2004

Executive Summary the Role of Ungulate Herbivory and Management on Ecosystem Patterns and Processes: A Problem Analysis

John G. Kie

Martin Vavra

EXECUTIVE SUMMARY

THE ROLE OF UNGULATE HERBIVORY AND MANAGEMENT ON ECOSYSTEM PATTERNS AND PROCESSES: A PROBLEM ANALYSIS

The purpose of this problem analysis is to identify knowledge gaps in forest management related to the interaction of herbivory, forest succession, and ecosystem patterns and processes; to identify critical research questions and designs to address and fill the knowledge gaps; to build and validate multi-scale models of herbivory effects on ecosystem patterns and processes as a fundamental paradigm for research and main tool for management applications; and ultimately, to provide a working document for an interagency, interdisciplinary team of scientists to implement the research designs to address the identified research questions.

In the western United States, foraging by wild ungulates has not been recognized as an ecological force as evidenced by the lack of their mention in land management plans. In Europe, the effects of ungulate herbivory are better recognized, but primarily for its impact on regeneration of conifers (Kräuchi et al. 2000).

Livestock grazing has long been recognized as an agent of change in composition, structure and production of plant communities (Fleischner 1994). However, recent increasing evidence indicates that ungulate herbivory, wild or domestic can have dramatic effects on ecosystem structure and function (Hobbs 1996, Augustine and McNaughton 1998). In northeastern Oregon recent findings indicate that wild ungulates can alter the successional pathway of understories following disturbance (Riggs et al. 2000) and impact grasslands (Johnson and Vavra 2001). Identifying how ungulate herbivory influences composition and structure of forest understories following disturbance is critical to the success of forest management over the next several years. Additionally, herbivory-induced changes in understory may affect productivity of native ungulate herds (Irwin et al. 1994) and increase the degree of interspecific competition among ungulates (Vavra and Riggs 2000).

Forest conditions in the western United States are such that major changes will be occurring in the next several years. Years of fire suppression, resulting forest ingrowth, and tree mortality caused by insect and disease outbreaks have all contributed to the development of forests that exist outside the natural range of variability and are susceptible to conflagrations (Quigley and Arbelbide 1997). The purposes of this Problem Analysis are: 1) summarize existing knowledge of the influence of herbivory on ecosystem structure and function, 2) provide application of this knowledge to identify research needs, and 3) provide a research approach to improve knowledge on herbivory effects that can be utilized by managers.

Following either large fires or fuels reduction treatments, secondary succession of both understory and conifer components is initiated. These areas often become focal points of ungulate herbivory. Recent literature reviews (Hobbs 1996, Augustine and McNaughton 1998) clearly indicate the important role of herbivory not only in modifying the composition of plant communities, but of ecosystems.

The issue of forest health in the interior Northwest has been adequately identified (Johnson 1994, Johnson et al. 1995, Langston 1995, Quigley and Arbelbide 1997, Hann et al. 1997). These publications also relate the human activities (extensive timber harvest, fire suppression, overgrazing, roading) that have led to the identified problems.

Wild and domestic herbivores should be considered agents of chronic disturbance, capable of influencing succession, nutrient cycles, and habitat characteristics, to extents equal to episodic fire or timber harvest (Riggs et al. 2000).

Augustine and McNaughton (1998) stated that species composition of plants can be dramatically altered by selective foraging of ungulates and that this phenomenon is a trademark of plant-ungulate relations. Augustine and McNaughton (1998) went on to include overstory species effects as well, and listed several species of coniferous and deciduous trees that were reported as herbivory intolerant.

Forest succession is a function of edaphic factors, the density and viability of seed and sprouting rootstocks, episodic disturbance regimes, and herbivores (Riggs et al. 2000). Herbivory alters the utilization profile of a plant community (palatable versus unpalatable plants) and thus can alter its successional trajectory. Herbivores influence growth, recruitment, and mortality rates of plants and may do so in ways correlated with plant density, frequency, or other neighborhood traits, or with competitive abilities (Huntly 1991). Herbivory is highly variable in space and in time, and these spatial and temporal patterns of herbivory can generate structure in plant populations, the existence of which strongly influences community dynamics.

When ungulate foraging reduces biomass and litter, and/or changes species composition, nutrient cycling and energy flow also can be altered (Augustine and McNaughton 1998). Herbivore-induced changes in composition of plant species caused by herbivory have important ramifications for nutrient cycling. If palatable nitrogen fixing plants are suppressed by ungulates less nitrogen may be available to the system. Herbivory following some timber harvest systems may create a lack of self-sufficiency in nitrogen on harvested units. As herbivores decrease the dominance of preferred plants in favor of unpreferred, and less degradable plants, rates of nutrient cycling and energy flow show decline (Pastor and Cohen 1997).

Herbivory-induced changes in plant species composition of forest understories and overstories have important ramifications for habitats of other species. Changes in understory structure and litter accumulations may be important to bird and small mammal populations. There is the potential that individual plant species and even entire plant communities may be put at risk (e.g., aspen (*Populus tremuloides*), bitterbrush (*Purshia tridentata*), Pacific yew (*Taxus brevifolia)*, and mountain mahogany (*Cercocarpus sp*) communities) (Parks et al. 1998, Vavra and Riggs 2000) and that vertebrate species dependent on these communities (e.g., cavity nesting birds in aspen stands) may diminish.

The potential role of herbivory as an important agent of chronic disturbance, and the resultant changes in successional trajectory imply that ungulates could be considered keystone species (Riggs et al. 2000). Disturbance agents rarely act alone (Rogers 1996). Other agents, such as drought and fire, or disease and insects most often act in concert across both time and space. To what extent and where herbivore impacts might be significant depends on the herbivore species, population densities, patch choices, and landscape patterns (Hobbs 1996). Additionally, scale is important in that small areas of disturbance may be used more heavily than large ones (Scott et al. 1982).

When ungulates modify the structure and composition of vegetation there is a cascading effect throughout the ecosystem. The suppression or elimination of nitrogen fixing plants reduces nitrogen accretion (Tiedemann and Berndt 1972, Bormann and

Gordon 1989, Knops et al. 2000, Riggs et al. 2000). The outcome of decreased nutrient availability is a loss of forest productivity over time (Riggs et al. 2000) and a potential change in overstory composition (Hobbs 1996, Alverson and Waller 1997).

The removal of fine fuels by ungulates may reduce ground fire frequency, but actually increases the opportunity for crown fires by enhancing the development of unpalatable trees and shrubs, providing ladder fuels (Hobbs 1996). After fire or other disturbance, as secondary succession occurs and food sources for herbivores increases, use by herbivores will also increase (Clary and Larson 1971, Lowe et al. 1978), possibly leading to plant composition changes and continuing the cycle of fire-prone landscapes.

Many factors other than food regulate the distribution of ungulates (Coughenour 1991b, Reismoser and Gossow 1996). Interference factors, such as postfire rehabilitation, logging, and fuels reduction practices may also redistribute ungulates across landscapes because of increased road traffic (Wisdom 1998).

High deer densities may reduce bird species diversity in forests, but selective logging practices may mitigate bird species diversity in the presence of concomitant high deer densities (DeGraaf et al. 1991). However, DeCalesta (1994) found that in managed forests the decline of songbird richness and abundance was linear with increasing deer numbers. The disparity in reports suggests that the extent of overstory removal, the numbers of deer (nutrient demand) and the inherent productivity of the landscape are important considerations.

If long-term herbivory has affected plant composition and nutrient cycling in forest vegetation, those changes should cause density dependent, negative feedback effects to ungulate population dynamics and weight gain of livestock (Klein 1970, Irwin et al. 1994).

Fire suppression, insects and diseases, herbivory and decreased logging have all interacted to produce conflagration-prone landscapes in the western United States. Given a repetition of weather conditions that occurred in the summer of 2000, large wildfires could continue in the West. Spending on post fire rehabilitation projects has increased during the past decade and probably will continue to increase (Robichaud 2000). The effectiveness of these projects may be in jeopardy given our lack of acknowledgement of herbivory effects following disturbance (Riggs et al. 2000). Current databases on post fire succession do not include herbivory as a component (Stickney and Campbell 2000).

If variation in herbivory regimes can modify the influence of episodic disturbances, then the significance of herbivores as change agents in the ecosystem is important to recognize in disturbance research (Riggs et al. 2000). Hobbs (1996) believed that the ability to fully understand and predict the ways that ungulates modify ecosystems remains a large task. Huntly (1991) specifically believed that field studies should be designed to evaluate the contributions of particular mechanisms to herbivore effects, not simply document whether plant communities differ when herbivores are present or absent. Long-term and large-scale studies are needed, as well as shorter-term and smaller scale studies in which the environments are manipulated so the full range of conditions can be evaluated.

The overall goal of future research for the Elk, Deer, and Cattle Interactions Team and its research partners is to quantify and integrate factors that affect ungulate resource selection in order to provide managers with reliable information to evaluate effects of management alternatives on long-term stability of ecosystems, ungulate productivity, and other wildlife populations. The proposed research will fulfill several goals and objectives of the Forest Service Strategic Plan, the Strategic Plan of the PNW Research Station and the Charter of the Managing Disturbance Regimes of the PNW Research Station.

The problem is important to managers faced with delivering programs for National Forest lands for sustainable forest ecosystem management, watershed health and restoration, recreation and compatible road systems. State fish and wildlife agencies charged with maintaining a viable recreation resource of fish and game, as well as healthy populations of non-game wildlife, need the best information possible to establish management objectives for ungulate populations to provide sufficient game animals for harvest without compromising other wildlife (non-game habitat) or ecological values (healthy biological communities). Additionally, the problem is important to the public which has voiced strong concern for the environment, including such things as biodiversity, and water quality and quantity; access to National Forest lands for recreation; and liberal opportunity for consumptive recreation (hunting and fishing).

Benefits accrued to managers will be the development of tools to provide better management of landscapes (silviculture, prescribed fire, fuels reduction, road access, livestock grazing, etc.) where ungulates are potentially important agents of chronic disturbance and may alter successional trajectories. State fish and wildlife agencies should be able to manage populations of big game with known impacts and tradeoffs on other wildlife and ecological resources. Research products will contribute to the pool of knowledge being developed to reach the goal of sustainable forest ecosystem management.

The identified problem, is an important component in the development of new management plans for National Forests in the West. Exact solution is not possible, but the next ten years of research will contribute to the knowledge base managers need in their journey toward sustainable forest ecosystem management and provide new questions for further research.

New directions of research for the Elk, Deer, and Cattle Interactions Team (EDCI) require the integration of an experimental approach with a modeling approach. Two possibilities exist, a) an approach that uses empirical results to build models, or b) an approach that builds hypothetical models based on extant information, and then tests model predictions via empirical experiments conducted at various scales. The latter approach best fits the EDCI as it provides for the integration of a wide array of specific research efforts conducted at various scales. This approach will also allow immediate interaction with the Interior Northwest Landscape Analysis Systems Project.

The overriding problem to identify is how ungulates modify successional trajectories in interior forest ecosystems. Some effort should be given to illustrate the potential for manipulation of herbivore factors (species, season of use, intensity of use) to develop different landscapes. Interactions are the next level of problem. If ungulates do in fact, modify the structure of forests, then various ungulate mixes should result in potentially different forest structures which would have various susceptibilities to fire, and the type of fire, e.g., ground or crown; large or small. Episodic disturbance, like fire, logging, or fuels reduction provides an interaction with herbivory whereby the influence of herbivory on successional trajectories is magnified following the disturbance. The third level of problem deals with the secondary effects of altered forest structure.

THE ROLE OF UNGULATE HERBIVORY AND MANAGEMENT ON ECOSYSTEM PATTERNS AND PROCESSES: A PROBLEM ANALYSIS

Purpose

The purpose of this problem analysis is to identify knowledge gaps in forest management related to the interaction of herbivory, forest succession, and ecosystem patterns and processes; to identify critical research questions and designs to address and fill the knowledge gaps; to build and validate multi-scale models of herbivory effects on ecosystem patterns and processes as a fundamental paradigm for research and main tool for management applications; and ultimately, to provide a working document for an interagency, interdisciplinary team of scientists to implement the research designs to address the identified research questions. More specifically, the document provides research direction for the Elk, Deer, and Cattle Interactions Team of the La Grande Forestry and Range Sciences Laboratory, Pacific Northwest Research Station, Forest Service for the next 10 years. Research will be focused on the Starkey Experimental Forest and Range, but extensive field locations on National Forest lands will be required for validation and extension of results to region-wide application.

