6 | 3,5,6 | 3,5 | |
| | Madison | 4,5,6 | 3,4,5,6 | 3,5,6 | ? | ? | 3,5,6 | 3,5 | |
| | Yellowstone | 4,5,6 | 3,4,5,6 | 3,5,6 | | | 3,5,6 | 3,4,5,6 | |
| | Henry's | 4,5,6 | 3,4,5 | 3,4,5 | | | 3,5,6 | 3,5 | |
| | Snake | 4,5,6 | 5,6 | 3,5,6 | | | 3,5,6 | 3,4,5,6 | |

Environmental Threats (Stressors)

1 Altered hydrology

2 Altered channel

3 Herbivory

4 Invasive species

5 Climate change/Drought

6 Recreation

from excessive bank destabilization by ungulate use.

Example of specific measurements for indicator: Width-depth ratios at selected reach types along rivers of different sizes, along with geographic measurements of river sinuosity can be combined to offer an “index” metric for channel dimensions. Just the width-depth ratio on selected reaches may be satisfactory.

c. *Riparian wildlife species.*

Resource Monitored: Abundance of potential indicator wildlife/avian species.

Justification: Riparian avian community structure may be used as a wildlife species indicator of riparian condition. Species diversity of riparian avian communities, including presence and/or absence of certain species that have been identified as species commonly found in “healthy” or “degraded” riparian vegetation, can be used as a surrogate of riparian condition, including linear connectivity of riparian patches along a river.

Comment: Many studies have used presence and abundance of resident birds at select times of the year to demonstrate potential sources and sinks of avian populations. Riparian communities are usually the source of birds and thus any changes or loss of bird species and/or population composition may be an important indicator of riparian condition.

Example of specific measurements for indicator: Presence and abundance measurements taken within specific sized plots for 10 minutes at a number of sites along selected reaches of rivers of concern can be used as the metric for this indicator.

d. *Exotic plants.*

Resource Monitored: Exotic plant component of riparian plant community.

Justification: One of the biological stressors in the riparian conceptual model, exotic plants, may also be a useful indicator of riparian vegetation condition. Increasing presence of exotic plant species has greatly altered many riparian systems in the West. A degraded riparian community may be altered primarily because of the presence of exotic species. If a relationship between altered condition and abundance of exotic species can be established, cover and diversity of exotic plant species in the riparian zone may be a useful long-term indicator.

Comment: For this indicator to be useful, a relationship between riparian condition and exotic plant presence, especially for herbaceous species, needs to be established. Recent literature ad-

resses increasing exotic plant presence in riparian areas, but a statistical connection between presence and riparian degradation is not well developed.

Example of specific measurements for indicator: The metric would be percentage cover of specific exotic species within riparian vegetation. This will only be useful if that percentage can be related to reduced function of the riparian area. This percentage should be determined by establishing permanent transects in selected representative riparian areas within the three GRYN parks. The transects will be used to sample woody vegetation, while small quadrats (e.g., 1x1 m plots) along the transects will be used to sample herbaceous vegetation.

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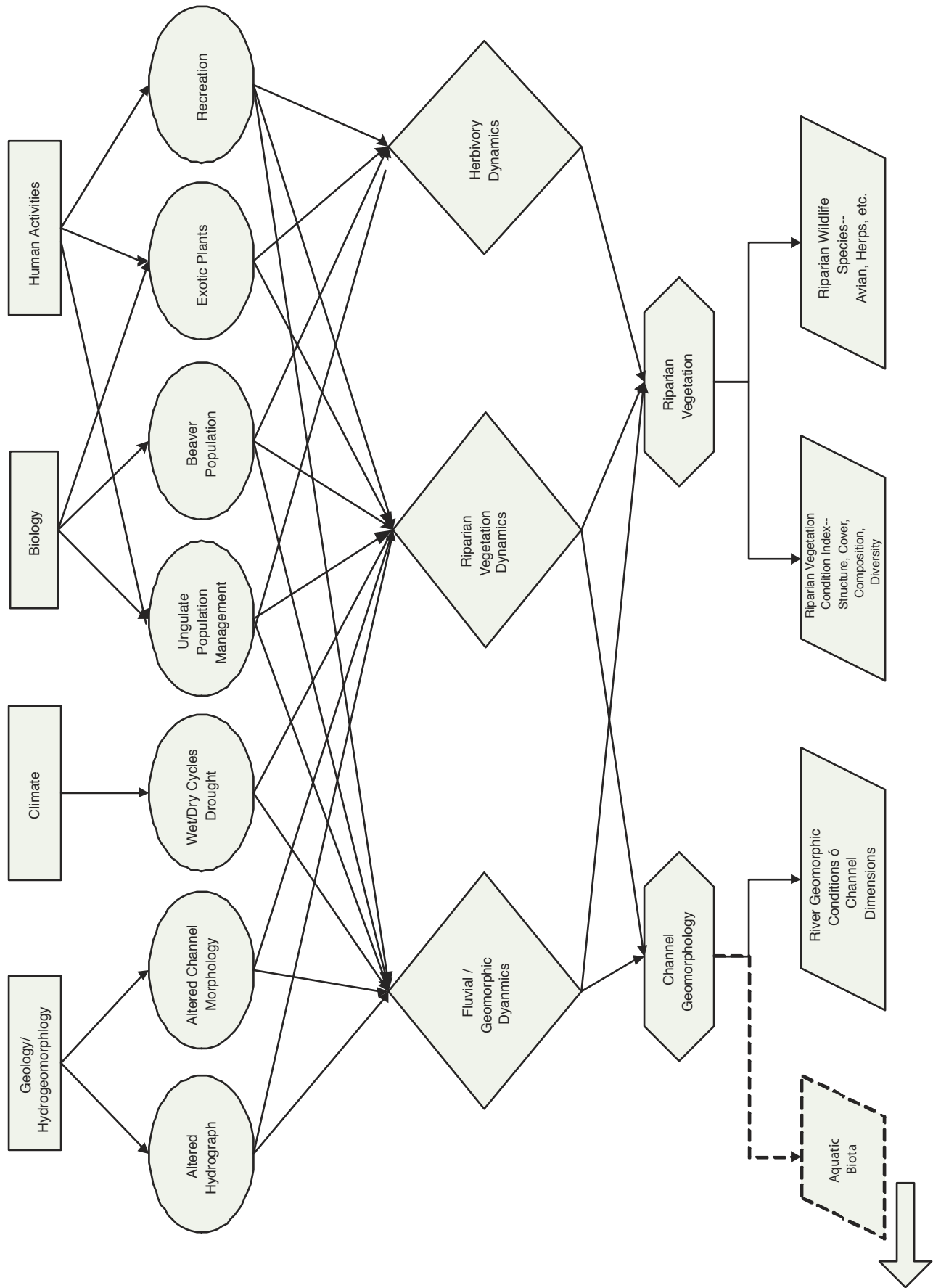


