

# INFLUENCES OF ADJACENT FOREST MANAGEMENT ACTIVITIES OF MIGRATORY ELK OF MOUNT RAINIER NATIONAL PARK

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#### INTRODUCTION

Mount Rainier National Park (MORA) was created by Act of Congress in 1899 to protect a portion of the natural and scenic resources of the Cascade Mountains. Among the most significant of these resources is the mountain itself, a 14,411-foot dormant volcano that contains the largest glacial system in the conterminous United States. The park is also renowned for its expansive subalpine meadows and forests that are enjoyed by thousands of park visitors each year and which provide habitat for a great diversity of native flora and fauna of the Cascade Mountains.

Observations that elk (<u>Cervus elaphus</u>) herds were increasing in MORA prompted concern that high densities of elk could threaten unique ecological values of the park. That concern was first expressed in 1962 when an initial aerial survey of elk revealed that densities summering in the park far surpassed previous expectations. Subsequent monitoring, beginning in the early 1970's, revealed that elk populations were continuing to increase in the northeastern part of the park and that population growth, if unabated, could become a concern to park management (Bradley 1982, Cooper 1987).

Bradley and Driver (1981) suggested that population increases of elk in MORA were related to land-management activities outside the park. Prior to modern logging practices extensive forests adjoining the park may have been deficient in important elk forages (Bradley 1982). A notable exception, however, occurred along the floodplain corridors of major river systems, where a variety of seral and old-age forest communities provided abundant forage and undoubtedly supported a viable elk population. In the 1950's and 1960's the primary elk winter range north of Mount Rainier National Park was intensively logged. Widespread patch-cutting provided additional foraging areas adjoining the floodplain, which may have enabled elk populations to increase during the 1970's.

Logging activities are of particular interest to park managers currently because they may continue to influence elk populations and range trends within the park. On the one hand, secondary forest succession resulting from past logging activities may have diminished carrying capacities of winter ranges abutting the park (Raedeke and Lemkuhl 1984). On the other hand, current and future forest management practices which include renewed patch-cutting of Douglas-fir (Psuedotsuga menziesii), thinning of regenerating stands, and harvesting second-growth red alder (Alnus rubra) stands, could enhance carrying capacity of winter ranges and enable elk populations to maintain themselves or resume growing.

The purpose of this study was to evaluate long-term consequences to migratory elk that summer within MORA of forest management activities in the White River drainage. The White River, which drains the park's northeastern quadrant, was selected for study because elk populations there have grown in the last decade, and human activities continue to influence winter range and elk populations adjoining the park.

This study was designed to provide answers to park managers on important questions concerning the status of elk in the White River drainage. Specifically, we address the following questions:

- What is the logging history and successional status of elk winter and spring ranges outside the park?
- 2. How do nutritional qualities of elk winter range compare to pristine conditions?
- 3. In what manner can we expect nutritional qualities of elk winter range (and therefore, possibly elk population trends) to change under current and future forest management activities?

Three major segments of this report correspond to each of the above questions. In the chapter entitled "The Elk Range" we describe current habitat conditions in managed forests of the White River. In the segment on "Elk-winter range relationships" we present results on forage production outside the park, and we discuss diets and nutrient availability of old growth and cutover portions of the White River range. In the segment on "Elk-habitat modeling" we present results of habitat models developed for forecasting elk habitat trends in the White River area.

#### CH 1: THE ELK RANGE

#### Elk Population Trends

The relative abundance of elk inhabiting MORA's northern summer range has been monitored from aerial surveys since 1974 (survey techniques and study design are described by Bradley 1982). Because not all elk present were observed during aerial surveys and no attempt was made to correct for unseen elk, the surveys provide only an index of relative elk numbers, not absolute densities.

Indices of elk abundance on the northern summer range increased from a population low of 200 in 1974 to a population high of 660 in 1984 (Finite Rate of Annual Increase (R) = 1.12; unpublished data, S. Schlegel, Mount Rainier National Park). Since 1984, however, indices of abundance have decreased steadily to a low of 450 in 1988 (R = 0.91). Overall, elk populations increased on MORA's northern summer range during the 1970's and early 1980's and now appear to be decreasing.

Population trends of elk on MORA's summer range may be related both to habitat conditions and to legal and illegal harvest of elk outside the park. MORA's northern elk herd inhabits two game management areas (GMU) of the Washington Department of Wildlife during the winter (GMU's 466 and 472). From 1974 until 1986, the legal harvest was limited to bulls-only in these two GMU's and averaged 235 bulls per year; no cows were harvested legally. Since 1986, in addition to the general bull-only harvest, Native Americans have harvested antlerless elk. Although harvests by Native Americans are not well-documented, legal harvest by Native Americans is estimated to have averaged approximately 100 elk per year in 1987 and 1988 (pers. comm. R. Spencer, Washington Dept. of Wildlife).

#### Seasonal Ranges of Elk

Cooper (1987) described movement patterns of three separate home range groups of elk that inhabit high-elevation summer ranges within MORA and low-elevation winter ranges along the White River. Summer ranges encompassed the areas surrounding Governors Ridge, Brown Peak, and Bear Park at the headwaters of tributaries of the White River (Fig. 1.1). Elk migrated from summer ranges to lower elevations following the first heavy snowfalls in October or November (Cooper 1987).

Elk wintered in two primary winter ranges along the White River. One subpopulation, referred to as the North Boundary Herd, wintered predominantly in old-growth forests in bottomlands of the White River near the northern boundary of MORA (10.0 km²) (Fig. 1.2). Two additional subpopulations wintered approximately 12 km downriver in second growth forests that were managed for timber production primarily by Weyerhaeuser Company, and to a much lesser extent, by Washington Department of Natural Resources and the United States Forest Service. These two subpopulations, referred to as the Gold Hill (7.2 km²) and Crystal Village (8.7 km²) herds, were named after prominent features in each area. Crystal Village was a housing development built on a subdivision of cutover Weyerhaeuser lands. Elk inhabiting these

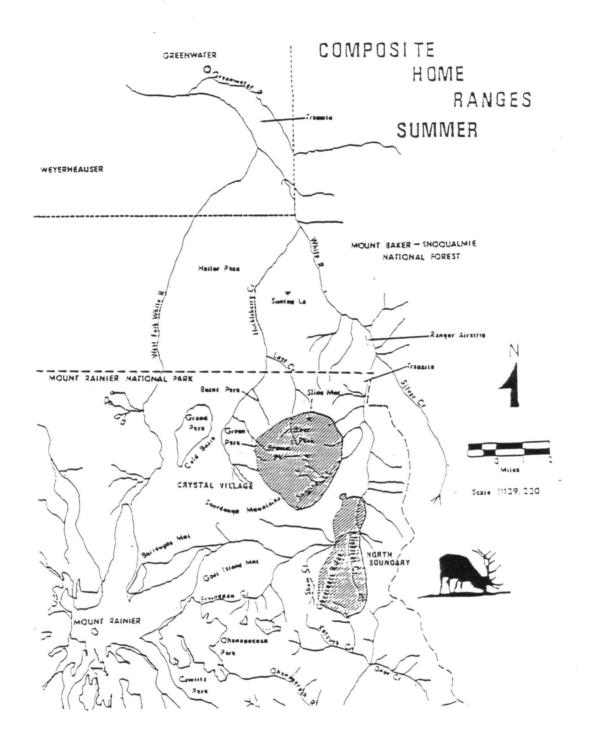


Fig. 1.1. Summer ranges of elk that winter in the upper White River drainage, Washington  ${\bf r}$ 

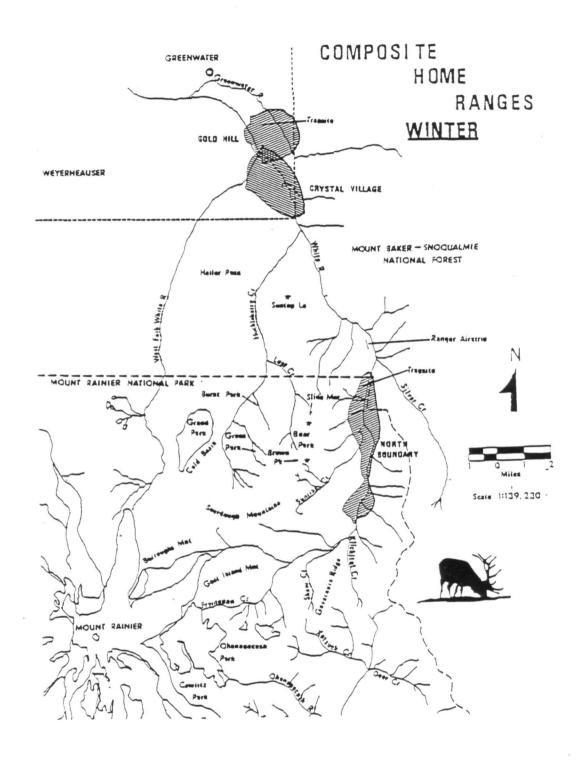


Fig. 1.2 Winter ranges of elk in the upper White River drainage, Washington

two broadly different areas, i.e. predominantly old-growth forests within MORA and second growth forests outside the park, formed the basis for studying relationships between forest management practices and diets of elk (Ch. 2).