Introduction

In the western United States, foraging by wild ungulates has not been recognized as an ecological force as evidenced by the lack of their mention in land management plans. Aber et al. (2000) made no reference to ungulate herbivory, either wild or domestic, in their publication "Applying ecological principles to management of the U. S. National Forests". Likewise, in a survey on forest health issues in British Columbia conducted by Nevill et al. (1995), research priorities for insects and diseases were of greater importance than mammals. Mammals mentioned were voles, hares/rabbits, squirrels, beavers, porcupines and deer. Elk were not mentioned although they are common in parts of British Columbia. Only porcupines warranted significant attention. In Europe, the effects of ungulate herbivory are better recognized, but primarily for its impact on regeneration of conifers (Kräuchi et al. 2000).

Livestock grazing has long been recognized as an agent of change in composition, structure and production of plant communities (Fleischner 1994). However, recent increasing evidence indicates that ungulate herbivory, wild or domestic can have dramatic effects on ecosystem structure and function (Hobbs 1996, Augustine and McNaughton 1998). In northeastern Oregon recent findings indicate that wild ungulates can alter the successional pathway of understories following disturbance (Riggs et al. 2000) and impact grasslands (Johnson and Vavra 2001, but see Coughenour 1991a, Singer 1995). For the purposes of this document ungulate herbivory will refer to both wild and domestic unless otherwise specified. Identifying how ungulate herbivory influences composition and structure of forest understories following disturbance is critical to the success of forest management over the next several years. Additionally, herbivory-induced changes in understory may affect productivity of native ungulate herds (Irwin et al. 1994) and increase the degree of interspecific competition among ungulates (Vavra and Riggs 2000).

Forest conditions in the western United States are such that major changes will be occurring in the next several years. Years of fire suppression, resulting forest ingrowth, and tree mortality caused by insect and disease outbreaks have all contributed to the development of forests that exist outside the natural range of variability and are susceptible to conflagrations (Quigley and Arbelbide 1997). As a result, management actions are being planned (National Fire Strategy 2000) to reduce tree density and fuels, and increase prescribed burning. Concomitant with management activities will be the continuing risk of conflagrations on areas yet to be treated. Vast landscapes have been and may continue to be altered by wild fire. For example, 17% of the Wallowa-Whitman National Forest has burned in the last 10 years. These disturbances will set in motion secondary plant succession that will be influenced by herbivory. The purposes of this Problem Analysis are: 1) summarize existing knowledge of the influence of herbivory on ecosystem patterns and processes, 2) provide application of this knowledge to identify research needs, and 3) provide a research approach to improve knowledge on herbivory effects that can be utilized by managers.

The Problem

In the National Forests of the Blue Mountains, a high percentage of commercial tree species, such as Douglas-fir and true firs, have died as a result of overcrowding on drier sites, drought, and insects (Johnson et al. 1995, Quigley and Arbelbide 1997). Traditional forest management practices (fire exclusion, harvest practices) (Johnson et al. 1995) and livestock grazing (Belsky and Blumenthal 1997) have contributed substanially to the current situation (Hann el al. 1997). Additionally, because of the aforementioned influences, stands exist at higher tree densities (live and dead) than occurred historically, creating ladder fuels that have dramatically increased the risk of conflagrations covering very large acreages. These conditions are typical of forested lands throughout the West (Covington and Moore 1994, Quigley and Arbelbide 1997). In the coming years it can be expected that conflagration fires will continue to occur on forests where excessive fuel build-ups have occurred, and that extensive fuels reduction projects will be initiated.

Following either large fires or fuels reduction treatments, secondary succession of both understory and conifer components is initiated. These areas often become focal points of ungulate herbivory for two reasons: 1) vegetation developing after disturbance is often more palatable to ungulates; and 2) surrounding untreated or unburned forest communities with dense canopies contain limited forage in the understory.

Only rudimentary data exists (Riggs et al. 2000) but strongly implicates ungulate herbivory as a significant agent in altering successional trajectories following disturbance (fire, logging, fuels reduction) in the Blue Mountains. Raedeke (1988) related that selective feeding of forest animals can result in complete changes in the structure, composition, and productivity of the forest. In general, plant communities within exclosures are more diverse than the surrounding forest community subjected to continual herbivory.

Recent literature reviews (Hobbs 1996, Augustine and McNaughton 1998) clearly indicate the important role of herbivory not only in modifying the composition of plant communities, but of ecosystems. In the Blue Mountains herbivory has long been recognized to be a competitive factor in ungulate relationships (Cliff 1939, Pickford and Reid 1943) and in suppressing the understory shrub component (Mitchell 1951). However, the role of herbivory is not well recognized in the predominant management paradigms, both in the Blue Mountains and in all forest ecosystems of the western U.S. (Riggs et al. 2000).

Supporting Literature

As previously noted the issue of forest health in the interior Northwest has been adequately identified (Johnson 1994, Johnson et al. 1995, Langston 1995, Quigley and Arbebide 1997, Hann et al. 1997). These publications also relate the human activities (extensive timber harvest, fire suppression, overgrazing, roading) that have led to the identified problems. Livestock grazing, particularly late in the nineteenth century and early in the twentieth century, has been identified as a causative agent (Belsky and Blumenthal 1997). However, the impacts of increasing numbers of wild ungulates as the twentieth century progressed, has not been well addressed (Riggs et al. 2000). Hobbs (1996) made the case that native ungulates are important agents of change in ecosystems by three processes: regulation of process rates, modification of spatial mosaics, and action as switches controlling transitions between alternative ecosystems states. Huntly (1991) identified the impact of herbivores on plant regeneration as a powerful, yet relatively little studied mechanism influencing vegetational diversity. Wild and domestic herbivores should be considered agents of chronic disturbance, capable of influencing succession, nutrient cycles, and habitat characteristics, to extents equal to episodic fire or timber harvest (Riggs et al. 2000).

Succession

Following disturbance in forests, understory vegetation is often considered undesirable, competitive and in need of control in relation to desired growth of the commercial tree component. In the past, herbicides were commonly used by managers to suppress understory vegetation (Cleary et al. 1978). With the curtailment of herbicide use, controlled grazing with livestock was pursued as an alternative (Sharrow et al. 1992, Huntsinger 1996). However, in some cases herbivory results in unwanted browsing of the regenerating conifers (Reimoser et al. 1999, Reimoser and Gossow 1996). On the other hand, controlled livestock grazing can enhance seedling physiological status (Karl and Doescher 1993) and significantly improve tree growth (Sharrow et al. 1992) in the short term immediately following regeneration treatments. This perceived benefit of herbivory might have underlying negative affects on the ecological integrity of the treated community in the long term, and has not been investigated.

Jones (2000) reviewed the effects of cattle grazing and reported that cover of grasses and shrubs, as well as total vegetation biomass often was reduced. Riggs et al. (2000) reported that in the Blue and Wallowa Mountains of eastern Oregon, understory biomass in ungulate exclosures was 2.1 times greater inside than outside enclosures, and forest-floor biomass was 1.5 times greater inside than outside. Shrub biomass was influenced more by ungulates than was grass or forb biomass. Mazancourt and Loreau (2000) stated that herbivory in general, could lead to species replacement in plant communities. Augustine and McNaughton (1998), in their review stated that species composition of plants can be dramatically altered by selective foraging of ungulates and that this phenomenon is a trademark of plant-ungulate relations. The authors noted that by altering the competitive relations among plants, differential tolerances of co-occurring plant species appear to be important determinants of how woody and herbaceous plant communities respond to herbivory. Anderson and Briske (1995) concluded that herbivore-induced modifications of competitive interactions are most likely to drive species replacement in grasslands characterized by high and consistent resource availability. These conditions often occur after disturbance, making disturbed areas focal points of herbivory (Miller and Krueger 1976, Miller et al. 1981). Hulme (1996) concluded that regeneration is a fundamental process underlying vegetational diversity at a local scale and that temporal and/or spatial variations in the impact of selective seed and/or seedling predators feeding in a density- or frequency-dependent manner may greatly facilitate the coexistence of numerous plant species within the same habitat.

Augustine and McNaughton (1998) went on to include overstory species effects as well, and listed several species of coniferous and deciduous trees that were reported as herbivory intolerant. Healy (1997) found that white-tailed deer interrupted the sequence of stand development and simplified understories in eastern oak forests. Likewise, Alverson and Waller (1997) found that white-tailed deer abundance reduced the size and number of hemlock seedlings and explained the widespread regenerative failure of eastern hemlock. The literature review of Alverson and Waller (1997) also indicated that white-tailed deer substantially altered tree, shrub and herbaceous components of plant communities. Using moose exclosures, McInnes et al. (1992) concluded that browsing by moose influences long-term structure and dynamics of the boreal forest ecosystem, which has important implications for forest ecosystem management. In Poland, Dzieceolowski (1980) found that with exclusion from deer, 25 plant species increased in numbers, but with herbivory only 3 increased. Both number of plant species and number of individual plants were affected by herbivory. Allen et al. (1984) reached similar conclusions in a New Zealand forest where herbivore exclusion increased species abundance of all but unpalatable shrubs and turf-forming species.

Ungulate herbivory shapes vegetation pattern in Northwest U. S. coastal coniferous forests (Woodward et al. 1994, Schreiner et al. 1996). Research by these authors indicated that ungulates maintained a reduced standing crop, increased species richness of forbs, and determined the distribution, morphology, and reproductive performance of several species of shrubs. Woodward et al. (1994) stated that the extent to which herbivores can change forest ecosystem processes might depend on the scale and magnitude of other disturbances. All of the observations are consistent with available information in interior forests.

Forest succession is a function of edaphic factors, the density and viability of seed and sprouting rootstocks, episodic disturbance regimes, and herbivores (Riggs et al. 2000). Herbivory alters the utilization profile of a plant community (palatable versus unpalatable plants) and thus can alter its successional trajectory. Herbivores influence growth, recruitment, and mortality rates of plants and may do so in ways correlated with plant density, frequency, or other neighborhood traits, or with competitive abilities (Huntly 1991). Moreover, herbivory may increase, offset, or generate reciprocal negative interactions among plants (Huntly 1991). Herbivory is highly variable in space and in time, and these spatial and temporal patterns of herbivory can generate structure in plant populations, the existence of which strongly influences community dynamics.

Contrary to the above discussion, Stohlgren et al. (1999) sampled 26 grazing exclosures on grasslands in Colorado, Wyoming, Montana and South Dakota and reported that (1) grazing probably has had little effect on native species richness at landscape scales; (2) grazing probably has had little effect on the accelerated spread of most species of exotic plants at landscape scales; (3) grazing has changed local plant species and life-form composition and cover, but spatial variation is considerable; (4) soil characteristics, climate, and disturbances may have greater effect on plant community species diversity than do current levels of grazing; and (5) few plant species show consistent, directional responses to grazing or cessation of grazing. The study areas were grazed by wild ungulates common to the western United States and domestic cattle or sheep. However, vegetation in many of the sampled locations evolved with large numbers of native herbivores so the plant communities were the evolutionary result of herbivory. Effects in the interior Northwest, which lacked the extensive herds of herbivores, would be expected to be different.

Nutrient cycling

When ungulates foraging reduces biomass and litter, and/or changes species composition, nutrient cycling and energy flow also can be altered (Augustine and McNaughton 1998). Additional causative agents listed by these authors were: 1) altering plant chemical composition during digestion, 2) altering inputs from utilized plants to the soil due to changes in the root system or leaf-litter quality, and 3) altering plant and soil microenvironments. These 3 agents allow animal dung and urine, through mineralization, to contribute directly to the pool of nitrogen that is readily available for plant growth; this process decreases the carbon to nitrogen ratio at the forest floor, which increases litter decomposition rate (Pastor et al. 1993, Pastor and Cohen 1997). In some cases, higher availability of soil nitrogen enhances the productivity of deciduous species, while low availability enhances conifer production (Hobbs 1996).