FIGURE 25 General riparian model.

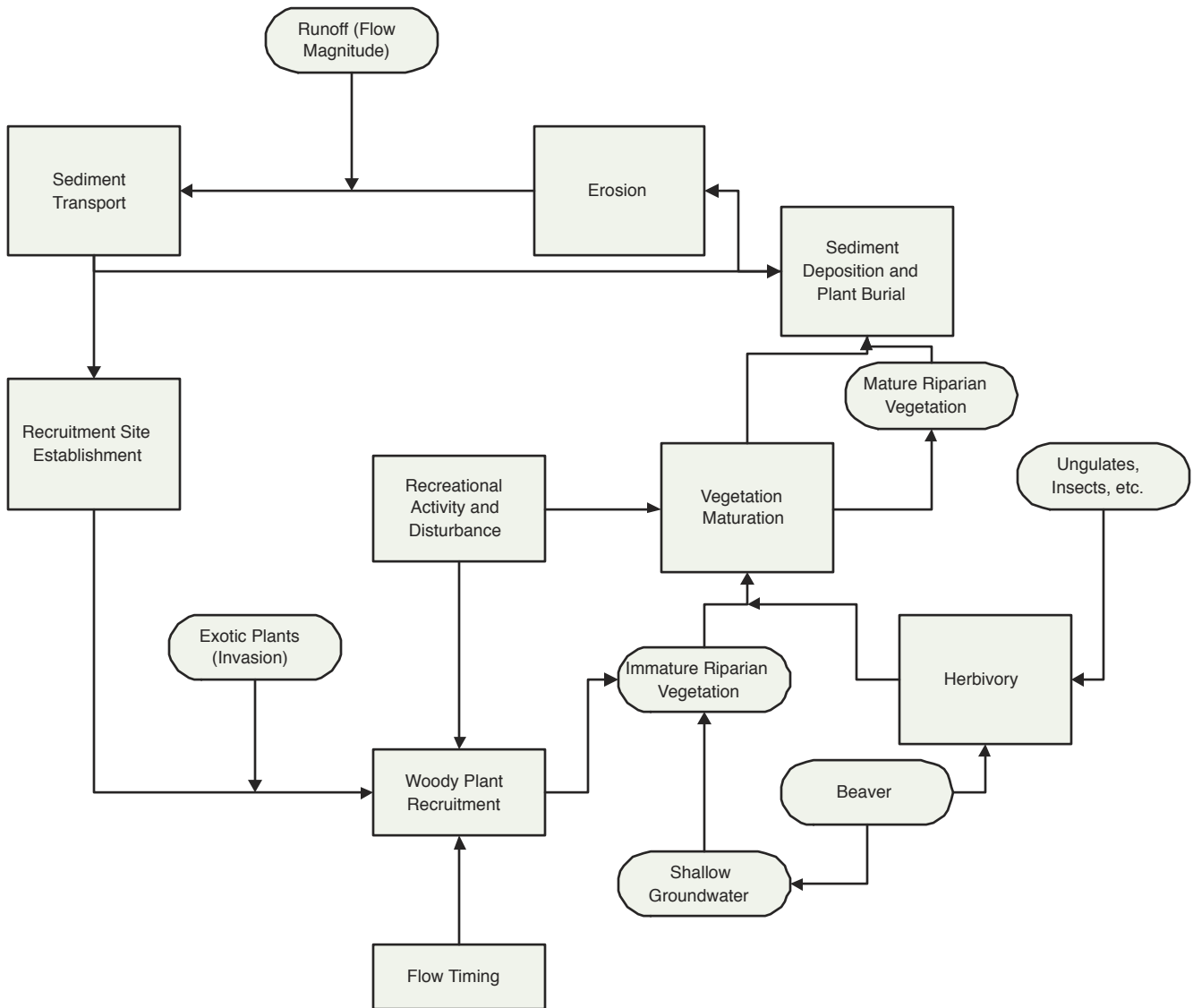


FIGURE 26 Riparian vegetation dynamics submodel.