Spring movements of elk were variable in the White River (Cooper 1987). Elk in the North Boundary and Gold Hill herds inhabited winter ranges until early July. Elk in the Crystal Village herd, in contrast, moved approximately 4 km south in late May to a distinct spring range. These elk inhabited a mid-elevation spring range until early July, at which time they migrated farther upslope to summer range within MORA. Spring range of the Crystal Village herd was located on Weyerhaeuser and USFS lands on the northeastern-most end of Huckleberry Ridge (Fig. 1.3). This spring range, like the winter range, was managed primarily for timber production.

#### Climate

Cooper (1987) summarized historical weather records from a weather station in Greenwater, Washington, within the elk winter range (Table 1.1). Climate in the study area is generally cool and moist, with wet, mild winters and comparatively dry, cool summers. Forty-year average winter temperatures ranged from 31 F during January to 39 F during November and March. Average minimum temperatures, however, ranged from 10 F to 20 F in January and March, respectively.

Winter snowfall has been exceedingly variable in the study area (Table 1.1). Although average mid-winter accumulations of snow vary only between 10-20 inches, maximum snow accumulations for a month have ranged between 0-69 inches. Particularly heavy accumulations of snow have occurred periodically, for example during 1949 (72 in), 1950 (60 in), 1957 (36 in), 1959 (36 in), and 1969 (36 in). Since 1970, snowfall winters for the most part has been average or below average. Winter 1986-87, during this study, was mild and snow depths never exceeded 14 inches.

# Physiography and Vegetation

Winter ranges were on bottomlands and low-lying alluvial terraces of the White River and ranged in elevation from approximately 640-960 m. Winter range of the North Boundary herd, within MORA, was constrained by steep valley side-slopes. Winter ranges at lower elevations outside the park were also delimited by mountain slopes, but alluvial terraces were broader than upriver and adjoining slopes were less steep.

Vegetation on winter ranges was representative of the <u>Tsuga heterophylla</u> vegetation zone (Franklin and Dyrness 1973). Specific plant associations reflected temperature and moisture gradients (Henderson and Peters 1984, Franklin et al. in prep.). <u>Thuja plicata/Lysichitum americanum</u> habitat types occurred on poorly drained, wetland sites. Overstories were dominated by western red cedar (<u>T. plicata</u>) and western hemlock (<u>Tsuga heterophylla</u>). A wide variety of wetland sedges and herbs were usually found in the understory in association with skunkcabbage (<u>L. americanum</u>).

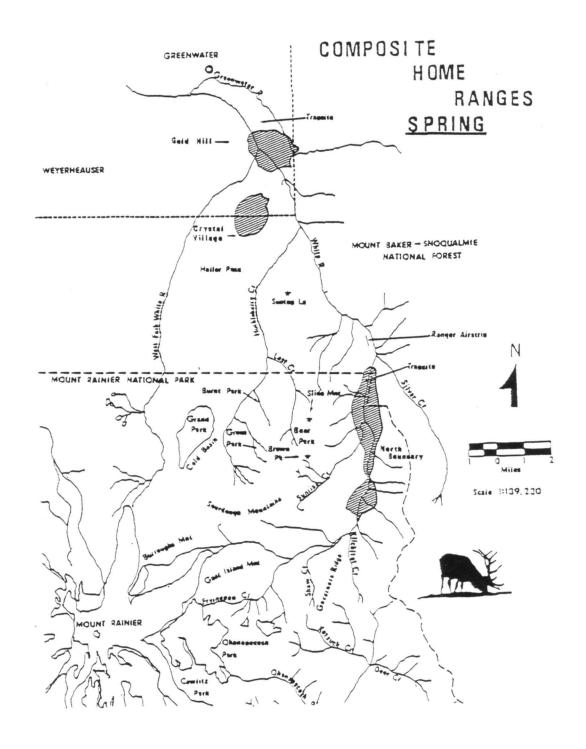


Fig. 1.3. Spring ranges of elk that winter in the upper White River drainage, Washington  ${\bf r}$ 

Table 1.1. Forty-year average weather conditions during winters, 1939-1980, Greenwater, Washington. Table from Cooper 1987. Data from U. S. Department of Commerce Climatological Data, National Climatic Center, Ashville, North Carolina.

40-Year		8	Month		
Average of:	Nov	Dec	Jan	Feb	Mar
Temperature (F)	38.6	33.6	31.4	36.4	38.8
Minimum Temperature (F)	19.6	16.3	10.1	18.4	20.3
Total Snowfall (In) (Range)	5.4 0-24	16.4 0-80	24.0 0-99	13.8 0-62	12.5 0-48
Maximum Snow Depth (In) (Range)	2.7 0-12	10.4	19.5 0-54	15.0 0-69	11.8 0-4]

T. heterophylla (TSHE)/Oplopanax horridum, and TSHE/Achlys triphylla habitat types were found on mesic bottomlands along the White River. Overstory dominants included Douglas-fir, western red cedar, and western hemlock. Sitka spruce (Picea sitchensis) occurred in a few low-elevation sites, and Pacific silver fir (Abies amabilis) increased in abundance at higher elevations. Variable understories were dominated by vine maple (Acer circinatum), salmonberry (Rubus spectabilis), devil's club (Oplopanax horridum) and a variety of moist-site forbs and ferns.

TSHE/Berberis nervosa and TSHE/Gaultheria shallon habitat types occurred on well-drained alluvial terraces and xeric uplands throughout the winter range. Overstories were dominated by Douglas-fir and western hemlock, with increasing amounts of Pacific silver fir at the higher elevations. Understories were characterized often by dense coverage of salal (Gaultheria shallon) and Oregongrape (Berberis nervosa). Variable herbaceous layers were dominated often by pipsissewa (Chimaphila umbellata) and twinflower (Linnaea borealis).

Recent logging activities have reduced mature forests on managed elk winter range outside MORA. Managed forests consisted of a mosaic of seral forest communities. Grass/sedge-dominated communities formed on cutover T. plicata/L. americanum habitat types. Grass/sedge communities were characterized by sparse regenerating overstories of Sitka spruce and dense herbaceous mats of hydrophyllic grasses, sedges and forbs. Red alder (Alnus rubra) communities formed on cutover TSHE/Oplopanax horridum and TSHE/Achlys triphylla habitat types. Red alder communities, as the name denotes, are dominated by red alder. Conifer reproduction is generally sparse, and consists of grand fir (Abies grandis), western red cedar, Sitka spruce or western hemlock. The dense herbaceous understory is often dominated by salmonberry and a variety of grasses, sedges and forbs. Seral forests of TSHE/Gaultheria shallon or Berberis nervosa habitat types are generally dominated by dense stands of regenerating Douglas-fir, variable understories of salal and Oregongrape, and low coverage of grasses and forbs.

For purposes of describing post-logging trends in forage production, the gradient of vegetation on managed forests in the study area was classified into 14 plant communities based on general soil moisture regimes, dominant cover characteristics, and age since overstory harvest (Table 1.2). Plant communities comprising a mesic sere corresponded largely to vegetation found on T. plicata/L. americanum, TSHE/O. horridum, and TSHE/A. triphyllum habitat types along the riverine bottomlands. Plant communities comprising a xeric sere corresponded to vegetation found on TSHE/G. shallon and TSHE/B. nervosa habitat types of adjoining terraces and uplands.

A variety of 21-40 year old plant communities were found in managed forests throughout the White River (Table 1.2), reflecting complex underlying influences of soils and past forest management activities. Red alder and grass/sedge communities, described above, formed on moist to wet bottomland sites 21-40 years after logging. Unthinned PSME forests corresponded to dense, regenerating Douglas-fir stands, 21-40 years old, that had not been pre-commercially thinned within 5 years. Thinned PSME stands, in contrast, were regenerating forests pre-commercially thinned within 5 years. Sparse

Table 1.2. Proportional abundance of 14 plant community-age classes of commercial forests on winter and spring ranges in the White River.

Community/age-class	Winter range	Spring range
Mesic Sere		
0-10 yrs 11-20 yrs 21-40 yrs/Red Alder 21-40 yrs/Grass-Sedge 200+ yrs/Douglas-fir 200+ yrs/Red Cedar	0.004 0.008 0.132 0.051 0.000	0.000 0.025 0.000 0.000 0.000
Subtotals	0.200	0.025
Xeric Sere		
0-10 yrs 11-20 yrs 21-40 yrs/Unthinned PSME 21-40 yrs/Thinned PSME 21-40 yrs/Sparse PSME 21-40 yrs/PSME-POIR 120-200 yrs/PSME 200+ yrs/PSME	0.017 0.049 0.378 0.236 0.023 0.083 0.001	0.000 0.536 0.078 0.000 0.079 0.178 0.000
Subtotals	0.800	0.975
Totals	1.000	1.000

PSME stands formed on xeric uplands where inadequate soil development and moisture appeared to inhibit forest regeneration. PSME-POTR communities were 21-40 year-old stands of Douglas-fir and cottonwood which formed on shallow river alluvium following logging.