Herbivore-induced changes in composition of plant species caused by herbivory have important ramifications for nutrient cycling. If palatable nitrogen fixing plants are suppressed by ungulates less nitrogen may be available to the system. Knops et al. (2000) found that in a regularly burned oak savanna in Minnesota, deer exclusion significantly influenced ecosystem nitrogen pools and caused ecosystem productivity to more than double. The authors indicated that deer exclusion increased the abundance of a native legume. Legumes played a critical role in replacing fire-induced nitrogen losses and herbivory negatively impacted these pools by the extirpation of the legume during secondary succession.

Herbivory following some timber harvest systems may create a lack of self-sufficiency in nitrogen on harvested units. If during secondary succession, a nitrogen fixing understory component is present, nitrogen self-sufficiency is maintained, even with large sustained losses of nitrogen in harvested biomass (Bormann and Gordon 1989). Nitrogen fixation by snowbrush (C*eanothus velutinus*) during early succession was sufficient to prevent nitrogen limitation throughout the entire succession sequence (Binkley et al. 1982). Soil carbon also increased 40 to 60 percent over 12 years. However, Tiedemann and Berndt (1972) reported that snowbrush was totally consumed by herbivores and absent outside exclosures. If the nitrogen-fixing plants are removed from the system by herbivory, nitrogen self-sufficiency can be expected to be lost.

Because herbivores feed selectively, their food items usually have higher nutrient contents than vegetation not consumed (Wisdom and Thomas 1996). These same highly digestible plants are also those that if allowed to become litter would decompose relatively rapidly, and thus, are decomposed even more rapidly when passed through the G-I tract of an herbivore. As herbivores decrease the dominance of preferred plants in favor of unpreferred, and less degradable plants, rates of nutrient cycling and energy flow show decline (Pastor and Cohen 1997).

Holland et al. (1996) concluded that aboveground herbivory can increase plant carbon fluxes below ground, thus increasing resources available to soil organisms. However, Ford and Grace (1998) found that aboveground biomass, belowground production, soil elevation and the expansion of the root zone decreased due to herbivore activity. Their conclusion was that herbivores could have a negative effect on soil-building processes.

However, where moose population density was controlled by predation, a positive feedback loop increased current annual production of vegetation through fertilization and browsing (Molvar et al. 1993, Crete and Manseau 1998). Fecal deposition and hence, nitrogen deposition occurred on sites selected by moose for foraging, whereas those not selected by moose did not, of course receive the added nitrogen benefit.

Habitat Characteristics

Herbivory-induced changes in plant species composition of forest understories and overstories have important ramifications for habitats of other species. Changes in understory structure and litter accumulations may be important to bird and small mammal populations. There is the potential that individual plant species and even entire plant communities may be put at risk (e.g.,aspen (*Populus tremuloides*), bitterbrush (*Purshia tridentata*), and Pacific yew (*Taxus brevifolia)*, mountain mahogany (*Cercocarpus sp*)communities) (Parks et al. 1998, Vavra and Riggs 2000) and that vertebrate species dependent on these communities (e.g., cavity nesting birds in aspen stands) may diminish. Population declines have been severe for several neotropical migratory species associated with large, mature forest, grassland, shrub, and young-second growth habitats (Petit et al. 1995). McShea and Rappole (1997) showed that habitat structural diversity, both vertical and horizontal, has a direct relation to the number and density of bird species. The authors gave two principal explanations: 1) increased structural diversity provides more niches and, 2) increased structural complexity decreases nest predator efficiency. The previous section on succession describes the general effects of ungulates on habitat structural diversity.

In managed forest stands the proportion of migrant birds was highest in the early and late years of the rotation and lowest in the middle years (Schwab and Sinclair 1994, Donald et al. 1998). Early successional habitats were more variable in quality than later stages and hence, their bird communities more responsive to the effects of grazing or management (Donald et al. 1998). Herbivory probably had a greater impact on early successional stage because emerging seedlings were rapidly and totally consumed (Riggs et al. 2000), causing composition and structural changes in early successional stands.

In managed forest stands in Pennsylvania, DeCalesta (1994) studied the influence of deer density on songbirds. The author found that upper canopy and ground nesting birds were unaffected by increasing deer densities. However, songbirds that were intermediate canopy nesters declined 27% in species richness and 37% in abundance from the lowest to the highest deer densities. A threshold existed for species richness but the decline in abundance was linear. McShea and Rappole (2000) studied songbirds in protected forests that had deer exclosures. With the exclusion of deer, they found an increase in both intermediate canopy nesters and ground nesters that were migrants. Several resident birds showed a decrease with deer removal. However, these residents were species of stable or increasing populations nationally while the migrants were decreasing species.

Thinning forest overstories appeared to mitigate the influence of heavy deer browsing in a study by Degraaf et al. (1991). Unthinned stands with high deer densities had sparse woody understories and little ground cover, while unthinned stands with low deer density had moderately dense woody understories and moderate ground cover. Thinned stands with few deer had dense, tall woody understories and moderate ground cover; thinned stands with many deer had sparse woody understories and lush ground cover. Understory changes associated with high deer densities were apparently offset by effects of thinning so that thinned stands supported more breeding bird species.

Small mammal populations could be impacted by multiple disturbance effects because of their need for diverse understory vegetation (Clough 1987) that provides cover and food (Carey and Johnson 1995). Small mammals play an important role in maintaining the productivity of coniferous forests of the Pacific Northwest through the dissemination of mycorrhiza-forming fungal spores (Raedeke 1988).

Understory vegetation and coarse woody debris accounted for a major part of the variation in abundance of six of eight species of small mammals in managed forest stands (Carey and Johnson 1995). Among 5 seral stages of forest in the Coast Range of Oregon, Gomez and Anthony (1998) found that total captures of small mammals was greatest in deciduous stands and progressively lower from shrub to old-growth. Clough (1987) found the richness and diversity of small mammals was lowest where the ground and shrub layers were sparse, as on logged areas treated with herbicide or under a mature forest canopy.

Given that small mammals need diverse understories to maintain viable populations, intensive herbivory could negatively impact species diversity, richness, and abundance of small mammals, especially if logging practices remove most of the remaining slash from the site. Literature exists on the impacts of livestock grazing on small mammals, but little is known about effects from wild ungulates (McShea, personal communication) Joubert and Ryan (1999) observed small mammal assemblages on heavily grazed and moderately grazed lands and found that larger and more diverse small mammal assemblages were found on the moderately grazed lands. Reynolds and Trost (1980) found small mammal diversity and relative density were reduced on grazed versus ungrazed sagebrush habitats. However, Johnson (1982) refuted the findings of Reynolds and Trost (1980) through his findings that small mammal abundance was more specific to background site conditions than to grazing treatments. Livestock grazing caused a 50 percent decrease in abundance of small mammals in grazed versus grazing-excluded areas in a desert wetland (Hayward et al. 1997). On the other hand, Heske and Campbell (1991) and Bich et al. (1995) found that livestock exclusion promotes an increase or decrease in rodent population, depending on species.

Brooks (1999) stated that research has demonstrated that even-aged regeneration harvests, notably clearcutting, can have major and long-lasting detrimental effects on forest amphibians. However, the author found that crown thinning in the presence of high and low deer densities did not have a significant effect on the number of redbacked salamanders. He suggested that a stand disturbance, where a large percentage of the canopy was retained and that resulted in an increase in cover of understory vegetation, would result in no long-term effect on forest-floor salamanders.

Human disturbance

Herbivory does not affect habitat characteristics equally across landscapes. Ungulate distribution is the result of many complex interacting factors. Ungulates confront their environment at several scales from regional down to feeding patch (Vavra and Riggs 2000). The attractiveness of habitats chosen at any particular scale depends not only on food supply, but also on food-independent factors such as terrain conditions, climate, edge effect, interference and competition impact, and thermal and hiding cover (Reimoser and Gossow 1996). Road density and traffic have a negative influence on elk distribution, in that elk avoid habitats near roads open to traffic (Rowland et al. 2000), with avoidance increasing with rate of traffic (Wisdom 1998). By contrast (Wisdom 1998) found that mule deer selected areas increasingly closer to roads with increasing rates of traffic, with the magnitude and direction of selection directly opposite of elk (Wisdom 1998). In a related article, Johnson et al. (2000) observed that in spring mule deer resource selection was inversely affected by elk. Interferences, such as roads, then, may actually cause a loss of habitat (Wisdom 1998, Rowland et al. 2000), a concentration of animals on a smaller portion of the landscape, and an increase of herbivory effects in the areas selected by the ungulates.

Increased levels of off-road motorized and non-motorized recreation, particularly all-terrain vehicles (ATVs), horseback riding, mountain biking, and hiking, also may substantially influence ungulate distributions, and hence, the spatial variation and magnitude of herbivory effects on forest landscapes. The comparative and cumulative effects of these off-road recreational activities on deer and elk, however, have not been studied under experimental conditions that use appropriate treatments, treatment levels, and controls. Such research was recently proposed for Starkey, and a pilot study is now underway (Wisdom and Johnson 2001). If this study is implemented over 3 or more years, results will assist managers in further evaluating the effects of human disturbances on ungulate herbivory as well as on animal performance.

Implications

The previous sections have dealt with the impacts of herbivory on succession, nutrient cycling, and habitat characteristics. The potential role of herbivory as an important agent of chronic disturbance, and the resultant changes in successional trajectory imply that ungulates could be considered keystone species (Riggs et al. 2000). Disturbance agents rarely act alone (Rogers 1996). Other agents, such as drought and fire, or disease and insects most often act in concert across both time and space. To what extent and where herbivore impacts might be significant depends on the herbivore species, population densities, patch choices, and landscape patterns (Hobbs 1996). Additionally, scale is important in that small areas of disturbance may be used more heavily than large ones (Scott et al. 1982). In Arizona, clear-cuts smaller than 20 acres received heavy use by deer and elk, but evidence of activity declined as opening size increased (Reynolds 1966).

When ungulates modify the structure and composition of vegetation there is a cascading effect throughout the ecosystem. The suppression or elimination of nitrogen fixing plants reduces nitrogen accretion (Tiedemann and Berndt 1972, Bormann and Gordon 1989, Knops et al. 2000, Riggs et al. 2000). Likewise, changes in composition of plant species caused by herbivory may result in litter accumulations that are degraded at a slower rate (Pastor and Cohen 1997), thereby affecting energy flow and nutrient cycles. The outcome of decreased nutrient availability is a loss of forest productivity over time

(Riggs et al. 2000) and a potential change in overstory composition (Hobbs 1996, Alverson and Waller 1997).

The removal of fine fuels by ungulates may reduce ground fire frequency, but actually increases the opportunity for crown fires by enhancing the development of unpalatable trees and shrubs, providing ladder fuels (Hobbs 1996). Belsky and Blumenthal (1997) attributed the lack of understory and the development of ladder fuels to livestock grazing. Unpalatable shrubs and conifers that may increase as herbivory reduces the amount of palatable shrubs present, often contain secondary compounds that are flammable, more so than the palatable species, further increasing the risk of high intensity fires (Hobbs 1996). After fire or other disturbance, as secondary succession occurs and food sources for herbivores increases, use by herbivores will also increase (Clary and Larson 1971, Lowe et al. 1978), possibly leading to plant composition changes and continuing the cycle of fire-prone landscapes.

In the western United States, aspen and riparian plant communities have been identified as two of the most degraded of community types. Aspen communities in the Intermountain West have declined 60 percent since European settlement (Amacher and Bartos 1997). Riparian areas are generally in degraded conditions because of past and even present improper livestock grazing (Armour et al. 1994, Fleischner 1994). The role of wild ungulates in maintaining these degraded conditions following the removal of livestock is often ignored. However, Opperman and Merenlender (2000) found that deer herbivory substantially reduced the rate of recovery of woody riparian species within degraded riparian corridors where livestock had been removed. Kay (1994) reported significant effects of elk herbivory on willows (*Salix* spp.) in Yellowstone National Park.