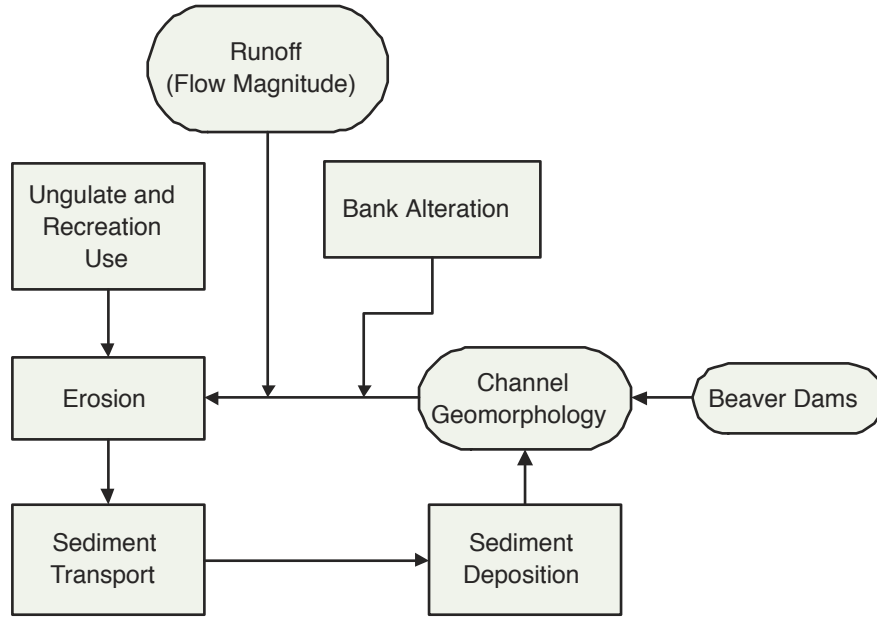


FIGURE 27 Riparian fluvial geomorphology dynamics submodel.

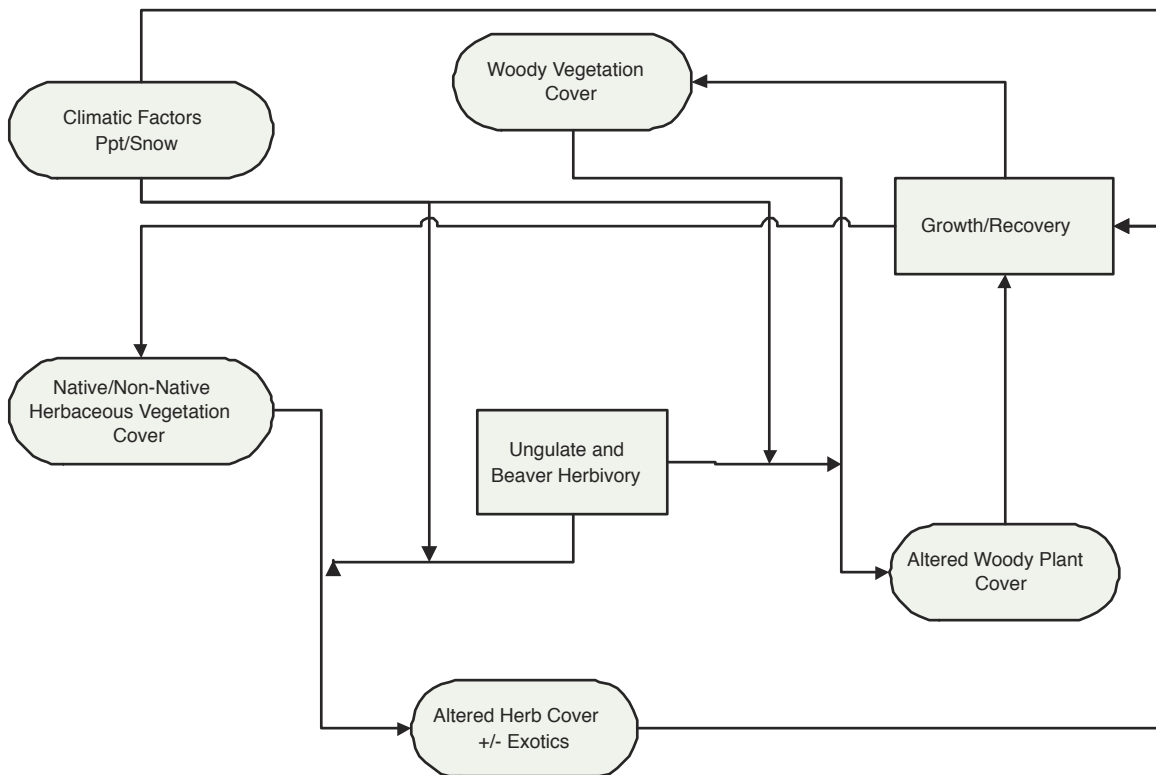


FIGURE 28 Riparian herbivory dynamics model.