# Forest Management Practices

Clearcutting was the primary silvicultural practice throughout the managed winter and spring ranges. The majority (90%) of winter range was clearcut between 1950-69 (Table 1.3). Only 2% of the commercially merchantable forests have been left standing as old-growth forest on the managed winter range. Harvesting of old-growth forests occurred more gradually and over a longer period on spring home ranges of elk than on winter ranges at lower elevations. Nonetheless, only 11% of the commercially valuable forests have been left uncut on elk spring range in the White River (Table 1.3).

A variety of forest management practices are employed routinely in the White River to maximize reforestation. Clearcut areas are frequently broadcast burned to remove logging slash, or slash is sometimes piled and burned. Following reduction of slash, nursery-stock seedlings of Douglas-fir are planted at a rate of approximately 200-600 seedlings/acre. Competing hardwood vegetation, primarily red alder and vine maple, are controlled where needed through aerial applications of herbicide. Regenerating stands of Douglas-fir are precommercially thinned generally to a density of approximately 300 trees/acre at approximately 15-25 years of age. Although most reforestation involved planting nursery stock of Douglas-fir, as described above, western red cedar, noble fir (Abies procera), and lodgepole (Pinus contorta) or white pine (Pinus monticola) are planted occasionally on wet sites, frost pockets and dry sites, respectively.

Table 1.3. Logging history of elk winter and spring ranges in the White River. Table values are proportions of home ranges logged during each 5-year interval (1945-1985).

Years Harvested	Winter Range	Spring Range
1945-49 1950-54 1955-59 1960-64 1965-69 1970-74 1975-79 1980-85 Mature (120 years) <sup>b</sup> Old-growth (200+ years) <sup>b</sup>	0.00 0.28 0.35 0.16 0.11 0.06 Ta 0.02 T	0.01 0.14 0.07 0.11 0.00 0.24 0.32 0.00 0.00
Total	1.00	1.00

a T is < 0.01

b Unharvested forests

#### CH. 2: ELK-WINTER RANGE RELATIONSHIPS

Elk are important economic and ecologic components of montane and subalpine ecosystems of the Cascade Mountains. Nearby urban centers enhance the recreational value of large elk herds in the Mount Rainier ecosystem, both for viewing opportunities and for traditional consumptive uses. But high densities of elk resulting from forest management activities could cause unacceptable impacts to subalpine meadows on summer ranges within Mount Rainier National Park (MORA). As demands for elk, timber, and park recreational resources increase, better understanding of relationships between logging and nutritional limiting factors of elk populations will be needed to accommodate diverse resource management objectives in the region.

Factors limiting elk populations are poorly understood in the western Cascades and Pacific coastal forests. Most studies have concluded that availability of digestible energy, particularly during winter, is the most limiting nutritional factor (Schoen 1977, Janz 1983, Leslie et al. 1984). Dietary nitrogen levels are generally thought to meet minimum ecological requirements provided that concentrations of protein-binding phenolic compounds do not interfere significantly with protein digestion (Janz 1983, Leslie et al. 1984). Recent studies, however, suggest that insoluble tannin-protein complexes may result in protein deficiencies for elk consuming browse diets in the Pacific Northwest (Hanley et al. 1987, Happe et al., in prep).

Evaluating effects of forest management activities on winter nutrition of elk requires information on availability of nutrients, and composition and quality of elk diets following logging. Previous studies have documented vegetation trends following logging in the Cascade Mountains (Dyrness 1973, Long and Turner 1975). Those studies, however, emphasized peak standing crop biomass during summer, and failed to distinguish between phytomass available and unavailable to browsing herbivores. Previous researchers also have documented diets of elk in the Cascade Mountains (Schoen 1977, Merrill et al. 1987) and nearby coastal forests (Janz 1983, Leslie et al. 1984). None, however, have compared diets and nutritional planes of elk inhabiting distinct stages of forest succession.

The goal of this study was to determine influences of recent logging practices on winter nutrition of elk in the White River drainage, Washington. Specific objectives were (1) to compare available biomass of elk forages among various plant communities and successional stages on managed forests adjacent to MORA, (2) to compare composition and nutrient levels of elk diets from unmanaged old-growth forests within MORA and adjacent managed second-growth forests, and (3) to compare forage values among plant communities on managed elk range.

#### Methods

# Forage Biomass Trends

Standing crop biomass of available elk forage was estimated in 14 plant communities outside MORA along the White River from 7 October 1986-15 April 1987. Available forage was defined as principal forage species available

above snow and below 225 cm in height. Principal forage species were those that comprised at least 1% of the reported autumn-spring diets of elk from throughout the Pacific Northwest (Swanson 1970, Schoen 1977, Janz 1983, Leslie et al. 1984, Harper 1985, Merrill et al. 1987). Plant communities chosen for sampling included a chronosequence of stand ages present on the managed forest, both on mesic bottomlands and on comparatively xeric uplands (Table 1.2).

Available biomass was measured in 3 - 8 randomly selected replicate stands of each plant community. Autumn standing crops were measured using 10 1-m<sup>2</sup> frames systematically placed along a 100-m transect in each sample stand. Canopy coverages and heights were measured for principal forbs, grasses, sedges, evergreen shrubs, and abscised leaves of deciduous trees. Additionally, current years shoots (>4 cm) of deciduous shrubs, conifers and ferns were counted and tabulated according to their heights above ground: 0-25, 26-50, 51-75, 76-100, and 101-225 cm.

Autumn biomass of forbs, grasses, sedges, evergreen shrubs, and abscised leaves were determined from cover and/or height measurements using simple linear regression models. Regression models relating biomass to cover were developed for individual species of principal forbs, evergreen shrubs and abscised leaves. General models based on cover and height were developed for grasses and sedges (Appendix I). Regression models were developed from clipping and weighing vegetation within 12 .25-m² plots after estimating species coverage and height. These plots were distributed randomly throughout the study area within strata containing low, moderate, and high coverage of each species. Vegetation in each plot was clipped to a height of 1 cm, and was oven-dried prior to developing regression models.

Autumn biomass of deciduous shrubs, conifers and ferns was determined as a product of twig density (twigs/ $m^2$ ) and average dry weight of twigs (g/twig). Average oven-dried weights of twigs were determined from random samples of 50-284 twigs of each species obtained from throughout the study area (Appendix II).

Seasonal changes in available biomass were described throughout the winter by monitoring canopy coverage of principal forages within 100 1-m² permanently staked plots. Plots were located systematically along 10 100-m transects distributed randomly among 5 plant communities (2 transects per community) on managed forests adjacent to MORA. Species cover was estimated on 1 November, 15 January, 15 February, and 15 April 1986-87. Seasonal correction factors were developed for adjusting autumn estimates of available biomass based on ratios of winter cover:November cover in the permanent reference plots. If correction factors were not available for a principal forage species or specific plant community, correction factors for similar species and plant communities were substituted.

#### Forage Quality

<u>In vitro</u> digestible dry matter (IVDDM) and crude protein (CP) levels were determined throughout a winter for 34 principal forages of elk. Composite samples of each principal forage were collected on or about 1

November, 15 January, 15 February and 15 April 1986-87. Composite samples were collected from a minimum of 20 plants throughout the study area and consisted of plant parts believed to be selected by elk. Plant parts selected by elk, which in all cases consisted of current year's growth, were determined by examining adjacent browsed plants. Samples of deciduous shrubs collected during November contained both leaves and stems, which were separated prior to conducting nutritional analyses. Shrubs collected later in winter consisted of stem material only. All samples were oven-dried at 40 C within 6 hours of clipping, were ground through a 1 mm sieve, and were then stored in airtight plastic bags at room temperature until they were analyzed. IVDDM was determined using the two-stage procedures of Goering and Van Soest (1970) using inoculum from a fistulated heifer maintained on ryegrass hay and supplemental grain. Crude protein was measured using the micro-Kjeldahl technique (Horowitz 1980:858).

# Diet Composition and Quality

Composition and quality of winter diets of elk were compared between an unmanaged forest ecosystem within MORA and a managed forest ecosystem adjacent to the park. Four composited fecal samples were obtained on each site on or about 1 November, 15 January, 15 February, and 15 April 1986-87 for dietary analyses. Composited samples consisted of 10 fecal pellets from each of 5-8 individual elk within a herd. Composited samples were obtained from each of 4 replicate elk herds on each study site (4 sample dates x 2 study sites x 4 replicates = 32 samples). All samples were stored frozen until they were oven-dried and ground through a 1-mm sieve in preparation for analysis.

Diet composition was determined from microhistological examination of fecal fragments following procedures of Sparks and Malechek (1968). Frequencies of occurrence of each plant species were determined from 20 microscope fields-of-view on 20 microscope slides prepared from each composited fecal sample. Frequencies were converted to percentage relative density (Fracker and Brischle 1944), which was assumed to be proportional to oven-dried weight.

Relative preferences of major forage classes in elk diets were assessed using Ivlev's Electivity Index (Ivlev 1961). Relative preference indices (RPI) (i.e., Ivlev's index) compared proportions of forage classes in diets to proportions of each forage class available in the environment. Available forage was determined from availability in each plant community weighted by the area of each community within the composited home range of elk (Cooper 1987). RPI of forage classes may range from -1, indicating complete absence in the diet, to +1, indicating maximum preference.

Nutritional quality of elk diets was estimated from botanical composition of diets and nutrient content of specific forages. Dietary levels of IVDDM and CP were computed following Westoby (1974) as the nutrient value of each forage weighted by its proportion in the seasonal diet. If nutrient data were absent for a specific forage, mean levels for similar species were substituted.