Likewise, aspen communities often lack regeneration because of herbivory by livestock, wild ungulates, or both (Kay and Bartos 2000). Old-age aspen stands that have not regenerated for 80 years are common in the Intermountain West (Mueggler 1989).

Many factors other than food regulate the distribution of ungulates (Coughenour 1991b, Reismoser and Gossow 1996). Interference factors, such as postfire rehabilitation, logging, and fuels reduction practices may also redistribute ungulates across landscapes because of increased road traffic (Wisdom 1998). Herbivores may then be concentrated on less than the totally available habitats, increasing the deleterious effects of herbivory on used habitats. In that light, Wisdom and Thomas (1996) demonstrated how road density can substantially change the distribution of elk and the resulting areas where foraging occurs.

High deer densities may reduce bird species diversity in forests, but selective logging practices may mitigate bird species diversity in the presence of concomitant high deer densities (Degraaf et al. 1991). However, DeCalesta (1994) found that in managed forests the decline of songbird richness and abundance was linear with increasing deer numbers. The disparity in reports suggests that the extent of overstory removal, the numbers of deer (nutrient demand) and the inherent productivity of the landscape are important considerations. In the short-term, fire and other disturbance effects usually reduce small mammal numbers, but in the long term, following disturbance, an increase in numbers is likely due to the surge of herbaceous and seed-producing plants (Ream 1981). Although the influence of wild ungulates on small mammals is not well documented (McShea, personal communication), livestock grazing has been shown to have an effect (Reynolds and Trost 1980, Heske and Campbell 1991, Birch et al. 1995).

Avian and small mammal richness and abundance then, may be initially impacted by disturbance like fire or logging, and may change over time in quite different ways according to the concomitant intensity of herbivory.

Ungulates are known to utilize areas of recent disturbance because of the relatively large quantities of palatable and nutritious forage present (Miller and Krueger 1976, Miller et al. 1981, Irwin and Peek 1983). In a previous section we have shown that ungulates can change the composition of understories to more unpalatable species. These same species are often less nutritious, often because they contain secondary compounds which inhibit digestion (Hobbs 1996). Thus, if long-term herbivory has affected plant composition and nutrient cycling in forest vegetation, those changes should cause density dependent, negative feedback effects to ungulate population dynamics and weight gain of livestock (Klein 1970, Irwin et al. 1994). A recent compilation of productivity in selected elk herds in the Northwest (Cook 1999) (Table 1) clearly indicates that in some areas both east and west of the Cascade Mountains declines are occurring. Although providing large elk populations is not a primary objective on Forest Service-administered lands, lost recreation opportunities may be important. Schommer (1991 a,b) reported that deer and elk hunter recreation-days declined 350 and 210 percent, respectively, from 1975 to 1990 on the Wallowa-Whitman National Forest. This decline resulted in an annual loss to northeastern Oregon communities of 8 to 10 million dollars. If declining productivity of big game and declining local revenues are linked to ecological conditions in the National Forests, then criticism of the Forest Service by the public is possible.

Table 1. **POPULATION TRENDS OF SELECTED ELK HERDS IN THE NORTHWEST USA**

Herd	Change
- **Blue Mtns (WA)**	**30% decline**
- **Olympic (WA)**	**30% decline**
- **Nooksack (WA)**	**80% decline**
- **North Rainier (WA)**	**50 – 70% decline**
- **South Rainier (WA)**	**30 – 50% decline**
- **Blue Mtns (OR)**	**30% decline**
- **Clearwater Basin (ID)**	**25% decline**

Fire suppression, insects and diseases, herbivory and decreased logging have all interacted to produce conflagration-prone landscapes in the western United States. Given a repetition of weather conditions that occurred in the summer of 2000, large wildfires could continue in the West. Spending on postfire rehabilitation projects has increased during the past decade and probably will continue to increase (Robichaud 2000). The effectiveness of these projects may be in jeopardy given our lack of acknowledgement of herbivory effects following disturbance (Riggs et al. 2000). Current databases on postfire succession do not include herbivory as a component (Stickney and Campbell 2000). These same authors went on to say that most studies of succession in the northern Rocky Mountains have been reconstructions of plant community change by sampling forest stands of different ages, with the underlying assumption that each sampled stand of different age will succeed to the next older sample. The authors warned that combining the fragmentary records of stand ages for sampling can lead to unknown and possibly substantial errors. Ignoring herbivory effects would make matters worse. Stickney and Campbell (2000) further stated that the lack of a continuous record of change in composition prevents recognition of the emplacement, extirpation, and development patterns of species within the succession that collectively constitute the seral pathway.

Hulme (1996) summarized the situation by stating that the role of seed/seedling predators in vegetational diversity (and therefore avian, mammalian and amphibian diversity) will remain a matter of speculation until directly comparable studies are undertaken on the relative rates of plant recruitment in the presence and absence of seed and seedling herbivores along gradients of plant species diversity. If variation in herbivory regimes can modify the influence of episodic disturbances, then the significance of herbivores as change agents in the ecosystem is important to recognize in disturbance research (Riggs et al. 2000). The authors also firmly stated that this would require much more than retrospective analysis of a handful of old exclosures. Scientists must be challenged to integrate herbivory into disturbance research at scales meaningful to managers. Huntly (1991) earlier voiced the same opinion. Huntly specifically believed that field studies should be designed to evaluate the contributions of particular mechanisms to herbivore effects, not simply document whether plant communities differ when herbivores are present or absent. Long-term and large-scale studies are needed, as well as shorter-term and smaller scale studies in which the environments are manipulated so the full range of conditions can be evaluated.

Hobbs (1996) believed that the ability to fully understand and predict the ways that ungulates modify ecosystems remains a large task. He further stated that our predictive ability depends on the ability to "scale-up" findings obtained in studies on physiology and behavior at the level of the individual animal to studies of populations, communities and whole ecosystems.

Research Overview

The overall goal of future research for the Elk, Deer, and Cattle Interactions Team and its research partners is to quantify and integrate factors that affect ungulate resource selection in order to provide managers with reliable information to evaluate effects of management alternatives on long-term stability of ecosystems, ungulate productivity, and other wildlife populations (Strategy for Ungulate Research 2001). Part of that goal is understanding the role of ungulates in driving ecosystem processes within the Blue Mountains Ecoregion, e.g., effects of herbivory on forest structure and succession and associated ecosystem properties. This effort is presented in this Problem Analysis.

Research conducted by partners outside SEFR will address topics on how ungulate productivity is driven by ecosystem characteristics include nutrient intake, competition among ungulates, and management activities (silviculture, grazing, recreation, roads/traffic, hunting) that affect distributions and productivity of wild ungulates and the role of predation (both hunters and mammalian predators) with ungulate productivity (Strategy for Ungulate Research 2001).

The proposed research will fulfill several goals, objectives and priorities of the Forest Service Strategic Plan, the Strategic Plan of the PNW Research Station and the Charter of the Managing Disturbance Regimes Program (MDR) within the Pacific Northwest Research Station. Table 2 illustrates specific portions of the Forest Service Strategic Plan Goals and Objectives (USFS 2000), and the PNW Station Research Goals and Priorities (PNWRS 2002) applicable to the Problem Analysis. Within the Charter of the MDR research potentials from this Problem Analysis will address Problem 1, Integrated Issue: Managing disturbance regimes to restore and enhance ecosystem health in the Pacific Northwest and Alaska. Under the Component category, several problems will be addressed; 3) Understanding and managing fuels, fire, and smoke; 4) Understanding and managing forest and rangeland dynamics; 6) Understanding and managing disturbance effects on plant and animal habitats; and 7) Understanding and managing the influence of ungulates on disturbance processes and succession.

The problem is important to managers faced with delivering programs for National Forest lands for sustainable forest ecosystem management, watershed health and restoration, recreation and compatible road systems. State Fish and Wildlife agencies charged with maintaining a viable recreation resource of fish and game, as well as healthy populations of non-game wildlife, need the best information possible to establish management objectives for ungulate populations to provide sufficient game animals for harvest without compromising other wildlife (non-game habitat) or ecological values (healthy biological communities). Additionally, the problem is important to the public, which has voiced strong concern for the environment, including such things as biodiversity, and water quality and quantity; access to National Forest lands for recreation; and liberal opportunity for consumptive recreation (hunting and fishing).

To better identify research needs, two meetings were held in the fall of 2000. La Grande Ranger District personnel, Range Conservationist and Fisheries/Watershed Staff, and the Area Plant Ecologist supported problem identification. Their needs involve identification of the potential for prescribed disturbances (fire, fuels reduction, logging) to improve upland forage conditions and the possible redistribution of herbivores (wild and domestic). Particular interest was voiced for the potential decreased use of riparian zones. Along a similar vein, concern was expressed for continued effort in determining the impact of herbivory on riparian hardwoods and the long-term projections of such. In areas where prescribed disturbance or wild fire occurs knowledge of successional trajectories following those disturbances is needed. Wildlife Biologists from the Malheur, Umatilla, and Wallowa Whitman National Forests, and the Regional Range Conservationist were involved in the second meeting. This group was impressed with the results of the initial findings from the Starkey Project. They were unanimous in their belief that the information needed delivery in a form for managers to use. In regards to the new direction for research, the group again gave unanimous support. Feedback from the meeting included continued effort on the relationship of livestock grazing and big game habitat use/selection, forage consumption and nutrition/energetics. Information on the impacts of wild ungulates on plant communities, diversity and succession both with and without disturbance is needed. Hardwood utilization in both uplands and riparian zones was noted as an area of concern. Specific questions asked were: do wild and domestic ungulates affect hardwood communities differently and who eats what and when?

Benefits accrued to managers will be the development of tools to provide better management of landscapes (silviculture, prescribed fire, fuels reduction, road access, livestock grazing, etc.) where ungulates are potentially important agents of chronic disturbance and may alter successional trajectories. State fish and wildlife agencies should be able to manage populations of big game with known impacts and tradeoffs on other wildlife and ecological resources. Research products will contribute to the pool of knowledge being developed to reach the goal of sustainable forest ecosystem management. This will be the prime benefit to the public. Enhancement of the recreation

Table 1. Goals, objectives and priorities of the Forest Service Strategic Plan (2000) and the PNW Strategy for the Future (2002) that can be addressed by the research outlined herein.

	Starkey Potential	Starkey Priority
Forest Service Strategic Plan Goals		
Ecosystem health		
Obj. 1.a Improve and protect watersheds	X	1
1.b Provide ecological conditions for species	X	1
1.c Restore forest and grasslands to health	X	1
Multiple benefits to people	X	
2.a Improve recreation	X	2
2.c Improve sustainable levels of use	X	1
Scientific and technical assistance	X	
3.b Increase the effectiveness of information	X	1
3.c Improve the knowledge base	X	1
Research Priorities for Entering the 21st Century PNWRS		
Goal 1. Understanding ecological, social and economic systems		
Priority 1.1 Understanding terrestrial ecological systems	X	1
Priority 1.2 Understanding aquatic and riparian ecological systems	X	3
Goal 2. Asses the status and trend of ecosystems And natural resources and their uses		
Priority 2.3 Develop monitoring protocols and data analysis techniques	X	1
Goal 3. Develop science-based options for informed management		
Priority 3.1. Manage riparian and aquatic area for multiple values	X	2
Priority 3.2 Restore ecosystems at risk	X	1
Priority 3.3 Develop recreation options	X	2
Priority 3.4 Produce wood within sustainable frameworks	X	2
Priority 3.5 Create operational strategies for conservation of biodiversity	X	1
Goal 4. Communicate science findings and enhance their application		
Priority 4.1 Respond to emerging issues	X	2
Priority 4.2 Bridge the gap between information generation and its use	X	1

experience by providing more esthetically pleasing landscapes with a diversity of plant communities and associated wildlife species and development of environmentally compatible road systems is an additional benefit.