WETLAND ECOSYSTEM NARRATIVE CONCEPTUAL MODEL

(author: Duncan Patten)

Wetlands are often a transition between aquatic and terrestrial ecosystems possessing some traits from both systems (Mitsch and Gosselink 2000). Wetlands are a primary source of biodiversity and this holds true for the GRYN area (Elliot and Hektner 2000). Wetlands play an important role in watershed hydrology, reducing flood peaks (Johnston 1994b), and improving stream water quality (Johnston 1991). Wetlands are highly variable and are found in many different conditions that have appropriate hydrology for wetland development. Most wetlands in the GRYN have been mapped by the USFWS in its NWI program. The more common wetland types (not necessarily based upon the NWI descriptions) within the GRYN area are, (a) depression or pothole wetlands, (b) willow community wetlands, (c) spring or seep wetlands, (d) beaver dam wetlands, and (e) herbaceous wetlands or wet meadows. Although several ecosystem types such as riparian systems may resemble wetlands, they do not have all the appropriate characteristics for true wetland status (NRC 1995). Willow wetlands, however, may occur in riparian conditions. Chadde et al. (1988) defined 62 wetland communities in the northern range of YNP, some dominated by non-wetland plant species. The true wetland nature of some of these community types may be questionable based upon the definition presented below. The following definition of wetlands from a National Research Council report (NRC 1995) explains those features required for wetlands and mentions potential for alteration of those features, an issue discussed in this report.

“A wetland is an ecosystem that depends on constant or recurrent, shallow inundation or saturation at or near the surface of the substrate. The minimum essential characteristics of a wetland are recurrent, sustained inundation or saturation at or near the surface and the presence of physical, chemical, and biological features reflective or recurrent, sustained inundation or saturation. Common diagnostic features of wetlands are hydric soils and hydrophytic vegetation. These features will be present except where specific physiochemical, biotic, or anthropogenic factors have removed them or prevented their development” (NRC 1995).

Wetland Drivers

The general description of wetlands presented above points out the importance of hydrology as a primary controlling factor of wetland

development, occurrence and maintenance (Mitsch and Gosselink 2000). Other factors that influence and/or alter hydrological events (i.e., inundation of wetlands) are also dominant drivers of wetland ecosystems. These external factors, for example climate and geomorphology, play an important role in general wetland occurrence and extent. Biological factors also play a role in wetland formation through feedback responses to hydrological processes (Mitsch and Gosselink 2000). Factors or stressors that influence the magnitude of climatic and geomorphic external factors, and also control vegetation and soil characteristics of wetland sites, are presented in Figure 29 (“Wetlands”) as human and biotic drivers. These stressors, discussed in the following section, include: altered hydrology, introduction of exotic plants, occurrence and management of ungulates, beaver, and predators.

Stressors

- a. **Upland Erosion:** Many wetlands are located in depressions, or in drainages that may be influenced by upslope erosional processes, often exacerbated by extreme wet climatic periods, and sometime by human activities, or natural processes such as fires, that destabilize slopes. Sediment (or alluvium) moving downslope will fill depression wetlands and small drainages, thus reducing or eliminating the wetland.
- b. **Wet/dry cycles:** Climate is highly variable, but when extremes of long-term wet or dry cycles occur they may alter the hydrology that controls wetland occurrence. Long-term droughts have caused many wetlands in the West to decline in size or dry up, thus eliminating many of the associated species commonly found in wetland communities. Contrarily, long-term wet periods may expand, or even create, wetlands. Longevity of these wetlands may be solely dependent on continued wet climatic cycles.
- c. **Altered Hydrology:** The significance of hydrology in the formation and maintenance of wetlands becomes more obvious when the hydrology is altered through human activities. Three forms of hydrological alterations have been found to greatly modify wetlands. One is the prevention of inflows of water from natural sources which eventually may dry up the wetland. On the other hand, new or increased surface flows into low lying areas may form wetlands where they have not occurred. Groundwater withdrawal can lower the water table that supports wetland inundation, and/or maintenance of continually wetted soils re-

sulting in wetland losses. Groundwater decline is not always related to human activities as long-term droughts may result in decreased water percolation to groundwater and thus reduction of wetland ecosystems that are supported by a shallow water table or spring activity.

- d. **Biological Stressors:** Plants and animals may modify wetland composition, structure and diversity.
- e. **Exotic plants:** Throughout the country, exotic plants have been introduced into every kind of ecosystem. Wetland plants from other continents are found in wetlands in the U.S.A., and plants from other locations may also migrate by human means into areas where they are not native. Consequently, many of the wetlands within the GRYN region no longer have the pristine plant community composition from the past. Exotic plants may out-compete with native plants resulting in highly modified wetland communities.
- f. **Ungulates:** Native ungulates may play a role in modification of wetlands. High density ungulate populations may alter vegetation composition or modify the geomorphic setting of wetlands. Management of ungulates plays a role in numbers and locations of ungulate herds.
- g. **Beaver:** Beaver, once very common in the GRYN and then scarce, is making a comeback in some areas of GRYN. Beaver can alter flowing streams and create wetlands, especially on secondary channels of large rivers, and small creeks (Johnston 1994a). In many parts of the West, beaver once created strings of wetlands where rivers now occur. Reintroduction of beaver may eventually increase the extent of wetlands within the GRYN in the future.
- h. **Predators:** Coyotes, wolves and other predators may indirectly play a role in wetland development and extent by controlling ungulates and beavers. Lack of predators becomes a wetland stressor because of their role in influencing the herbivores that modify wetlands.