Two-factor analysis of variance was used to determine significant seasonal and site differences in composition and quality of elk diets. If diets varied among seasons, Fisher's protected LSD test was used to determine significance of all pairwise seasonal comparisons.

# Relative Forage Values of Plant Communities

Traditionally, forage values have been compared among plant communities on the basis of available forage biomass. Such comparisons may be misguided if forages vary widely in digestible energy or in palatability. Therefore, we derived an index for comparing relative forage values of plant communities based on estimates of forage biomass, digestibility, and dietary preferences of elk. Seasonal forage value indices (FVI) were computed for each plant community as the sum of digestible dry matters of forage classes weighted by forage preference indices of elk. Specifically, FVI was computed for each plant community as follows:

 $FVI = \sum_{i=1}^{n} DDM_{i} \times RPI_{i}$ 

where: FVI = Forage Value Index,

 $\mathtt{DDM_i} =$  biomass of digestible dry matter of forage

class i  $(g \text{ IVDDM/m}^2)$ , and

RPI; = Relative Preference Index of forage class i.

n = number of forage classes

It was necessary to rescale Ivlev's RPI, as described in the previous section, so that it ranged from 0, indicating complete avoidance, to 1, which indicated maximum forage preference. Although influences of forage availability and nutrient content on diet selection remain poorly described in the literature, we believe that the above formulation, although simple, describes the nutritional interactions of nutrient quality and preference in a biologically reasonable way.

#### Results

#### Forage Biomass Trends

Seasonal trends of forage availability were influenced strongly by variation in snowpacks. Snowfall occurred sporadically throughout winter, but snow accumulated for only a two-week period prior to and during the January vegetation sampling period. Accumulation of snow averaged 25 cm under open canopies, 22 cm in alder communities, 20 cm in 30-yr-old Douglas-fir communities and 14 cm under old-growth forests. Excluding the January sampling period, our data reflect snowfree conditions during the remainder of winter.

Biomass of available forage was greatest during November and was least during January following a snowfall (Table 2.1). Biomass increased from February to April following disappearance of snow and initiation of green-growth. Mid-winter snowfall covered nearly all forbs, grasses, ferns and abscised leaves during January. Many grasses and sedges were matted down following snow melt; thus, availability of grasses and forbs remained low in February. Availability of grasses and forbs increased from February to April, reflecting an interplay between rapid plant growth and intensive cropping by elk. Evergreen shrubs, primarily low-lying (< 50 cm) salal and Oregongrape were largely covered by snow in January, although elk were observed pawing through snow to feed on low evergreens during this period, so our estimates of availability may underestimate the true amounts accessible to browsers. Availability of deciduous shrubs and conifers were less affected by snow than were low evergreen shrubs, and availability was relatively constant throughout winter.

Post-logging patterns of forage succession differed between mesic bottomlands and xeric uplands in the White River drainage (Fig. 2.1). Grasses, forbs and deciduous shrubs were more abundant in mesic than in xeric plant communities. Grasses and forbs were abundant for up to 40 years in grass-sedge communities that developed on wet sites after logging. Standing water, dense herbaceous vegetation, and intensive herbivory all appeared to inhibit overstory establishment and to perpetuate a long-lived herbaceous community. Grasses and forbs were also abundant in red alder communities that occurred extensively in bottomlands of the White River following logging. Grasses and forbs decreased in red alder communities approximately 20-40 years following logging, after a dense overstory of red alder had developed. Although the development of a red alder overstory reduced availability of grasses and forbs, abscised alder leaves were an abundant and important forage for elk during leaf-fall in October and November.

The xeric sere was strongly dominated by evergreen shrubs, primarily salal and Oregongrape (Fig. 2.1, Table 2.1). Grasses, forbs and deciduous shrubs reached peak biomass during the first 15 years following logging. After approximately 15 years, regenerating Douglas-fir shaded out herbs and shrubs. Evergreen shrubs increased in the early stages following logging and remained abundant in mid- and late-seral stages of succession.

Successional patterns of forage development were variable in 20-40 yearold Douglas-fir forests on xeric uplands. Conifers, deciduous shrubs, and forbs were more abundant on poorly stocked Douglas-fir forests, which developed on poor sites, than on more productive sites (Table 2.1). Greater sunlight and abundant low branches of Douglas-fir resulted in greater availability of forage in poorly stocked forests.

Thinning practices produced negligible forage benefits for elk in 20 year-old Douglas-fir forests (Table 2.1). Conifers were more available in thinned than in unthinned forests; however there were only slight differences in availability of deciduous shrubs, evergreen shrubs and grasses. Understory responses to thinning, if any, would have persisted only a short time until canopies reduced by thinning once again closed over. It appeared that herbaceous forages important to elk had already declined by the time

Table 2.1. Mean standing crop-biomass (g dry matter  $(DM)/m^2$ ) of available forage (current annual growth < 225 cm in height) in 14 plant communities along the White River on four sampling dates, 1986-87.

Plant Community	Forage Class	1 Nov	15 Jan	15 Feb	15 Apr
Mesic Bottomlands					
0-10 years (6) <sup>a</sup>	Conifers Decid. shrubs Evergr. shrubs Forbs Ferns Grasses Leaves	1 20 4 21 3 36 Tb	1 10 1 T 0 0	1 20 3 4 1 10 0	1 20 3 23 T 8 0
10-20 years (6)	Conifers Decid. shrubs Evergr. shrubs Forbs Ferns Grasses Leaves	16 38 4 12 2 30 10	16 30 T T 0 0	16 36 3 3 1 8 0	16 36 3 12 T 7 0
20-40 years/ Red Alder (8)	Conifers Decid. shrubs Evergr. shrubs Forbs Ferns Grasses Leaves	5 10 1 6 6 23 18	5 6 1 T 0 0	5 10 T 2 2 5 0	5 10 T 10 2 14 0
20-40 years/ Grass-Sedge (8)	Conifers Decid. shrubs Evergr. shrubs Forbs Ferns Grasses Leaves	13 15 T 9 1 53 T	12 6 T T 0 0	13 11 T 2 1 6	13 11 T 12 T 20 0
20-40 years/Black Cottonwood (8)	Conifers Decid. shrubs Evergr. shrubs Forbs Ferns Grasses Leaves	7 4 5 7 4 16 24	6 2 1 T 0 0	7 3 5 2 2 3 0	7 3 5 8 2 10 0

Table 2.1. (cont.)

Plant Community	Forage Class	1 Nov	15 Jan	15 Feb	15 Apr
200+ years/	Conifers	3	3	3	3
Douglas-fir (4)	Decid. shrubs	5	5	5	5
	Evergr. shrubs	4	1	4	4
	Forbs	4	0	1	5
	Ferns	6	T	4	3
	Grasses	3	0	3	2
	Leaves	T	0	0	0
200+ years/Western		2	2	2	2
Red Cedar (4)	Decid. shrubs	9	8	9	9
	Evergr. shrubs	2	0	T	т
	Forbs	5	T	2	8
	Ferns	10	T	5	4
	Grasses	11	0	9	8
	Leaves	1	0	0	0
Xeric Terraces and	<u>Uplands</u>				
0-10 years (6)	Conifers	5	5	5	5
0 10 1011	Decid. shrubs	. 8	3	8	8
	Evergr. shrubs	4	1	4	4
	Forbs	14	0	4	14
	Ferns	T	0	T	T
	Grasses	8	0	2	2
	Leaves	0	0	0	0
10-20 years (7)	Conifers	83	80	83	83
. , ,	Decid. shrubs	15	4	10	10
	Evergr. shrubs	16	2	14	14
	Forbs	13	T	5	11
	Ferns	1	0	$\mathbf{T}$	${f T}$
	Grasses	18	0	5	5
	Leaves	2	0	0	0
20-40 years/	Conifers	4	4	4	4
Unthinned	Decid. shrubs	2	1	1	1
Douglas-fir (8)C	Evergr. shrubs	26	5	26	25
	Forbs	4	0	1	4
	Ferns	3	T	2	1
	Grasses	6	0	5	4
	Leaves	T	0	0	0

Table 2.1. (cont.)