The Starkey Experimental Forest and Range is critical to the implementation of the proposed research. At SEFR use of the telemetry system allows exact verification of ungulate use of various plant communities and disturbance regimes. Ungulate density is known and manipulation of such is possible. Various confounding influences such as roads, traffic and ATV use can be identified and controlled. Development of exclosures, stocking density treatments, and vegetation manipulation can be centralized and controlled. Research at scales (both spatial and temporal) applicable to management is not possible without a facility like SEFR. Most importantly, the 10+ years of data on ungulates and plant communities is invaluable for the proposed studies.

The identified problem, to determine the effects of ungulate herbivory and management on ecosystem patterns and processes, is an important component in the development of new management plans for National Forests in the West. Exact solution is not possible, but the next ten years of research will contribute to the knowledge base managers need in their journey toward sustainable forest ecosystem management and provide new questions for further research. Sustainability is not an endpoint, but a trajectory or pathway that does not end (Vavra 1996). Information obtained from addressing the identified problem will provide better direction to that trajectory.

Research Approach

New directions of research for the Elk, Deer, and Cattle Interactions Team (EDCI) require the integration of an experimental approach with a modeling approach. Two possibilities exist, a) an approach that uses empirical results to build models, or b) an approach that builds hypothetical models based on extant information, and then tests model predictions via empirical experiments conducted at various scales. The latter approach best fits the EDCI as it provides for the integration of a wide array of specific research efforts conducted at various scales. This approach will also allow immediate interaction with the Interior Northwest Landscape Analysis Systems Project.

The issue of scale is critical in the design of research so that results are meaningful and readily transferable to management. The proposed research will include intensive projects designed to identify forage preferences of ungulates at the patch (small) scale as the basis for predicting ungulate effects on successional trajectories. Projects on SEFR that evaluate the effects of ungulates on succession following disturbance (fuels reduction and prescribed fire) and the influence of these disturbances on ungulate distribution will occur at the mid-scale, more applicable to management. These projects will allow a steady stream of data collection, in short through long temporal scales, following disturbance. Previous studies have not been designed this way, but have instead been retrospective analyses of exclosures (Riggs et al. 2000) whereby exact mechanisms could only be identified by speculation. The suggestions and concerns in ungulate effects research design expressed by Huntly (1991), Hulme (1996) and Hobbs (1996) are incorporated into the research designs presented in this Problem Analysis.

The overriding problem to identify is how ungulates modify successional trajectories in interior forest ecosystems. Some effort should be given to illustrate the potential for manipulation of herbivore factors (species, season of use, intensity of use) to develop different landscapes. Interactions are the next level of problem. If ungulates do in fact, modify the structure of forests, then various ungulate mixes should result in potentially different forest structures which would have various susceptibilities to fire, and the type of fire, e.g., ground or crown; large or small. Episodic disturbance, like fire, logging, or fuels reduction provides an interaction with herbivory whereby the influence of herbivory on successional trajectories is magnified following the disturbance. The third level of problem deals with the secondary effects of altered forest structure. Nutrient cycling and energy flow may be modified by herbivory. Potentially, changes in forest productivity and further changes in structure may occur. Vegetation changes may lead to altered habitats and a reduction in biodiversity.

The proposed research direction will be facilitated by several completed and ongoing studies. Exclosure research at Hoodoo, Mottet, and Hall Ranch (Riggs et al. 2000) provide baseline data for development of models on grand fir (*Abies grandis*) and Douglas-fir (*Psuedotsuga menzesii*) habitat types. Ongoing Research at Starkey with resource selection functions (Johnson et al. 2000) and the forage allocation model (Johnson et al. 1996), and new research (see following section, studies 1.1 and 2.1) will provide the basis for a regional herbivory model. The resulting model will be incorporated with state and transition models (Hann et al 1997 and Hemstrom et al. 2001) now in use to include herbivory effects. The ongoing elk stocking rate study and proposed studies 2.2, 2.3, and 3.1 will provide information on the effects of herbivory and disturbance on changes in successional trajectory understory vegetation. Finally, the third level of research problem, the role of ungulates in ecosystem function will be addressed with research partners and new funding sources. These are identified in studies 4.1, 4.2, 4.3, and 4.4. The end product is an ungulate keystone effects model.

The three levels of research problems identified are addressed by the following proposed studies. The resulting models should assist managers in answering questions regarding the role of herbivory in successional trajectory of forest understories and the same following disturbance; and how these trajectories in turn, will influence biotic and abiotic factors of ecosystem function. Managers will have information on matching the level of disturbance with ungulate numbers to develop preferred vegetation assemblages and the resultant faunal assemblages.

The following studies and conceptual designs are proposed to address the three levels of problems just described. In many cases, additional funding and/or scientific skills will be required to initiate specific studies.

Proposed Research

Current funding

1. MULTI-SCALE MODELING AND VALIDATION OF UNGULATE HERBIVORY EFFECTS ON ECOSYSTEM PATTERNS AND PROCESSES

Study 1.1 Modeling Effects of Ungulate Herbivory on Forest Vegetation Dynamics.

Background: While succession in forests is typically assumed to progress and regress predictably to and from climax plant associations (i.e., based on traditional succession theory of Clements [1936]), evidence is growing that succession can be controlled or altered in non-linear ways by chronic herbivory (Riggs et al. 2000, Jenkins and Starkey 1996, Peek et al. 1978, Schreiner et al. 1996). Consequently, forest succession may operate as a set of states and transitions, much like the models developed and validated for rangeland ecosystems (Westoby et al. 1989, Laycock 1991). Indeed, it now seems possible that the veracity of many "climax" associations is questionable on this basis (Peek et al. 1978, Riggs et al. 2000, Schreiner et al. 1996). Variation in the herbivory regime (i.e., variation in the herbivore species, and/or timing, duration, or intensity of grazing) can vary the trajectory of forest succession, and even vary its endpoint. Thus, to predict landscape vegetation dynamics with confidence, one must understand the herbivory regime and its influence on forest succession in the form of vegetation states and transitions and potential thresholds. Moreover, one must understand the interactions of herbivory with episodic disturbances of fire, insects, disease, and silvicultural treatments, all of which can vary dramatically in frequency and intensity and their subsequent effects on succession. Finally, one must understand these relations at scales relevant to management and science.

Information Needed: Conceptual and predictive models need to be built and validated at multiple spatial scales to understand and evaluate the effects of ungulate herbivory on dynamics of understory and overstory vegetation in a holistic manner for forests of the Blue Mountains. These models could operate as state and transition models of succession that account for effects of herbivory in combination with all other major disturbance regimes, as such regimes change both the understory and overstory composition and structure of forests and the associated ecosystem processes. Moreover, the potential for ungulate herbivory to dramatically affect forest understories (Riggs et al. 2000), combined with the potential for substantial interaction effects with other disturbance regimes, demands that multi-scale models be designed and tested as part of formal research on herbivory.

Models built at stand and watershed scales are needed, with additional scaling to subbasin and province likely required for robust management inference. These multi-scale models are proposed as "umbrella" models that will integrate research findings from all herbivory and related studies proposed in this problem analysis and in the Starkey research strategy. The models specifically need to evaluate the effects of herbivory in concert with joint effects of fire, insect and disease, and other disturbance events, including human activities. All herbivory studies proposed in our problem analysis would provide parameter estimates on which these multi-scale models would be built and/or validated.

Study Design: Models of forest succession now exist in research and management to address the dynamics of change in forest overstories in relation to disturbances of fire, insects, disease in the Blue Mountains. These models were built and parameterized with the use of the Vegetation Dynamics Development Tool (VDDT, Beukema and Kurz 1995, as cited and used by Hann et al. 1997, Hemstrom et al. 2001, Hemstrom et al. in press).

We will use a similar approach for the *a priori* construction of herbivory-disturbance regime models to design and integrate all proposed herbivory research, as this type of modeling provides the greatest utility for robust, multi-scale research inferences and management applications. We will specifically build on existing VDDT models of overstory succession now in use by National Forests of the Blue Mountains.

We will make the following changes to these models to accommodate the herbivory regime for management and research: (1) both overstory and understory dynamics of forest succession will be modeled, including potential interactions between each; (2) effects of herbivory will be modeled as a single agent, and as an agent interacting with disturbances of fire, insects, disease, silviculture, and other human activities; (3) models will be spatially- and temporally-dynamic, providing capability to reliably predict effects on succession over small or large areas, and over short or long time periods; (4) models will be built for the major forest vegetation types of Blue Mountains (grand fir, Douglas-fir, and ponderosa pine types); (5) models will explicitly accommodate variation in the herbivore species, and/or timing, duration, or intensity of grazing as input variables; (6) study designs outlined in our problem analysis will be refined to address recognized weaknesses in the *a priori* models of herbivory effects, particularly to address parameters estimates that most need improvement through research; and (7) *a priori* models will be validated with the implementation of all research proposed in this problem analysis in combination with past and on-going research on effects of non-herbivory disturbances on vegetation dynamics.

Stand–level models will be built directly from results of past, traditional, fine-scale research as well as stand-level research proposed in this problem analysis (e.g., see studies below). Models will be developed for each plant community type (or cover type) and structural stage for which research is targeted (primarily ponderosa pine, Douglas-fir, and grand fir types and associated structural stages). For modeling and mapping at stand scales, stands would be defined in terms of the remote-sensing methods used in relation to the pixel size (mapping unit) employed; this will require explicit, *a priori* development of accurate methods to translate stand-level research results to collections of pixels that define a stand and groups of stands on a landscape. For watershed-, subbasin-, and province-level modeling, effective scaling of both "bottom up" and top down" processes is needed (Peterson and Parker 1998); bottom-up processes consist of local mechanisms that operate at specific locations (fine-scales), whereas top-down processes consist of regional mechanisms that operate over large geographic areas (broad-scales). Both types of processes must be integrated in a nested, hierarchical framework for multi-scale modeling (Peterson and Parker 1998), developed as a formal study, as opposed to modeling as an afterthought. Because spatial variability and spatial characteristics vary dramatically and uniquely by spatial scale in relation to bottom-up and top-down processes, careful design and testing of models is needed as part of formal research, particularly as an effective mechanism for integrating all herbivory studies described here in relation to other disturbance events of fire, insects, disease, and human activities. The foundation for such modeling may be the state-and-transition models developed for forest potential vegetation types in the Blue Mountains from prior broad-scale modeling work (Hann et al. 1997, Hemstrom et al. 2001).

Advantages of Approach: The modeling approach described above provides the following advantages for herbivory management and research: (1) all disturbance regimes and management prescriptions for all major forest vegetation types are accounted for at any spatial and temporal scale desired; (2) the role of herbivory can be explicitly modeled in relation to all potential interactions with other disturbance regimes and management prescriptions on landscapes and over time; (3) sensitivity and validation of herbivory effects in relation to the interactive effects with other disturbance regimes can be tested in relation to a holistic suite of management prescriptions, as applied or hypothesized for any spatial scale and time frame; (4) spatial and temporal scales of effects can be modeled as dynamic processes, with scales adjusted to the appropriate biological context of the predictor and response variables of interest; for example, the effects of wildfire and herbivory operate as "top-down" processes over large landscapes, but also manifest in different ways at local scales as "bottom-up" processes (see Peterson and Parker 1998 for details about these processes and associated scales).

Both types of processes and associated scales can be accommodated efficiently with state and transition models, as expressed through the structure of VDDT models. For example, the response of birds or small mammals to top-down and bottom-up processes can be evaluated at scales of an animal's home range or the range of a population, both of which are unique to each individual or population of a species that might be targeted as a response variable. This dynamic, hierarchical scaling of predictor and response variables, and associated ecological processes (e.g., use of hierarchical spatial scales in Fig. 3), is a fundamental underpinning of herbivory research and its applications in management.