Processes

The interaction of several stressors within the context of a functional wetland will result in a modified wetland as briefly discussed under “stressors”. However, the ecological processes (diamonds) in Figure 29 (“Wetlands”) that potentially lead to indicators may be a complex set of interactions which result in modifications to wetlands. None of the stressors act alone on existing wetlands, or in the creation of wetlands.

- a. **Depressional Wetland Dynamics:** Probably the simplest of the submodels developed to show dynamics of interactions of stressors is that related to filling of depressional wetlands. Precipitation and erosional processes interact to create and reduce wetlands. Alluvium washed into depressional wetlands, in time, may reduce or eradicate wetlands in its path. Although depressional wetlands may not be the most common in the GRYN, they do occur and several studies have shown rates of sediment deposition in these (Ref.). These studies may be interpreted to illustrate the possible increase in deposition rates in the depressional wetlands (and ponds) in GRYN resulting from high rangeland utilization by ungulates in wetland watersheds and adjacent to depressional areas.
- b. **Hydrological Dynamics:** As the primary driver of wetlands, hydrology and those factors that influence it, play an important role in extent of wetlands within the GRYN area. The amount of precipitation, a function of wet/dry cycles, is the primary controlling variable within the hydrological dynamics of the landscape that includes wetlands. The fate of precipitation, that is, what factors control its input to wetlands, becomes of prime importance in understanding wetland dynamics in GRYN. Figure 30 illustrates the complexity of the flow of water from precipitation to wetlands. Some water runs off into streams, lakes and human controlled or beaver created reservoirs. Some percolates into the ground and emerges as springs. Eventually, to form wetlands, these water sources must create standing water long enough to form hydric soils and allow wetland vegetation to establish.
- c. **Wetland Vegetation Dynamics:** The presence of wetland vegetation is one of the three properties that define a wetland. The other two are duration of inundation and presence of hydric soils. If appropriate wetland physical conditions exist, wetland vegetation will establish. Altered hydrology may enhance wetland vegetation establishment if the hydrological changes create periods of inundation, or prevent wetland formation if the changes reduce or eliminate inundation periods. Wetland vegetation structure and cover may be altered by herbivory by ungulates, beaver and other wetland herbivores. Wetland plant species composition is being altered by presence of introduced, exotic plants throughout the country, the GRYN being no exception.
- d. **Beaver Population Dynamics:** Beaver play a role as herbi-

vores, often altering the structure and cover of wetland plants (discussed above); however, the role of beaver may be more significant in the formation of physical conditions that form, and occasionally destroy, wetlands (Naiman 1988). Thus, the abundance and distribution of beaver in the GRYN area are important factors in presence (and demise) of wetlands. Beaver populations appear to be increasing in the GRYN area, some naturally and some through reintroduction. This increase, if not controlled by predators and humans, may eventually result in greater extent of wetlands.

Outcomes and Indicators

Within the GRYN area there are several wetland types that result from the interaction of natural hydrogeomorphic processes with stressors that control or alter features of the wetlands (i.e., hydrology, soils and vegetation). These wetland types, mentioned in wetland descriptions earlier in this discussion are (a) depressional or pothole wetlands, (b) willow community wetlands, (c) spring or seep wetlands, (d) beaver dam wetlands, and (e) herbaceous wetlands or wet meadows. Each wetland type has its own unique set of characteristics, a consequence of all of the drivers and stressors creating it, however, some basic parameters or metrics are common to all. These include the fundamental structure and composition of the wetlands, and the associated species. Obviously, vegetation composition may be primarily woody or herbaceous, but metrics such as cover or species composition can be used as indicators for all wetland types.

Another set of wetland parameters that may also be used as indicators relates to the status of wetland associated species, such as birds and amphibians. Both of these species assemblages have been found to be useful indicators of wetland status.

1. Wetland Vegetation Parameters

Resource Monitored: Plant species composition, cover, abundance, or diversity for each wetland type (i.e., depression, willow, spring, beaver dam, and herbaceous wetlands).

Justification: The high biological diversity of wetlands is found in the plant community as well as associated animal communities and populations. The plant community is the foundation of the wetland ecosystem. It responds to the hydrological events that create inundation and hydric soils. Wetland plants, especially obligate wetland plants, are limited to wetland physical conditions. Consequently, plant associations in wetlands change in

response to the magnitude of stressors that may alter the influence of hydrology or ability of the plants to establish and grow in wetland conditions. These changes, when determined in different types of wetlands will, over time, signal both short-term and long-term local and regional wetland changes.

Comment: Abundance is a term often applied to quantification of some ecosystem or community parameter. Because wetlands plant communities tend to be dense, estimates of cover of individual species may be the best metric to use. Cover classes (e.g., 1-5) may be appropriate. Sampling vegetation cover at representative wetlands of each type, when present, will produce data on increasing or decreasing cover of individual species and the whole community. This type of sampling will also produce data on community composition and species diversity.