Plant Community	Forage Class	1 Nov	15 Jan	15 Feb	15 Apr
20-40 years/	Conifers	11	10	11	11
Thinned	Decid. shrubs	4	2	3	3
Douglas-fir (8)d	Evergr. shrubs	28	5	27	26
	Forbs	3	0	1	3
	Ferns	1	T	1	1
	Grasses	8	0	7	6
	Leaves	0	0	0	0
20-40 years/	Conifers	40	39	40	40
Sparse	Decid. shrubs	7	1	3	3
Douglas-fir (8) e	Evergr. shrubs	28	4	26	26
	Forbs	9	0	3	7
	Ferns	1	T	T	T
	Grasses	9	0	7	6
	Leaves	T	0	0	0
120 years/	Conifers	1	1	1	1
Douglas-fir (3)	Decid. shrubs	T	T	${f T}$	T
	Evergr. shrubs	45	8	40	40
	Forbs	0	0	T	T
	Ferns	0	0	0	0
	Grasses	0	0	0	0
	Leaves	0	0	0	0
200+ years/	Conifers	4	4	4	4
Douglas-fir (3)	Decid. shrubs	1	1	1	1
-	Evergr. shrubs	91	15	82	81
	Forbs	T	0	T	1
	Ferns	T	T	T	T
	Grasses	0	0	0	0
	Leaves	0	0	0	0

Sample size (number of stands sampled, each with 10 1-m $^2$  frames) b T = Less than 0.1 g DM/m $^2$  Regenerating stand not thinned within 5 years d Regenerating stand thinned within 5 years e Poorly-stocked regenerating stand

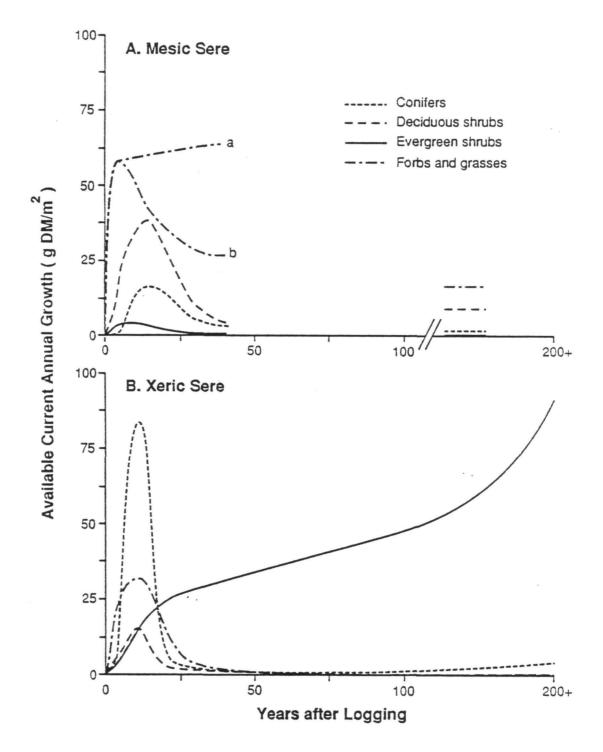


Fig. 2.1. Successional patterns of available current annual growth (g DM/m $^2$ ) following logging on mesic and xeric sites along the White River, Washington. Successional patterns shown for grass-forbs in mesic seres correspond to grass-sedge (a) and red alder (b) successional pathways (see text). Successional patterns for xeric seres correspond to unthinned 20-40 year old Douglas-fir stands.

stands were thinned at approximately 18-20 years of age. Additionally, heavy accumulation of slash in thinned forests may have reduced sunlight and hindered forage.

# Forage Quality

IVDDM and CP contents of forages followed the same seasonal pattern; each tended to be highest during November and April and lowest during midwinter (Table 2.2). Grasses, forbs, and deciduous shrubs increased in nutritive value between mid-winter and April during spring green-up. Grasses and forbs contained the highest level of IVDDM and CP throughout winter, reflecting low lignin contents and high proportions of cell contents (Cook 1972). Aquatic forbs, such as water parsley (Oenanthe sammentosa) and American veronica (Veronica americana) were succulent all winter and provided a limited, yet highly nutritious, winter forage on hydric sites. Evergreen shrubs, conifers, and deciduous shrubs contained low levels of IVDDM and CP during winter. Among browse species, trailing blackberry (Rubus ursinus) was the most nutritious. Swordfern (Polystichum munitum) was high in CP and low in IVDDM. In contrast, horsetail rush (Equisetum arvense), here considered a fern, was highly digestible during spring green-up.

# Diet Composition and Quality

Seasonal differences in diet selection by elk reflected seasonal changes in forage availability. Elk consumed more forbs, grasses and deciduous shrubs during autumn, when a variety of foods were available, than during winter (Fig. 2.2). A wide variety of forbs and grasses were eaten during fall (Appendix III). Abscised leaves of red alder and black cottonwood (Populus trichocarpa) were the most prevalent deciduous shrubs in the fall diets (5-13% of diet). Other important shrubs included willows (Salix spp.), huckleberry (Vaccinium spp.), trailing blackberry, and salmonberry.

Elk consumed more conifers and evergreen shrubs during winter than during fall and spring (Fig. 2.2), particularly when snow covered low-lying forages during January. Important evergreens included Pacific yew (<u>Taxus brevifolia</u>), western red cedar, western hemlock, trailing twinflower, and salal (Appendix III). Elk switched from eating evergreens to eating a variety of forbs and grasses as soon as green grasses and forbs were available during spring (Fig. 2.2, Appendix III).

Relative preferences of elk for the major forage classes were ranked each season using Ivlev's RPI (Fig. 2.3). Although there was considerable seasonal variation in forage preference, the following general ranking of preference was evident: grasses and forbs > ferns > deciduous shrubs > evergreen shrubs > conifers. Relative preferences of forage classes were not correlated with either average IVDDM or CP of forage classes (P > 0.05).

Diets of elk differed between old-growth, unmanaged forests of MORA and nearby managed forests (Fig. 2.2). Differences appeared to be related to differences in forage availabilities. For example, grasses and forbs were more abundant in seral than in climax stages of forest succession (Table 2.1), and they were more prevalent in the diets of elk in managed than in

Table 2.2. Percentage IVDDM and CP in principal elk forages<sup>a</sup> in the White River, WA.

Species	1 Nov		15 Jan-1	5 Feb	15 Ap	15 Apr	
	IVDDM	CP	IVDDM	CP	IVDDM	CP	
Shrubs							
Acer circinatum	44	4					
Alnus rubra	32	11	29	8	39	23	
Oplopanax horridum	43	7	22	•	95		
Populus trichocarpa	43	4					
Rosa spp.		-	33	4	53	23	
Rubus spectabilis	34	6	29	5	43	20	
Rubus ursinus	46	8	48	10	50	20	
Salix spp.			27	5	42	22	
Sambucus racemosa	40	6					
Spiraea douglasii	25	5					
Vaccinium parvifolia	37	7	37	6	64	13	
Vaccinitati parviroria	3,	,	3,		•		
Average	38.	6	34	6	48	20	
<u>Forbs</u>							
Epilobium angustifolium			50	14	47	22	
Fragaria virginiana			30		51	15	
Hypochaeris radicata			69	9	79	15	
Lotus spp.	53	9	0,5		, ,	10	
Oenanthe sarmentosa	74	16	67	21	79	24	
Trifolium spp.	64	16	43	17	68	24	
Veronica officionale	44	5	52	8	00	24	
Veronica americana	60	12	32	0	63	23	
veronica americana	00	12			03	23	
Average	59	12	56	14	67	21	
<u>Ferns</u>							
Equisetum arvense					60	15	
Polystichum munitum			29	11			
Conifers							
Abies grandis			37	5			
Psuedotsuga menziesii			37	5	33	5	
Taxus brevifolia	40	6	39	5	44	5	
Thuja plicata	34	7	33	4	40	4	
Tsuga heterophylla	54	,	35	5	34	5	
Ibaga incorropityIIa			33	5	54	9	
Average	37	6	36	5	38	5	
		-		-		-	

Table 2.2. (cont.)

Species	1 N IVDDM	íov CP	15 Jan-15 IVDDM	Feb CP	15 Apr IVDDM	CP
Evergreen Shrubs <sup>b</sup>						
Arctostaphylos uva-ursi Berberis nervosa Chimophila umbellata	39	5	39 39 34	5 6 6	42	6
<u>Gaultheria shallon</u> <u>Linnaea</u> <u>borealis</u>	28 36	5 6	29 33	4 5	32 47	10 4
Average	35	5	35	5	40	7
Grasses						
<u>Carex</u> spp. <u>Juncus</u> spp.	46	11	50 42	8 7	71	21
Unident.C	62	12	53	11	78	21

Principal forages comprised > 1% of the seasonal diet

Evergreen shrubs includes evergreen sub-shrubs

Values are means derived from 4 independent samples of unidentified grass species that were observed eaten by elk

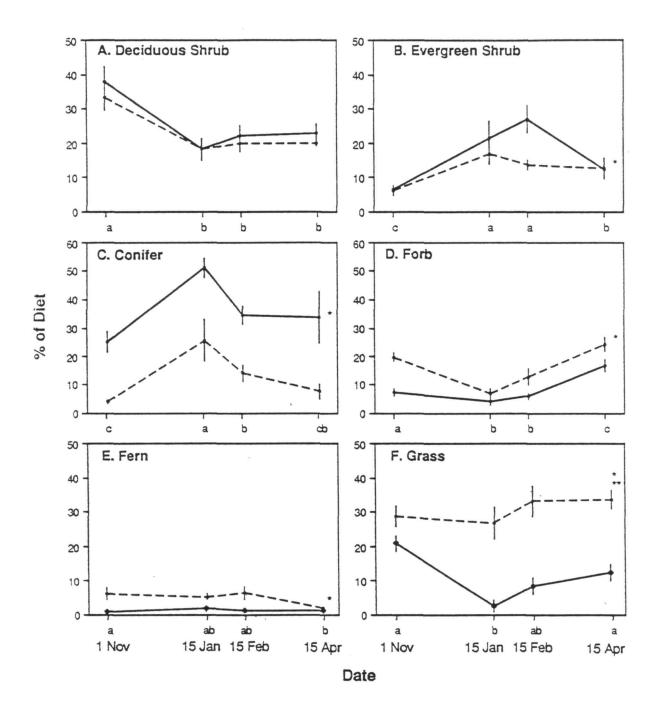


Fig. 2.2. Mean percentages (n = 4,  $\pm$ SE) of major forage classes in the seasonal diets of elk inhabiting urmanaged (——) and managed (——) forest ecosystems in the White River, Nov 1986- April 1987. Different letters between seasons indicate significant dietary differences (LSD test,  $\underline{P}$  < 0.05). \* indicates a significant site difference and \*\* indicates significant site X season interaction (ANOVA,  $\underline{P}$  < 0.05).