Lead Scientists: Mike Wisdom, Miles Hemstrom (PNW Research Station), Alan Ager (Umatilla National Forest), John Kie and Marty Vavra (PNW Research Station)

2. EFFECTS OF UNGULATE HERBIVORY ON FOREST SUCCESSION

Study 2.1. Retrospective effects of ungulate herbivory on forest structure across diverse environmental conditions in the Blue Mountains

Background. Feeding strategies of ungulates can be considered plastic in regard to forage availability and season of use. Ungulates can select various individual species within forage classes, grass, forbs or shrubs; as well as vary the amount of various classes of forage in the diet. In order to predict the effects of ungulate herbivory on a regional scale, data on forage preferences must be collected across a wide range of environmental variables that encompass different plant communities and across changes in nutritive quality that occur with season of the year.

Information needed. Limited exclosure data indicates ungulates significantly alter post-disturbance succession in the Blue Mountains (Riggs et al. 2000). Forest and understory composition and structure have serious implications for fire susceptibility, biodiversity, and productivity. We need to develop models that will predict the effects of herbivory on the composition and structure of forest stands across the Blue Mountains. We do not know the forage preferences of ungulates under post-disturbance conditions.

Study design. Seasonal forage preferences by elk, mule deer and cattle have to be identified to construct successional models for various plant communities common to the Blue Mountains. Additionally, post-disturbance successional trajectories with and without herbivory from exclosures throughout the Blue Mountains are required as supplementary data to be used in model development (see study 1.1). The National Forest System maintains Evaluation Plantations across the Blue Mountains that are fenced to exclude ungulates. These exclosures provide an excellent laboratory from which to develop region-wide forage preference models. This study will be initiated in 2001 with a reconnaissance of the exclosures and limited data collection on a pilot basis. Intensive sampling will begin summer of 2002 utilizing tractable animals to develop forage preference models. This study will provide baseline information for the development of herbivory models used in other sections of the project.

Advantages to approach. It is necessary to develop regional models of herbivore forage preference to provide the basis for further modeling efforts on herbivory impacts on forest vegetation dynamics. Utilizing the Evaluation Plantations is a cost effective way to accomplish this goal as fences are already in place. However, there is a need to sample recently disturbed (logged) plant communities to obtain data on early successional stages.

Lead scientists. Marty Vavra, John Kie, Mike Wisdom (PNWRS); Bob Riggs (Boise Cascade Corp.); Alan Ager, Umatilla National Forest; John Cook (NCASI)

Study 2.2. Effects of ungulate herbivory following fuels reduction on forest structure and succession

Background: Past exclosure studies have indicated that ungulates alter the trajectory of succession. However, current information is derived from retrospective studies of long-term exclosures (Riggs et al. 2000). Mechanisms influencing the observed plant communities are a matter of speculation since continuous data collection was not accomplished nor were consistent grazing treatments applied among exclosure locations. Studies are needed that document the influence of ungulate herbivory from the time of disturbance. Additionally, with the exception of one 1.6 ha exclosure that allows cattle use only (Riggs et al. 2000), there are no data on the influences of individual ungulate species or stocking density on succession.

Information needed: In order to develop landscape level models of ungulate effects on succession (study 1.1), data must be collected that identifies cumulative effects of ungulate herbivory, the roll of individual species of ungulate and the influence of stocking density of each ungulate. A continuous data stream from time of disturbance through the successional process is needed.

Study design: Three-way exclosures and stocking density paddocks will be built on locations immediately following fuels reduction treatments. Three-way exclosures will be used to document the successional trajectories over time as influenced by cattle, mule deer and elk; elk and mule deer; and total ungulate exclusion. Each exclosure will be replicated three times. Frequency of occurrence and percent basal cover will be recorded annually for each treatment. Standing crop will be collected from caged plots located in each treatment.

Enclosed paddocks will be constructed on sites where fuels reduction treatments were applied. These enclosed paddocks will be used for single species stocking density studies. Each of three replicates will contain individual paddocks that will enclose cattle, mule deer, and elk at high and low stocking densities. Animal numbers and/or days of use will be manipulated to achieve 25% and 50% forage utilization, based on weight. On-site evaluation of utilization will have to be made and adjusted for individual ungulate species preference for different forage classes. Early and late season grazing paddocks will be constructed. Frequency of occurrence, percent basal cover, and standing crop will be recorded annually. This study will provide data for study 1.1 and provide sampling locations for study 4.4.

Advantages of approach: The study as designed provides a continuous data stream of plant succession as influenced by ungulate species, species interactions, and stocking densities. Information will be utilized in model development under study 1.1. Detailed studies from point of disturbance event over time have not been accomplished. Previously, a limited number of exclosures were established and data collected at erratic intervals and by inconsistent methods. Fragmentary data from disparate stands can lead to unknown and possibly substantial errors. This design however, will provide a continuous record of change in composition that allows recognition of the emplacement, extirpation, and developmental patterns of species within the successions that collectively constitute the seral pathways as influenced by various herbivory regimes. The design also provides the laboratory for conducting study 4.4. Additionally, forage quality and quantity, and diet preference information collected can be utilized by cooperators on other aspects of ungulate research (Strategy for Ungulate Research 2001).

Lead scientists: Marty Vavra, John Kie, Mike Wisdom (PNW Research Station); Bob Riggs (Boise Cascade Corporation); Tim DelCurto (EOARC-OSU)

Study 2.3 Effects of varying densities of ungulates on forest structure and succession

Background: The effects of high densities of native ungulates on successional patterns of forest growth is necessary when attempting to evaluate harvest strategies, grazing strategies, and populations of non-game species in areas of varying herbivore densities. Large herbivores including both native species, such as elk and mule deer, and introduced species such as cattle have the potential to profoundly affect the structure and function of ecosystems (Bowyer et al. 1997, McNaughton 1985, Turner et al. 1997, Hobbs 1996, Stewart et al. 2002). The Starkey Experimental Forest and Range is ideal for conducting research of this nature. The automated telemetry system on Starkey, in conjunction with the ability to manipulate population densities of elk within the experimental forest, allow for research on the effects of varying densities of large herbivores on plant production and successional patterns. Moreover, these densities may be maintained over time and the effects on forest succession may be evaluated.

The Syrup Creek study area was divided into two parts, and since 1998 two different population densities of elk have been maintained. The east half of the Syrup Creek pastures has been stocked with a high-density population of elk (1 elk : 12 acres) and the west pasture has been maintained with a low-density population of elk (1 elk : 60 acres). The effects of these varying densities of elk on plant production have been monitored from 1998 through 2001 as a graduate student research project. Four major habitat types were defined for the study area 1) mesic forest characterized by grand fir (*Abies grandis*) overstory, 2) xeric forest dominated by ponderosa pine (*Pinus ponderosa*) overstory, 3) logged forest sites that were harvested during 1991and 1992, 4) xeric grasslands dominated by a few species of grasses such as Idaho fescue (*Festuca idahoensis*) and forbs such as low gumweed (*Grindelia nana*) (Stewart et al. 2002). To document the differences in levels of herbivory with controls (no herbivory) exclosures (32-m per side) were built with 3 replications in each study area and habitat type.

This graduate research project examined the effects of population density with grazing intensity and plant productivity. The telemetry system allowed for an independent measure of grazing intensity that is not based upon vegetation measurements, to date herbivory studies have been unable to evaluate grazing intensity independently of vegetation monitoring. Moreover the effects of varying population densities on animal condition was also evaluated from the handling facilities maintained on Starkey.

Information Needed: Information as to the long term affects of population densities of native ungulates on forest productivity is important in evaluating harvest strategies and non-game research in the pacific northwest. Moreover, forested areas in the pacific northwest are also used for grazing of domestic livestock and the effects of populations of native ungulates is important to understand prior to establishing grazing strategies in a given area. The knowledge of the effects of native ungulates on the composition of both woody and herbaceous plant species may then be applied and evaluated in multi-species systems.

Study Design: The design of the study will utilize the existing study design from the previous research including designated habitat types, exclosures, and densities of animals. The two population densities will be maintained in their current areas to evaluate long term changes resulting from the effects of the two population densities.

Hypotheses tested will be related to differences in vegetation structure and plant species composition among two population densities (high and low) of elk. We will test the hypothesis that high densities of elk will suppress shrub growth and diversity and that palatable shrub species will become more prevalent under low population density of elk. We will also test the hypothesis that at high population density elk will spend more time actively searching for forage thus movement patterns will be greater duration and area than the low density population.

Vegetation will be monitored at the peak of the growing season end June or early July when most species are present. Line transect surveys will be conducted within and outside each exclosure to monitor shrub composition and conifer regeneration. Within each transect daubenmire plots will be read to examine herbaceous species composition within and outside each exclosure site.

Measures of animal use of each exclosure site and differences in movement patterns of animals under high- and low-population densities will be evaluated using the automated telemetry system present on Starkey. Radio-telemetry data collected from elk and mule deer as part of the ongoing monitoring and research on ungulates at Starkey

Experimental Forest and Range. Data will be collected for a 7-month period each year between late March and early November.

Advantages of Approach: This study takes advantage of the automated radio-telemetry system in place at Starkey Experimental Forest and Range. Starkey personnel will monitor vegetation characteristics throughout the study as part of ongoing vegetation monitoring on Starkey. Use of current personnel and facilities on Starkey allows the study to proceed with no additional equipment, personnel, or funds.

Lead Scientists: John G. Kie, Marty Vavra (PNW Research Station), and Kelley M. Stewart (Institute of Arctic Biology)

3. INTERACTIONS OF UNGULATE HERBIVORY, FOREST FUELS, WILDFIRE, AND OTHER NATURAL DISTURBANCES

Study 3.1. Effects of fuels reduction at the stand and landscape scales on elk, mule deer, and cattle

Background: The Starkey Experimental Forest and Range was created in 1940 with the goal of furthering the emerging science of range management. Additionally, the creation of an experimental forest in this ponderosa pine-bunch grass type provided the opportunity for the Pacific Northwest Research Station to conduct research in the drier forest communities of the Region. The use of this dry forest type as a living laboratory provided a distinctive opportunity for researchers to study forest and range management practices of the Blue Mountains, in a controlled setting.

The components of a ponderosa pine-bunch grass system remain, in a large part to the limited harvest in the area the past few decades, and to successful fire suppression. Unfortunately, efforts have resulted in overstocked stands, high fuel loads, and a high percentage of mortality from insect attacks. The situation is not uncommon in the Blue Mountains for this type. Several studies have concluded that large acreages of trees located in eastern Oregon and Washington are crowded and stressed, making them vulnerable to insects and disease. They have also reported that woody fuels in these forests have accumulated to unnaturally high levels.

High fuel loads resulting from decades of fire suppression have increased the occurrence of catastrophic fires. These fires are more lethal and damaging to soils than those occurring under pre-settlement conditions. Recent history in the Blue Mountains supports the findings of the previously referenced reports. On the Wallowa-Whitman Forest alone, wildfire has burned over approximately 418,000 acres (17% of the total forest acreage) in the last ten years. Cost to suppress these fires was just short of $113,000,000.

This proposed Starkey research and restoration project presents an opportunity to launch an adaptive resource management (ARM) effort that can serve as a guidepost to the Intermountain West during the long restoration task ahead. ARM projects offer unique opportunities for collaboration between research and management. Rarely do research stations have the funds, personnel, and expertise to conduct land management activities at such a broad scale. Conversely, national forests lack personnel trained in experimental design and the infrastructure to conduct sound, scientific experiments. By combining the talents and resources of both Research and the National Forest System in a collaborative ARM project, benefits accrue that would be impossible for either branch operating independently. The value of such adaptive resource management efforts is such that many professional scientific organizations have called for their increasing use.

Information Needed: It is likely that in the near future, efforts to reduce fuel loadings throughout the Interior Columbia Basin will be greatly intensified. These efforts will include mechanical treatments, prescribed burning, and other techniques used in the past. They will, however, be tailored specifically for the Interior Columbia Basin, will include new techniques and prescriptions, and will include collaborative partnerships between management and research. We do not know how elk, mule deer, and cattle will respond to these treatments at either the stand or the landscape level.