Example of specific measurements for indicator: An example of a sampling scheme for determining species and total community cover, as well as species composition might be a series of random quadrats within a grid placed on the selected representative wetland, or stratified portion of the wetland if it is large. If the wetland has large woody species (e.g., willows), nested quadrats should be used (i.e., large (4x4 m) for woody and small (1x1 m) for herbaceous). The grid should be permanently marked to allow continued sampling of the same area of the wetland. Resampling (e.g., every 10 years) should be part of the long-term monitoring program.

2. Wetland associated species

Resource Monitored: Abundance of associated animal species (e.g., amphibians, birds, small mammals, etc.) in each wetland type (i.e., depression, willow, spring, beaver dam, and herbaceous wetlands).

Justification: Wetlands sustain a high diversity of associated species including, for example, birds, amphibians, small mammals, insects, etc. The abundance or presence of these species and/or the aggregate of these species (aka community) often act as surrogates for the condition or health of the wetland. Within a functional group, like birds, a change in composition of species from wetland specialists to generalists may indicate a change in food sources such as seeds and insects. In this way, the bird assemblage may be an easier metric to measure than comprehensive vegetation samples.

Comment: Avian (bird) species assemblages have been widely used

within the GRYN to determine the health of different ecosystems as well as avian source and sink vegetation communities. Riparian areas are a primary source and one could expect localized wetlands might also function in this capacity. Of the various associated species groups, the avian community probably is the easiest to sample, and long-term data sets for this group also exist for parts of the GRYN.

Example of specific measurements for indicator: Avian sampling includes regular (e.g., monthly) short-time (10 minute) visits to specific locations, in this case, specific wetland communities. The presence of every bird species within a pre-determined radius is recorded. The data can be organized into functional groups, such as resident, nesting migrants, neo-tropical migrants, etc. Sampling should be repeated on an annual or pre-determined time frame (e.g., every 1, 2 or 5 years) and this repeat sampling should be part of the long-term monitoring program.

3. *Beaver populations*

Resource Monitored: Presence of beaver activities (e.g., dams, mounds and/or bank burrows), and estimates of associated beaver numbers.

Justification: Beaver produce one kind of wetland within GRYN area that is associated with dams, ponds and elevated water tables. The presence or absence of beaver and these types of wetlands has reduced the diversity of wetlands and ecosystem types within the GRYN area. Consequently, biodiversity in valleys and along streams where beaver activity once occurred has declined. Beaver abundance tends to be cyclical, but some causes for these cycles may be related to human influence as well as changes in population of competitors for woody plants, predators and climate. There appears to be a resurgence of beaver in parts of the GRYN area. Although in many places with higher density human population the return of beaver is not welcome, within the natural areas of the GRYN region return of beaver is a sign of improving health of the landscape. For this reason, use of beaver population as an indicator (vital sign) may allow long-term evaluation of landscape health within those areas of the GRYN where beaver can occur and develop associated wetlands.

Comment: Within parts of the GRYN there has been some semblance of tracking beaver over the past few decades. A more systematic effort needs to be established that will not only determine

where they are located and how many might inhabit each location, but also will determine the trends in beaver expansion or decline and the associated movements or migration of beaver families.

Example of specific measurements for indicator: All beaver locations within GRYN should be mapped (GIS recorded). This can be done by a combination of remote sensing and ground-truthing. A representative number of beaver sites should be visited to determine the population size at each site, if this type of data doesn't presently exist. These data sets, location and site population should be archived and regular (2-5 years) resampling of the GRYN region for beaver should become part of the long-term monitoring plan.