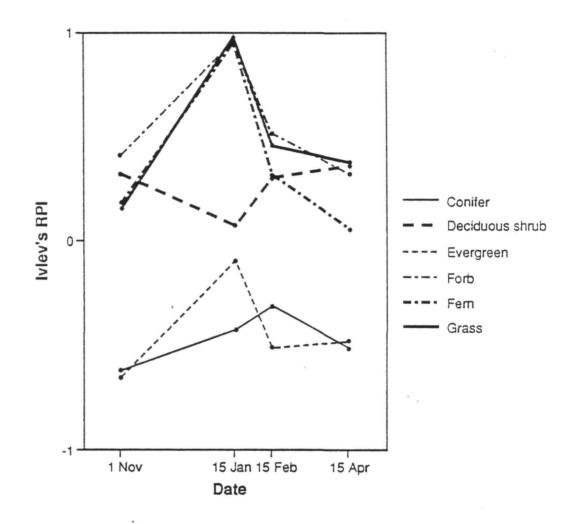


Fig. 2.3. Seasonal Relative Preference Indices (RPI) of forage classes in the White River, Nov 1986-April 1987.

unmanaged forests (Fig. 2.2). Evergreen shrubs were more abundant in climax than in seral communities, and they were more prevalent in the diets of elk in unmanaged forests of MORA than in adjacent managed forests. Additionally, abscised leaves of alder and cottonwood were more prevalent in the fall diets of elk in MORA than in the managed forests. Perhaps greater abundance of preferred grasses and forbs in the seral forest resulted in less use of deciduous leaves.

Seasonal and site differences in forage selection produced similar differences in dietary quality. Diets of elk on both study sites were highest in IVDDM and CP during April; they were intermediate during November, and they were lowest during January and February when elk ate mainly evergreen browse (Fig. 2.4). Highly nutritious spring diets reflected a high proportion of nutritious grasses and forbs in the diets.

Nutrient quality of elk diets was consistently greater in managed forests adjacent to MORA than in unmanaged forests within MORA (Fig. 2.4). The magnitude of that site difference varied seasonally (significant site x season interaction) for both IVDDM and CP. For both IVDDM and CP, dietary quality increased earlier in spring and more rapidly in the managed forest than in MORA. Seral communities in the managed forest provided a greater abundance of nutritious herbaceous forage earlier in the spring than did old-growth forests.

### Relative Forage Values of Plant Communities

Seasonal Forage Value Indices (FVI) of plant communities are presented in Fig. 2.5. Each vegetation class exhibited the same seasonal trend; FVI decreased from November to January, increased following snowmelt in February, and increased further following green-up beginning in February.

Overall, forage values were greater on mesic bottomlands along the White River than on xeric uplands within each age-class (Fig. 2.5). High forage values among mesic communities was related to abundant grasses and forbs, particularly during November and April. True forage values of mesic communities during April may have been greater than was actually measured because intensive grazing by elk reduced standing crop of many highly preferred grasses and forbs.

Forage values decreased with stand-age in both the xeric and mesic seres; however, the reduction in forage value was more pronounced in the xeric sere (Fig. 2.5). By 20 years of age overstory closure had reduced understory forage values in each of the xeric vegetation classes. Forage values remained high in 20-40 year-old red alder, grass-sedge and black cottonwood communities in the mesic sere. In both seres, mature forest communities contained lower forage values than did seral communities. Midseral Douglas-fir forest (~120 years) provided negligible forage values for elk.

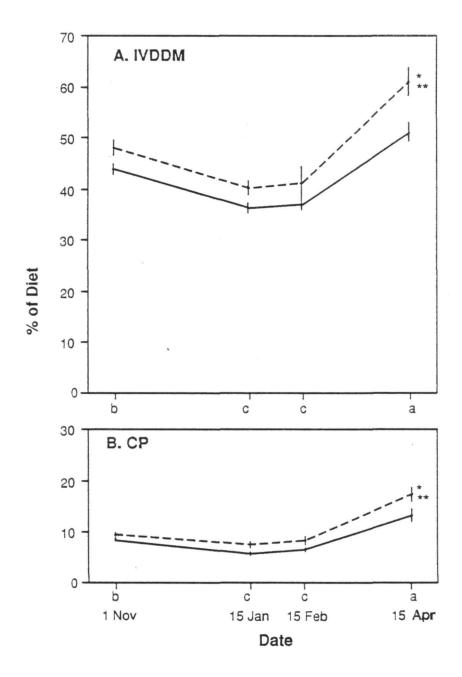


Fig. 2.4. Mean percentages (n = 4,  $\pm$ SE) of in vitro digestible dry matter (IVDDM) and crude protein (CP) in the seasonal diets of elk inhabiting unmanaged (——) and managed (——) forest ecosystems in the White River, Nov 1986- April 1987. Different letters between seasons indicate significant dietary differences (LSD test, P < 0.05). \* indicates a significant site difference and \*\* indicates significant site X season interaction (ANOVA, P < 0.05).

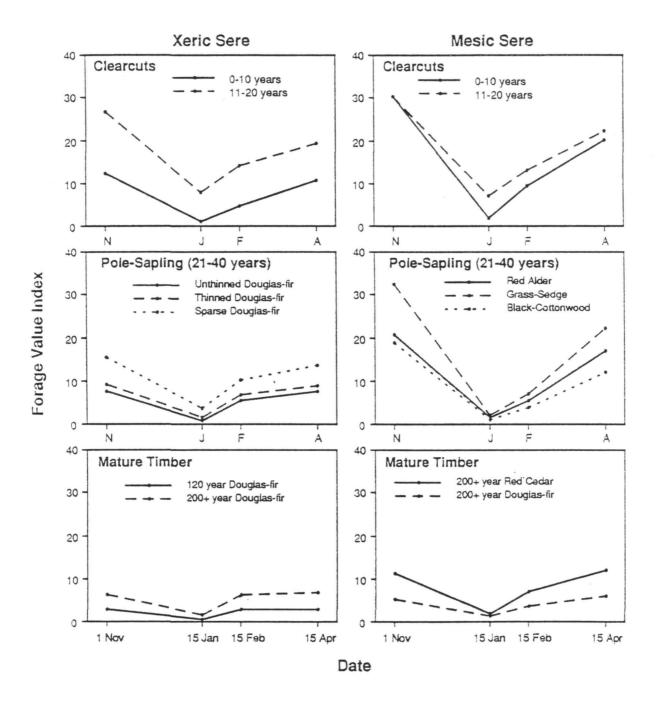


Fig. 2.5. Seasonal Forage Value Indices (FVI) of 14 plant communities on xeric and mesic sites along the White River, Nov. 1986-April 1987. See text for discussion of FVI.

#### Discussion

Post-logging successional patterns in the White River drainage are comparable to patterns previously reported for xeric uplands and mesic bottomlands in the Cascade Mountains (Long and Turner 1975, Hanley 1984). Succession on xeric uplands produced the now-classic picture of forage development that has emerged from comparable studies in the Pacific Northwest; i.e., clearcutting produces a pulse of forage that persists for approximately 8-20 years until the developing overstory shades out understory vegetation (Long and Turner 1975, Wallmo and Schoen 1980, Hanley 1984). Once overstory crown closure is complete, understories are often nearly devoid of elk forages. Understory development after complete crown closure was a long-term process marked by gradual thinning of forest overstories, increased lighting of the forest floor, and gradual increase of shrubs, primarily salal. Descriptions of succession from throughout the Cascade Mountains suggest that this pattern applies widely to montane forests in the Douglas-fir zone.

Successional patterns of forage development were variable on mesic bottomlands of the White River. Divergent successional pathways in riparian forests were probably related to complex patterns of alluvial deposition and soil moisture. Grass-sedge communities became established following logging in low-lying wet sites, whereas second-growth alder communities became established in better-drained bottomlands. Overall, successional pathways on bottomlands were distinct from those of uplands in containing a long-lived seral stage characterized by high productivity of grasses, forbs and deciduous shrubs.

Seasonal nutritive qualities of forages and dietary selections of elk were similar to broad patterns reported throughout the Pacific Northwest. Our findings upheld the general belief that grasses and forbs are preferred winter forages of elk, but that elk often consume less-digestible browses whenever availability of preferred forages limits rate of forage intake. In the White River, elk ate more herbaceous forage during autumn and spring than during winter, following trends in availability. Elk also consumed more grasses and forbs in managed forests, where seral bottomland communities provided abundant herbage, than in MORA. Use of evergreen browse, in contrast, was greatest in unmanaged forests where seral forest communities were limited, and in managed forests following a deep snow that restricted availability of herbaceous forage. Abscised leaves of alder and cottonwood also were important alternate forages of elk during autumn, especially in MORA where grasses and forbs were comparatively scarce. Alder also comprised 22-50% of the autumn of diets of elk and deer in Olympic National Park (Leslie et al. 1984), which suggests that deciduous leaves may be of greater importance to cervids during autumn than was previously believed.