Study Design: A program of fuel reduction will begin on Starkey Experimental Forest and Range in 2001. Fuel reduction treatments will be targeted at overstocked stands of true fir and Douglas fir that suffered heavy mortality during the spruce budworm outbreak in the late 1980s. Some fir stands on Starkey will be left untreated as experimental controls, and to allow additional research opportunities in the future. Stands will be subjected to appropriate fuel reduction activities, and overstory tree removal will be incorporated with an embedded timber sale contract.

Several hypotheses will be tested using radio-telemetry data collected from elk and mule deer as part of the ongoing monitoring and research on ungulates at Starkey Experimental Forest and Range. Data will be collected for a 7-month period each year between late March and early November. Pre-treatment data is available for previous years. Data for the 4-year period 1996-1999 will be used as a temporal experimental control. Spatial experimental control will be achieved by comparing animal use data from the treatment areas with those collected on the untreated fir stands. The distribution of open roads and associated traffic rates will be considered as covariates in all analyses.

Specific hypotheses to be tested include: 1) Elk and mule deer will be attracted to fuels treatment areas in autumn by the slash left on the ground following treatment activities because of the presence of lichens. This use will be associated temporally with foraging activity peaks in early morning and at dusk, 2) after the initial use of lichens, elk and mule deer will be attracted to the treatment areas because of increased production of preferred forages. This use will be associated temporally with foraging activity peaks in early morning and at dusk, 3) elk will competitively displace mule deer from newly-treated patches, thereby invalidating predictions made under the ideal-free distribution (Fretwell 1972, Populations in a seasonal environment. Monographs in Population Biology 5, Princeton University Press, New Jersey), 4) spatial memory (remembering where the treatments areas are located and the amount of forage in each) and exploratory trips (to find newly treated patches) will influence the process by which elk and mule deer use the fuels treatments areas. The resulting violation of the assumption of perfect knowledge will also invalidate the predictions made under the ideal-free distribution (Fretwell 1972), 5) the shape, size, and spacing of treatment patches will affect their use by elk and mule deer. These large herbivores will exhibit longer residence times in large patches, and those more isolated from similar patches. They will also make greater use of irregularly shaped patches than regularly shaped ones. Finally, they will be less likely to use patch core areas of small size because of the lack of security and escape cover, and 6) the size of home ranges used by elk and mule deer will be smaller in the south half of Starkey Experimental Forest and Range than in the north half, because treatment patches will be more numerous and in closer proximity to each other.

Advantages of Approach: This study takes advantage of the existing automated radio-telemetry system in place at Starkey Experimental Forest and Range. It allows the study to proceed with no additional equipment, personnel, or funds.

Lead Scientists: John G. Kie and Marty Vavra (PNW Research Station)

Additional funding required

4. THE ROLE OF UNGULATE HERBIVORY ON ECOSYSTEM FUNCTION

Study 4.1. Retrospective effects of ungulate herbivory on avian communities
Study 4.2. Experimental effects of ungulate herbivory on avian communities in relation to fire and fuels reduction
Study 4.3. Effects of fuels reduction and herbivory at the stand and landscape scales on small mammals
Study 4.4. Herbivory at multiple trophic levels on plant species diversity, rates of nutrient cycling, and annual net primary productivity

Timeline for Products

	2001-02	2002-03	2003-04	2004-05	2005-06	2006-07	2007-08	2008-09	2009-10	2010-11
1.1		Model Development →	Model Validation Testing	→	→	→	Publication			
2.1		Data Collection →	→	→	Publication					
			Model Incorporation	→	→					
2.2	Excl Const	Excl Const Data Collect	\Data Collect	→	→	→	→	Interim Publication	→	→
2.3	Data Collect	Thesis	Publications	→	→	→	→	Publication	→	→
3.1	Data Collect	→	→	→	→	→ Publication	→	→	→	→

Literature Cited

Aber, J., N. Christensen, I. Fernandez, J. Franklin, L. Hidinger, M. Hunter, J. MacMahon, D. Mladenoff, J. Pastor, D. Perry, R. Slangen, H. van Miegroet. 2000. Applying ecological principles to management of the U.S. National Forests. Issues in Ecology. 6:1-20

Allen, R.B., I.J. Payton, and J.E. Knowlton. 1984. Effects of ungulates on structure and species composition in the Urewera forests as shown by exclosures. New Zealand Ecological Soc. 7:119-130

Alverson, W.S. and D.M. Waller. 1997. The white tailed deer: a keystone herbivore. Wildl. Soc. Bull. 25:217-226

Amacher, M.C. and D.L. Bartos. 1997. Soil properties associated with various stages of succession in the aspen ecosystem. Abst. Form 50th meeting of Soc. Range Manage. Rapid City, SD

Anderson, V.J. and D.D. Briske. 1995. Herbivore-induced species replacement in grasslands: Is it driven by herbivory tolerance or avoidance? Ecological App. 5:1014-1024

Armour, C. et al. 1994. The effects of livestock grazing on western riparian and stream ecosystems. Fisheries. 19:9-12

Augustine, D.J. and S.J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. J. Wildl. Manage. 62:1165-1183

Belsky, A.J. and D.M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior West. Conservation Biology. 11:315-327

Beukema, S.J. and W.A. Kurz. 1995. Vegetation dynamics development tool user's guide. 2.0 beta. Unpublished report prepared by ESSA Technologies Ltd., On file with ESSA Technologies Ltd., #300-1765 West 8th Avenue, Vancouver, BC, V6J 5C6. Canada. 76p.

Bich, B.S., J.L. Butler, and C.A. Schmidt. 1995. Effects of differential livestock use on key plant species and rodent populations within selected *Oryzopsis hymenoides/Hilaria jamesii* communities of Glen Canyon National Recreation Area. Southwestern Nat. 40:281-287

Binkley, D., K. Cromack, and R.L. Fredriksen. 1982. Nitrogen accretion and availability in some snowbrush ecosystems. Forest Sci. 28:720-724

Bormann, B.T. and J.C. Gordon. 1989. Can intensively managed forest ecosystems be self-sufficient in nitrogen? Forest Ecology and Manage. 29:95-103

Bowyer, R.T., V. Van Ballenberghe, and J.G. Kie. 1997. The role of moose in landscape processes: effects of biogeography, population dynamics, and predation. Pp. 265-287 in Wildlife and landscape ecology: effects of pattern and scale (J.A. Bissonette, ed.). Springer-Verlag, New York.

Brooks, R.T. 1999. Residual effects of thinning and high White-tailed deer densities on Northern Redback salamanders in southern New England oak forests. J. Wildl. Manage. 63:1172-1180

Carey, A.B. and M.L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological App. 5:336-352

Clary, W.P. and F.R. Larson. 1971. Elk and deer use are related to food sources in Arizona Ponderosa pine. USDA- Forest Service, RMFRES, Res. Note. RM-202

Cleary, B.D., R.D. Greaves, and R.K. Herman. 1978. Regenerating Oregon's forests. Oregon State Univ., Extension Service, Corvallis, Oregon, 203 p.

Clements, F.E. 1936. Nature and structure of the climax. J. of Ecology 24:252-284

Cliff, E.P. 1939. Relationship between elk and mule deer in the Blue Mountains of Oregon. Fourth North American Wildlife Conference. US Forest Service, Portland, Oregon, USA

Clough, G.C. 1987. Relations of small mammals to forest management in northern Maine. Canadian Field-Nat. 101:40-48

Cook, J.G., L. Irwin, L. Bender, B. Johnson, and D. Boyce. 1999. Declining elk herd productivity: assessing habitat's role in the Pacific and inland Northwest. A Proposal.

Coughenour, M.B. 1991a. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. J. Appl. Eco. 28:71-82

Coughenour, M.B. 1991b. Invited synthesis paper: Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. J. of Range Manage. 44:530-542

Covington, W.W. and M. Moore. 1994. Southwestern Ponderosa forest structure, Changes since Euro-American settlement. J. Forestry. 39-47

Crete, M. and M. Manseau. 1998. Natural regulation of cervidae along a 1000 km latitudinal gradient: change in trophic dominance. Evolu. Ecol. 10

DeCalesta, D.S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. J. Wildl. Manage. 58:711-718

Degraaf, R.M., W.H. Healy, and R.T. Brooks. 1991. Effects of thinning and deer browsing on breeding birds in New England oak woodlands. Forest Eco. Manage. 41:179-191

Donald, P.F., R.J. Fuller, A.D. Evans, and S.J. Gough. 1998. Effects of forest management and grazing on breeding bird communities in plantations of broad-leaved and coniferous trees in western England. Bio. Conser. 85:183-197

Dzieciolowski, R. 1980. Impact of deer browsing upon forest regeneration and undergrowth. Ekologia Polska. 28:583-599

Fleischner, T.L. 1994. Ecological costs of livestock grazing in Western North America. Conservation Biology. 8:629-644

Ford, M.A. and J.B. Grace. 1998. Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. J. Ecology. 86:974-982

Fretwell, Stephen D. 1972. Populations in a seasonal environment. Monographs in Population Biology 5. Princeton University Press, New Jersey.

Gomez, D.M. and R.G. Anthony. 1998. Small mammal abundance in riparian and upland areas of five seral stages in Western Oregon. Northwest Sci. 72:293-302

Hann, W.J., J.L. Jones, M.G. Karl, P.F. Hessburg, R.E. Keane, D.G. Long, J.P. Menakis, C.H. McNicoll, S.G. Leonard, R.A. Gravenmier, and B.G. Smith. 1997. Landscape dynamics of the basin. *In:* T.M. Quigley and S.J. Arbelbide, (eds.) An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins. Gen. Tech. Rep. PNW-GTR-405. USDA Forest Service Pacific Northwest Research Sta. Portland, Oregon.

Hayward, B., E.J. Heske, and C.W. Painter. 1997. Effects of livestock grazing on small mammals at a desert cienaga. J. Wildl. Manage. 61:123-129

Healy, W.M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. P. 249-266. *In:* W.J. McShea, H.B. Underwood, and J.H. Rappole (eds.), The science of overabundance: deer ecology and population management. Smithsonian Institution Press, Washington, D.C., USA

Hemstrom, M.A., J.J. Korol, and W.J. Hann. 2001. Trends in terrestrial plant communities and landscape health indicate the effects of alternative management strategies in the interior Columbia River Basin. For. Ecol. Manage.

Hemstrom, M.A., M.J. Wisdom, M.M. Rowland, B.K. Wales, W.J. Hann, and B. Gravenmier. In press. Sagebrush-steppe vegetation dynamics and potential for restoration in the interior Columbia Basin, USA. Cons. Biol.

Heske, E.J. and M.C. Campbell. 1991. Effects of an 11-year livestock exclosure on rodent and ant numbers in the Chihuahuan Desert, southeastern Arizona. Southwest Nat. 36:89-93

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

Holland, J.N., W. Cheng, and D.A. Crossley. 1996. Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. Oecologia. 107:87-94

Hulme, P.E. 1996. Herbivory, plant regeneration, and species coexistence. J. Ecology. 84:609-615

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annu. Rev. Eco. Sys. 22:477-503

Huntsinger, L. 1996. Grazing in a California silvopastoral system: effects of defoliation season, intensity, and frequency on deerbrush, *Ceanothus intergerrimus* Hook. & Arn. Agroforestry Sys. 34:67-82

Irwin, L.L., J.G. Cook, R.A. Riggs, and J.M. Skovlin. 1994. Effects of long-term grazing by big game and livestock in the Blue Mountains Forest Ecosystem. USDA-Forest Service, Pacific Northwest Research Station, Gen. Tech. Rep.. PNW-GTR-325

Irwin, L.L. and J.M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. J. Wildl. Manage. 47:664-672

Jenkins, K. and E. Starkey. 1996. Simulating secondary succession of elk forage values in a managed forest landscape, western Washington. Environ. Manage. 20:715-724

Johnson, C.G. 1994. Forest health in the Blue Mountains: A plant ecologist's perspective on ecosystem processes and biological diversity. USDA- Forest Service, Pacific Northwest Res. Sta., Gen. Tech. Rep.. PNW-GTR-339

Johnson, K.N., J. Agee, R. Beschta, J. Beuter, S. Gregory, L. Kellogg, W. McComb, J. Sedell, T. Schowalter, and S. Tesch. 1995. Forest health and timber harvest on national forest in the Blue Mountains of Oregon.