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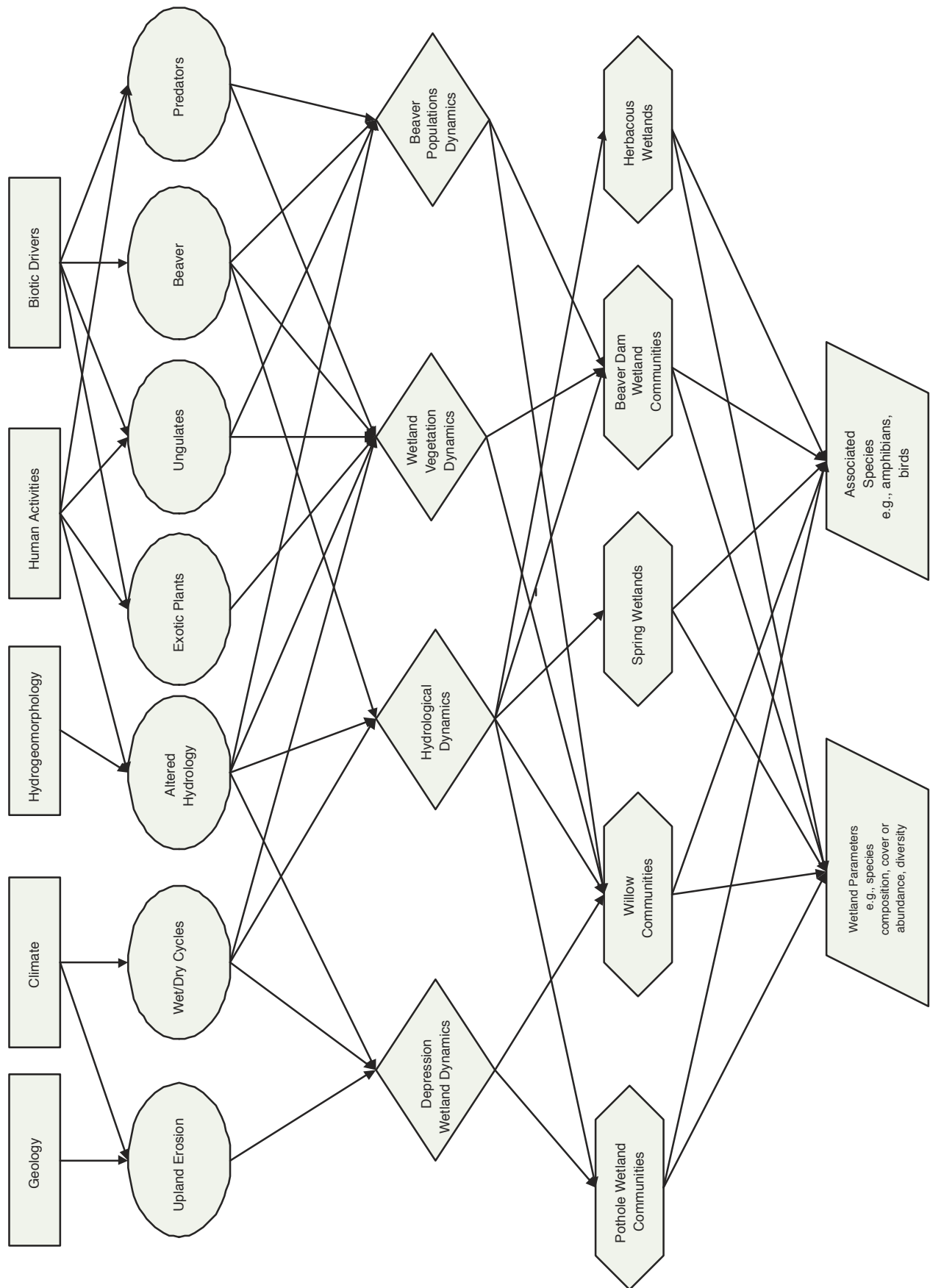


FIGURE 29 General wetland model.

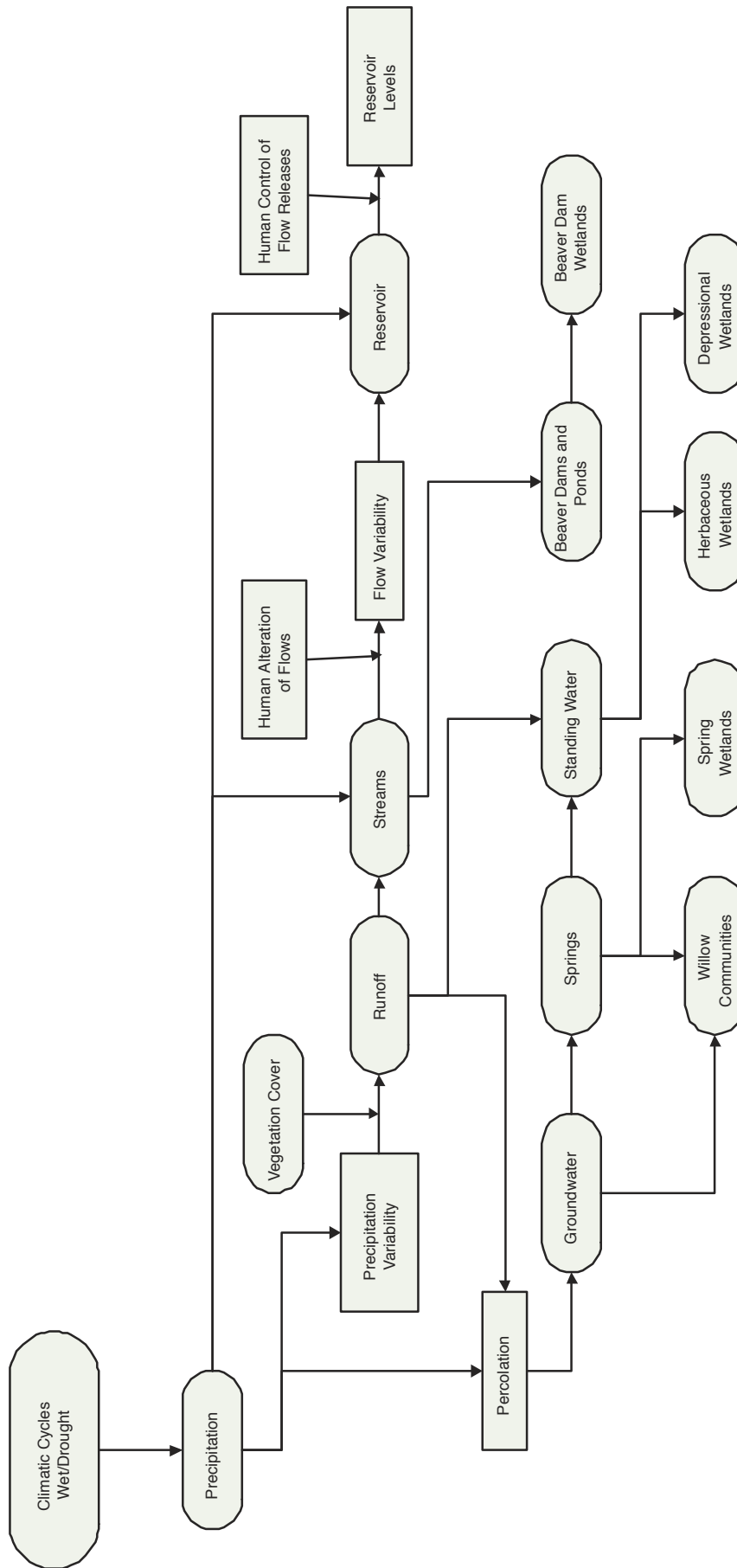


FIGURE 30 Wetland hydrology dynamics submodel.