Dietary CP levels in the White River drainage (5-8%) were within the range of values previously reported for Roosevelt elk during winter in the Pacific Northwest (7-8%, Janz 1983; 8.3%, Leslie et al. 1984; 8% (November), Merrill et al. 1987). Most investigators have considered those levels adequate for maintaining body weight over winter, assuming forage intake, digestible energy, and protein digestibility is adequate (Janz 1983, Leslie

et al. 1984). Few studies, however, have examined those assumptions critically. Dry-matter intake may be severely constrained during winter by low turnover rates associated with high lignin-cutin contents, cell structural characteristics of browse (Spalinger et al. 1986), or by limited ability of ruminants to detoxify or absorb phenolic compounds in browse (Robbins et al. 1987). Additionally, endogenous protein may be catabolized to help mitigate the effects of energy deficiencies. Furthermore, digestibility of protein is reduced depending upon concentrations of insoluble protein-binding phenolic compounds in the diet (Robbins et al. 1987). For example, Robbins et al. (1987) reported that conifer rations containing 6-8% CP contained only 0-3% CP that was digestible by deer. These findings suggest that dietary protein in the White River, as elsewhere in the Pacific Northwest, may be deficient.

Dietary IVDDM of elk during winter (35-40%) was above dietary levels reported for elk inhabiting nearby coastal regions (31-34%, Janz 1983; 25%, Leslie et al. 1984). Those differences may reflect different inoculum sources used in in-vitro digestion trials (Milchunas and Baker 1982) and differences in forage sampling methods, as well as real regional differences. Our results, however, agree with previous studies concluding that IVDDM of winter diets was insufficient for elk to meet daily energy requirements and animals could be expected to decline in body weight over winter. Daily energy requirements of ruminants have been approximated as 150 kcal/kg $^{0.75}$ / day (Robbins 1983). An average 250-kg cow elk, therefore, would require a daily intake of 5.1-5.9 kg DM/day, assuming a gross energy content of forage equal to 4.5 kcal/kg, a metabolizable energy coefficient of 0.85 (Hobbs et al. 1982), and assuming percent IVDDM of forage ranging from 35-40% (this study). Merrill et al. (1987) estimated that "average" elk were capable of consuming only 3.2 kg DM/day during November near Mount St. Helens, Washington. That estimate was derived from activity budgets, forage availability and foraging rates of elk on Mount Saint Helens, but it provides a general indication of relative deficiencies of winter diets in the White River.

Seasonal and site variability of dietary nutrients were related to availability of herbaceous forages. Dietary levels of IVDDM and CP were both greater in a managed forest, where herbaceous forage was comparatively abundant, than in an unmanaged forest ecosystem. In addition, dietary levels of IVDDM and CP decreased in early winter in both sites as availability of herbaceous forage decreased, and it increased markedly during spring greenup. Green-up and associated nutritional benefits, however, occurred approximately 2-3 weeks earlier in the managed than the unmanaged forests.

It is tempting to equate site differences in dietary qualities solely to influences of past forest management activities; however, geographic differences between study sites also played a role. Elk winter range within MORA was approximately 300m higher in elevation than winter range outside the park. After one January storm, snow depth averaged only 5 cm deeper on MORA winter range than on lower-elevation managed ranges. Accumulations resulting from that storm, however, persisted approximately two weeks longer within MORA than at lower elevations outside the park. Unfortunately, we cannot determine the relative influences of elevation and forest management

activities on dietary nutrient qualities of elk inhabiting these two winter ranges.

Cause of nutritional differences notwithstanding, enhanced nutrition of elk wintering outside MORA could have important consequences for populations of elk summering within the park. Improved winter nutrition would result in reduced weight-loss and mortality of cow elk, reduced pre-natal and neo-natal losses of calves (Thorne et al. 1976), greater fall weights of cows, and increased ovulation and pregnancy rates (Trainer 1971). These results were reflected in observations of higher calf:cow ratios and rates of population growth of elk inhabiting lower-elevation managed ranges outside MORA than of elk wintering within the park (unpubl. data, K. Cooper).

Relative foraging values of old-growth and immature forests are at the core of contemporary issues regarding management of remaining old-growth forests in the Pacific Northwest (Schoen et al. 1981, Bunnell 1985). Many wildlife managers believe that forage values of old-growth forests have been underestimated in the past relative to values of seral forests. Measurable benefits of old-growth forests have included greater standing crop biomass of forage (Bunnell and Jones 1984), reduced snow accumulation and greater availability of forage (Jenkins et al. 1990; Harestad et al. 1982), increased nutritional value of browse (Hanley et al. 1987, Happe et al., in prep.), and greater availability of arboreal lichens and litterfall in old-growth than in immature forests (Stevenson and Rochelle 1984).

Forage values measured along a successional sequence of plant communities in the White River, however, suggested that many seral forests provided forage values superior to those of old-aged forests during mild winters. Admittedly, we did not measure standing crops of arboreal lichens and litter, which Stevenson and Rochelle (1984) reported often exceeded biomass of ground-rooted vegetation in old-aged forests on Vancouver Island, BC. Nor did we compare forage values during prolonged periods following deep snow. Additionally, we measured forage values based on available biomass, forage digestibility, and forage preferences of elk, rather than based on just forage biomass. Previous studies reviewed by Bunnell and Jones (1984:413) indicated that old-age forests contained 2-20% as much biomass of key winter forages of black-tailed deer (Odocoileus hemionus columbianus), primarily salal, than did immature forests. We, too, measured 2-25X as much evergreen shrubs in old-age than in immature upland forests of the Douglasfir zone. We chose, however, to discount the importance of salal and Oregongrape in estimations of forage values because they were of such low preference by elk. Forage values of plant communities, one should expect, would differ for black-tailed deer and elk because of interspecific differences of foraging strategies and forage preferences (Hanley 1984).

Comparisons of forage values between xeric and mesic seres in the White River drainage revealed that forage values are influenced by a variety of unmeasured factors besides stand-age. Forage values computed for communities within a single age class often varied as much as between age-classes. For example, during November forage values of communities 11-20, 21-40 and >200 years old, differed by as much as 2.5X, 4.2X, and 2.0X within an age-class, respectively (Fig. 2.5). We suggest, therefore, that standard notions of

post-logging forage succession are too simple to warrant widespread application in forest management. Clearly, additional systematically conducted research is needed on successional trends of elk forages in a variety of riparian and upland forest associations throughout the range of elk.

The data presented above leave little question that clearcuts provided a significant increase in forage values for elk during mild winters. Clearly, however, this should not be construed to mean that clearcuts are better elk habitat than old-age forests. In both a managed and an ummanaged forest, elk foraged principally upon conifers and evergreen shrubs following a winter storm. Evaluation of Fig. 2.5 reveals that 12" of snow virtually negated forage values of many immature forests, which equalized forage values of different aged stands. Deeper or more prolonged snow than was observed in this study would result in further increases of forage values in old-age relative to immature forests. Previous studies of big game-forest management relationships have revealed that snow intercepting capabilities of old-age forests may increase accessibility of browse (Harestad et al. 1982), reduce energy costs of foraging (Parker et al. 1984), and enhance abilities of elk to conserve energy during nutritionally restrictive winters. Additional behavioral preferences of elk for old-age forest communities are likely to occur, but have been difficult to determine.

It seems clear from the results of this and comparable studies of elk-habitat relations that a mosaic of immature and old-age forest habitats is optimum for elk. Excessive harvesting of old-aged forests may increase ecological carrying capacity (sensu Caughley 1976) for elk during successive mild winters, but would likely result in greater density-dependent and -independent winter losses of elk during severe winters. Optimum proportions of forest ages, therefore, will vary as functions of prevailing snow characteristics, site-specific successional patterns of forage development, and big game management objectives.

#### CH. 3: ELK HABITAT MODELING

Habitat modeling is an important tool used in assessing influences of land-use developments on wildlife populations. Simulation procedures that link models of secondary forest succession and carrying capacity (the number of animals that can be supported per unit area of habitat) are particularly useful for predicting the long-term effects of forest management activities on big-game populations and habitats (Hett et al. 1978, Raedeke and Lemkuhl 1985, Jenkins and Wright 1987). Such models are generally very tractable, cost-efficient, and they enable managers to predict responses of wildlife to a variety of forest management activities without long-term and costly field experimentation (Raedeke and Lemkuhl 1985).

Two models of forest succession/carrying capacity have been developed for assessing responses of elk populations to forest harvesting activities near Mount Rainier National Park (MORA), Washington. One model, HABSIM, was developed for the National Park Service to determine possible influences of forestry practices on elk populations that summer within the MORA (Raedeke and Lemkuhl 1984, 1985). Another model, FORPLAN, was developed by the U.S. Forest Service to assist with long-term planning of timber and wildlife resources on the Gifford Pinchot National Forest adjacent to MORA (B. Ruediger, Gifford Pinchot National Forest, pers. comm.). Although the overall objectives and structure of the two models were similar, they produced markedly different predictions of elk population responses to logging. While such discrepancies cast obvious doubts on the predictive accuracy of one or both models, further examination of these differences would fulfill an important role of ecological modeling -- identifying deficiencies in ecological understanding and important areas of future research.