Johnson, M. 1982. Response of small mammals to livestock grazing in southcentral Idaho. J. Range Manage. 35:51-53

Johnson, B.K., J.W. Kern, M.J. Wisdom, S.L. Findholt, and J. G. Kie. 2000. Resource selection and spatial separation of mule deer and elk during spring. J. Wildl. Manage. 64:685-697

Johnson, C.G. and M. Vavra. 2001. Permanent monitoring points: An example of value and utility in the study of elk impacts on bunchgrass communities in Hells Canyon. Abstract. Society for Range Management Annual Meeting. February 2001.

Jones, A. 2000. Effects of cattle grazing on North American arid ecosystems: A quantitative review. Western. N. A. Nat. 60:155-164

Joubert, D.F. and P.G. Ryan. 1999. Differences in mammal and bird assemblages between commercial and communal rangelands in the Succulent Karoo, South Africa. J. Arid Environ. 43:287-299

Karl, M.G. and P.S. Doescher. 1993. Regulating competition on conifer plantations with prescribed cattle grazing. Forest Sci. 39:405-418

Kay, C.E. 1994. Aboriginal overkill: The role of Native Americans in structuring western ecosystems. Human Nature. 5:359-398

Kay, C. and D.L. Bartos. 2000. Ungulate herbivory of Utah aspen: Assessment of long-term exclosures. J. Range Manage. 53:145-153

Klein, D.R. 1970. Food selection by North American deer and their response to over-utilization of preferred plant species, p. 25-46. *In:* A. Watson (ed.), Animal populations in relation to their food resources. A symposium of The British Ecological Society, Aberdeen, March 24-25, 1969. Blackwell Scientific Publications. Oxford and Edinburgh.

Knops, M.H., M.E. Ritchie, and D. Tilman. 2000. Selective herbivory on a nitrogen fixing legume (*Lathyrus venosus*) influences productivity and ecosystem nitrogen pools in an oak savanna. Ecoscience. 7:166-174

Kräuchi, N, P. Brang, and W. Shönenberger. 2000. Forests of mountainous regions: gaps in knowledge and research needs. Forest Eco. and Manage. 132:78-82

Langston, N. 1995. Forest Dreams, Forest Nightmares. Univ. Washington Press, Seattle, Wash.

Laycock, W.A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. J. of Range Manage. 44:427-434

Lowe, P.O., Ffolliott, P.F., J.H. Dietrich, D.R. Patton. 1978. Determining potential wildlife benefits from wildfire in Arizona Ponderosa pine forests. USDA- Forest Service, RMFRES, Gen. Tech. Rep.. RM-52. 12p.

Mazancourt, C. and M. Loreau. 2000. Effect of herbivory and plant species replacement on primary production. American Nat. 155:735-754

McInnes, P.F., R.J. Naiman, J. Pastor, and Y. Cohen. 1992. Effects of moose browsing on vegetation and litter of the Boreal Forest, Isle Royale, Michigan, USA. Ecology. 73:2059-2075

McNaughton, S.J. 1985. Ecology of a grazing system: The Serengeti. Ecol. Monog. 55:259-294

McShea, W.J. and J.H. Rappole. 1997. Herbivores and the ecology of forest understory birds, p. 298-309. *In:* William J. McShea, H. Brian Underwood, and John H. Rappole (eds.), The Science of Overabundance: Deer ecology and population. Smithsonian Institution Press, Washington, D.C.

McShea, W.J. and J.H. Rappole. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conser. Bio. 14:1161-1170

Miller, R. and W. Krueger. 1976. Cattle use on summer foothill rangelands in northeastern Oregon. J. Range Manage. 29:367-371

Miller, R., W.C. Krueger, and M. Vavra. 1981. Deer and elk use on foothill rangelands in northeastern Oregon. J. Range Manage. 34:201-204

Mitchell, G.E. 1951. Status of browse on ranges of eastern Oregon and eastern Washington. J. Range Manage. 4:249-253

Molvar, E.M., R.T. Bowyer, and V.V. Ballenberghe. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia. 94:472-479

Mueggler, W.F. 1989. Age distribution and reproduction of aspen stands in the Intermountain Region. West. J. Appl. Forest. 4:41-45

Nevill, R.J., P.M. Hall, and J. Beale. 1995. Forest health research needs in British Columbia. Forestry Chron. 71:489-496

Opperman, J.J. and A.M. Merenlender. 2000. Deer herbivory as an ecological constraint to restoration of degraded riparian corridors. Rest. Ecol. 8:41-47

Parks, C.G., L. Bednar, and A.R. Tiedemann. 1998. Browsing ungulates – an important consideration in dieback and mortality of Pacific Yew (*Taxus brevifolia*) in a northeastern Oregon stand. Nor. Sci. 72:190-197

Pastor, J. and Y. Cohen. 1997. Herbivores, the functional diversity of plants species, and the cycling of nutrients in ecosystems. Theor. Pop. Bio. 51:1-15

Pastor, J., B. Dewey, R.J. Maniman, P.F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Eco. 74:467-480

Peek, J.M., F.D. Johnson, and N.N. Pence. 1978. Successional trends in a ponderosa pine/bitterbush community related to grazing by livestock, wildlife, and to fire. J. Range Manage. 31:49-53

Peterson, D.L. and V.T. Parker. 1998. Ecological scale: theory and applications. Columbia University Press, New York, NY, USA.

Petit, L.J., Petit, D.R., and T.E. Martin. 1995. Landscape-level management of migratory birds: looking past the trees to see the forest. Wildl. Soc. Bull. 23:420-429

Pickford, G. and E. Reid. 1943. Competition of elk and domestic livestock for summer range forage. J. Wildl. Manage. 7:328-332

PNWRS. 2002. Strategy for the future. Pacific Northwest Research Station publication 38p.

Quigley, T.M. and S.J. Arbelbide. 1997. An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins. USDA-Forest Service, BLM, Pacific Northwest Reg.. Gen. Tech. Rep. PNW-GTR-405. Portland, OR.

Raedeke, K.J. 1988. Forest management and wildlife in the Pacific Northwest. Northwest Environ. J. 4:263-278

Ream, C.H. 1981. The effects of fore and other disturbances on small mammals and their predators: an annotated bibliography. USDA- Forest Service, IFRES, Gen. Tech. Rep. INT-106

Reimoser, F., H. Armstrong, and R. Suchant. 1999. Measuring forest damage of ungulates: what should be considered. Forest Eco. Manage. 120:47-58

Reimoser, F. and H. Gossow. 1996. Impact of ungulates on forest vegetation and its dependence on the silvicultural system. Forest Eco. Manage. 88:107-119

Reynolds, H.G. 1966. Use of openings in spruce-fir forests by deer, elk, and cattle. USDA- Forest Service, Rocky Mountain Forest and Range Experiment Station. Research Note RM-63

Reynolds, T.D. and C.H. Trost. 1980. The response of native vertebrate populations to crested wheatgrass planting and grazing by sheep. J. Range Manage. 33:122-125

Riggs, R.A., A.R. Tiedemann, J.G. Cook, T.M. Ballard, P.J. Edgerton, M. Vavra, W.C. Krueger, F.C. Hall, L.D. Bryant, L.L. Irwin, and T. DelCurto. 2000. Modification of mixed-conifer forests by ruminant herbivores in the Blue Mountains Ecological Province. USDA- Forest Service, Pacific Northwest Reg. Research Paper PNW-RP-527. LaGrande, OR.

Robichaud, P.R., J.L. Beyers, and D.G. Neary 2000. Evaluating the effectiveness of postfire rehabilitation treatments. USDA- Forest Service, Rocky Mountain Research Station, Gen. Tech. Rep. RMRS-GTR-63

Rogers, P. 1996. Disturbance ecology and forest management: a review of the literature. USDA- Forest Service, Intermountain Research Station, Gen. Tech. Rep.. INT-GTR-336

Rowland, M.M., M.J. Wisdom, B.K. Johnson and J.G. Kie. 2000. Elk distribution and modeling in relation to roads. J. Wildl. Manage. 64:672-684

Schreiner, E.G., K.A. Krueger, P.J. Happe, and D.B. Houston. 1996. Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. Can. J. For. Res. 26:255-265

Schommer, T. 1991a. Analysis of big game statistics 1965-1990. Wallowa-Whitman National Forest. U.S. For. Ser., Wallowa-Whitman National Forest, Baker City, OR. 40pp.

Schommer, T. 1991b. Analysis of big game statistics 1965-1990. Wallowa-Whitman National Forest. Part II: Deer. U.S. For. Ser., Wallowa-Whitman National Forest, Baker City, OR. 59pp.

Schwab, F.E. and A.R.E. Sinclair. 1994. Biodiversity of diurnal breeding bird communities related to succession in the dry Douglas-fir forests of southeastern British Columbia. Can. J. For. Res. 24:2034-2040

Scott, V.E., G.L. Crouch, and J.A. Whelan. 1982. Responses of birds and small mammals to clearcutting in a subalpine forest in Central Colorado. USDA- Forest Service, Rocky Mountain, Research Note RM-422. Fort Collins, CO

Sharrow, S.H., W.C. Leininger, and K.A. Osman. 1992. Sheep grazing effects on coastal Douglas fir forest growth: a ten-year perspective. Forest Eco. Manage. 50:75-84

Singer, F.J. 1995. Effects of grazing by ungulates on upland bunchgrass communities of the northern winter range of Yellowstone National Park. Nor. Sci. 69:191

Stewart, K.M., R.T. Bowyer, J.G. Kie, N.J. Cimon, B.K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. J. of Mammalogy 83(1):229-244

Stickney, P.R. and R.B. Campbell, Jr. 2000. Data base for early postfire succession in northern Rocky Mountain forests. USDA- Forest Service, Rocky Mountain Research Station, Gen. Tech. Rep. RMRS-GTR-61CD

Stohlgren, T.J., L.D. Schell, and B.V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Eco. App. 9:45-64

Strategy for Ungulate Research. 2001. Draft document. Pacific Northwest Research Station publication. 13p.

Tiedemann, A.R. and H.W. Berndt. 1972. Vegetation and soils of a 30-year deer and elk exclosure in central Washington. Northwest Sci. 46:59-66

Turner, M.G., S.M. Pearson, W.H. Romme, L.L. Wallace. 1997. Landscape heterogeneity and ungulate dynamics: what spatial scales are important? Pp. 331-348 in Wildlife and landscape ecology: effects of pattern and scale (J.A. Bissonette, ed.). Springer-Verlag, New York.

USDA/FS. 2001. A collaborative approach for reducing wildland fire risks to communities and the environment. Misc. publ. 24p.

USFS. 2000. USDA Forest Service Strategic Plan. Forest Service publication 73p.

Vavra, M. 1996. Sustainability of animal production system: an ecological perspective. J. Animal Sci. 74:1418-1423

Vavra, M. and R. Riggs. 2000. The effects of ungulate herbivory and management on ecosystem patterns and processes. A Problem analysis. *In:* Evelyn Merrill and Larry Irwin (eds.), Perspectives of scale in ungulate ecology and management. In review.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. J. of Range Manage. 42:266-276

Wisdom, M.J. 1998. Assessing life-stage importance and resource selection for conservation of selected vertebrates. Dissertation, University of Idaho, Moscow, Idaho, USA.

Wisdom, M.J. and B.K. Johnson. 2001. Effects of off-road vehicle and other human activities on mule deer and elk: a proposal for manipulative research at the Starkey Experimental Forest and Range, northeast Oregon. Study proposal on file at Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850.

Wisdom, M.J. and J.W. Thomas. 1996. Elk. Pages 157-182. *In:* P.R. Krausman (ed.), Rangeland Wildlife. Society for Range Management, Denver, Colorado, USA.

Woodward, A., E.G. Schreiner, D.B. Houston, and B.B. Moorhead. 1994. Ungulate-forest relationships in Olympic National Park: Retrospective exclosure studies. Northwest Sci. 68:97-110