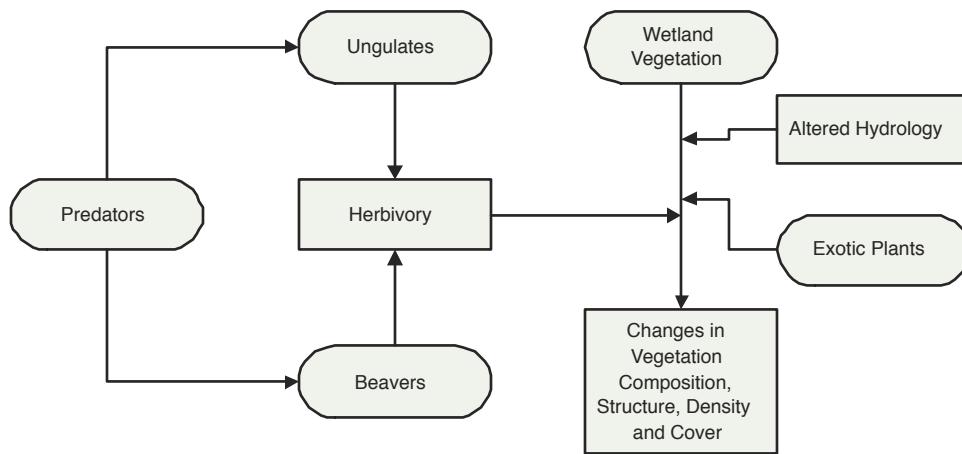


FIGURE 31 Wetland vegetation dynamics submodel.

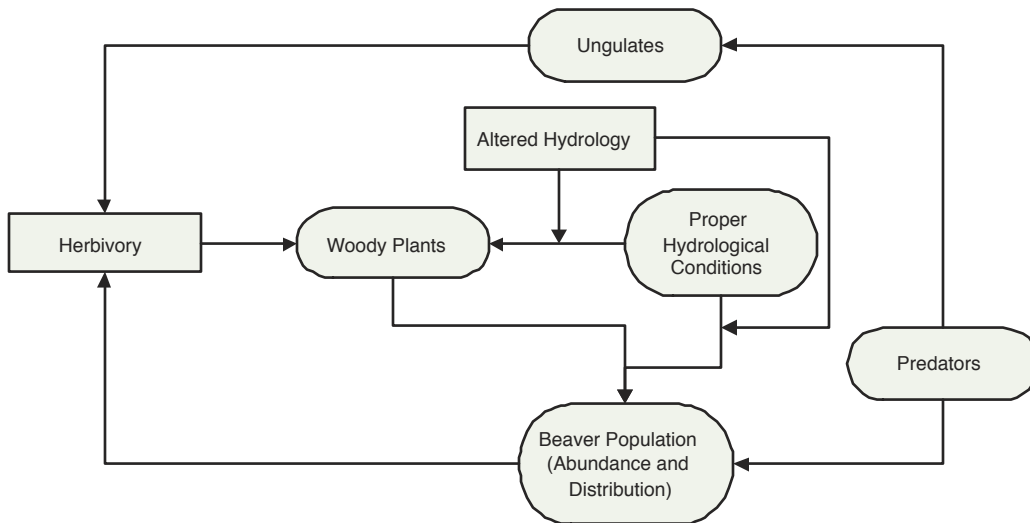


FIGURE 32 Wetland beaver population dynamics submodel.

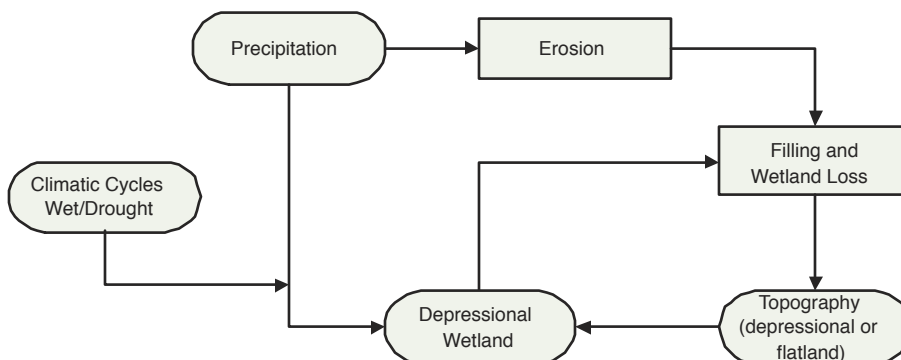


FIGURE 33 Depressional wetland dynamics submodel.