The purpose of this study was to review existing models of elk responses to forest harvesting and secondary succession in the MORA ecosystem, and attempt to resolve discrepancies between the two models. In so doing, we developed a new model, a hybrid of its predecessors that we believe draws the best features from both models using site-specific data obtained from this study. Unlike its predecessors, however, our model forecasts forage values of elk winter ranges rather than elk densities. That approach reflects our perspective that forage, although having an important influence on habitat quality, is a poor predictor of actual elk numbers. Lastly, we demonstrate several applications of our model by assessing the influences of harvesting rates, rotation lengths, thinning rates, hardwood conversions and winter snowfall on forage values in the White River drainage adjacent to MORA.

#### Review of Previous Models

Both HARSIM and FORPIAN were developed as tools for estimating future Potential Carrying Capacities (PCC) of elk winter ranges adjoining MORA (additionally FORPIAN has very broad capabilities of estimating a variety of future environmental qualities in the managed forest). PCC is defined as the maximum density of elk that a habitat can support at a specified time based on the available forage supplies and food-requirements of elk. Actual densities of elk may be less than PCC whenever factors other than forage

supplies limit the elk population (e.g., hunting, predation, disease, density independent mortality).

The concept of PCC used in HABSIM and FORPIAN differs from the interactive forage-based concept of ecological carrying capacity (ECC) described by Caughley (1976:217). ECC is the equilibrium density of herbivores that is established after a lengthy period of mutual interaction between herbivore and food supply. PCC, in contrast, is the density of herbivores capable of being supported by the food-supply at any specified time.

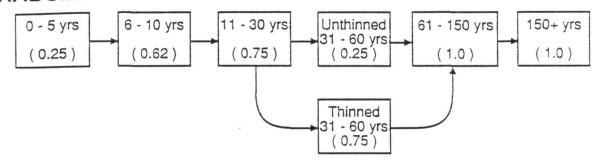
The structures of HARSIM and FORPIAN are very similar. Both models use a computer algorithm as a simple book-keeping tool to track acreages of several forest age-classes during the simulation period. The modeler must provide data on the initial acreages of each forest age-class, and an estimate of PCC of each. After each simulated time-step, each acre is advanced one unit of age, and a specified proportion of acreage exceeding rotation age is set to age 0, thus simulating harvest. PCC of the region is determined for each time-step by multiplying acreage of each forest age-class by its estimated PCC (i.e., elk/acre). Both models assume that PCC of forest age-classes is constant during the simulation period. Hence, each model implies that PCC is uninfluenced by environmental factors such as winter severity, human disturbance, spatial arrangements of habitat patches, or any interaction between elk and their food supplies (e.g., retrogressive succession, accelerated succession, response of plant production to herbivory).

Despite the conceptual similarities, HARSIM and FORPIAN consistently produce different patterns of elk population responses to timber harvest on winter ranges adjacent to MORA. HARSIM predicts that PCC of winter range will decline steadily following the initiation of logging (Raedeke and Lemkuhl 1984), whereas FORPIAN predicts that PCC will increase for approximately 20 years following harvest (B. Ruediger, GPNF, pers. comm.). FORPIAN, like HARSIM, predicts that PCC decreases after 21-60 years following logging; i.e., after regenerating overstories reach complete crown closure and shade out understory forages. The major discrepancy between models, therefore, occurs in the early stages of forest regeneration when HARSIM predicts declining habitat quality and FORPIAN predicts an increase in habitat quality.

Reasons for this discrepancy can best be appreciated by examining the sequences of post-logging forest succession incorporated in each model (Fig. 3.1). HABSIM incorporates six age-classes in the successional sequence (Fig. 3.1). HABSIM assumes that PCCs of forested age-classes are maximum in mature forests (60-150 years post-logging) and old-growth timber (stands > 150 years old), and that PCCs of immature, regenerating stands are less than in older forests. Given those relative rankings of carrying capacity, the model will always predict a decline in PCC whenever mature or old-growth stands are harvested.

FORPLAN, in contrast, allows for only three stages of forest succession after logging (Fig. 3.1). Immediately following logging, PCC of early-seral

# HABSIM



# **FORPLAN**

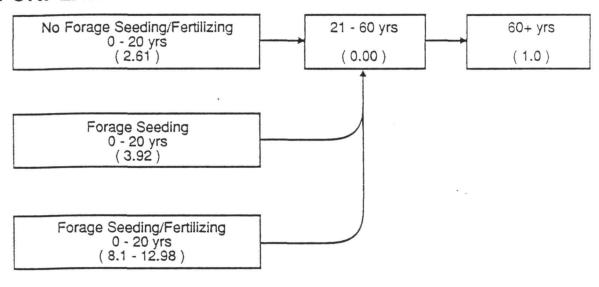


Fig. 3.1. Comparison of post-logging successional pathways and relative carrying capacities of forest age-classes used in the habitat models, HABSIM and FORPIAN. Relative carrying capacities in parentheses are expressed as fractions or multiples of PCC of mature forests ( > 60 years old).

clearcuts is presumed to be 2.6-13.0 times greater than PCC of mature forests (Fig. 3.1). Variable PCC of clearcuts reflects variable production of elk forage associated with three different management practices. FORPIAN assumes that PCCs of clearcuts declines to zero at 21 years post-logging, and then increases in mature stands of second growth (60 years +). High PCC weightings given to clearcuts causes FORPIAN to predict an increase in habitat quality for a limited time following logging.

Differences in PCC weightings used in the two models reflect different estimation techniques, as well as broadly different assumptions regarding factors limiting elk populations in the Pacific Northwest. Habitat weightings used in HABSIM are based largely on professional "guesses" at carrying capacity. Those weightings assume implicitly that deep snow eliminates many forage values of early seral clearcuts during winter, and that elk are limited primarily by forage available in mature coniferous stands during severe winters. Raedeke and Lemkuhl (1984) recognized that these assumptions present a conservative view of population limitation of elk in the western Cascades, and that elk may benefit in actuality from forage produced in clearcuts during mild winters. They concluded, however, that populations are limited in the long term by abilities of habitats to carry elk through severe winters.

Habitat rankings used in FORPLAN were based on forage production in the Siuslaw National Forest in the Coast Range of Oregon (B. Ruediger, GPNF, pers. comm.). PCC of each forest age—class was determined from estimated biomass of consumable forage in each age—class and estimated forage consumption by elk over a 120—day winter. Those computations of PCC assume implicitly that forage production in the Cascade Mountains of Washington is the same as in the Coast Range of Oregon. Furthermore, the procedure assumes that forages in clearcuts are available to elk during winter. The model fails to account for seasonal reductions of forage in clearcuts due to deep accumulations of snow and increased cover requirements of elk during severe winters.

Each of the models described above presents a simplistic picture of complex elk-range interrelationships in the Cascade Mountains. Comparisons of model predictions to observed elk populations in the White River do not support the simple modeling assumptions. Elk populations in MORA's northern elk range more than tripled from 1974-1984 (unpublished data, S. Schlegel, Mount Rainier National Park) during a period when predictions of PCC declined (Raedeke and Lemkuhl 1984:62). Raedeke and Lemkuhl suggested that opposing patterns were caused by an uncoupling of elk population and habitat trends, i.e., that elk populations colonized an understocked range at the time PCC of the winter range was declining. An alternative explanation is that elk populations increased in response to low levels of sport-harvest and increased forage available in clearcuts during a series of mild winters in the 1970s and early 1980s. Additionally, elk have been observed wintering at elevations as high as 3000' and above during recent mild winters (typically transitional spring range), which has enabled elk to exploit forage produced in clearcuts at elevations that are not usually accessible during normal winters (pers. comm., R. Spencer, Washington Dept. of Wildlife). Although these explanations would tend to support the assumptions of FORPIAN over

those of HABSIM, we stress that elk population trends following a series of severe winters may more closely resemble predictions of HABSIM than FORPIAN. Densities of elk wintering in the Cascade Mountains reflect a complex interplay between poorly understood forage successional patterns, cover requirements of elk, winter severity, and sport-harvest.

The above examination of model assumptions and performances fulfills an important function of ecological simulation. It points out deficiencies in our understanding of interacting components of ecological systems. And it points to specific improvements of existing models that would enhance model realism and predictive capabilities. Clearly additional research is needed on relationships among overstory canopy, snow depth, availability of preferred forages, and rates of nutrient acquisition in a variety of forest habitat types found in the western Cascade Mountains. Additional modeling efforts in the MORA ecosystem should incorporate site—specific measures of forage availability, more realistic patterns of post-logging forage succession, and influences of stochastic snowfall on elk habitat qualities.

### Model Development

The model developed below, like HABSIM and FORPLAN, links models of successional patterns with habitat quality to permit long-term assessment of forest management activities on elk habitats in the MORA ecosystem. Unlike either of its predecessors, the model incorporates site-specific data on elk distribution, forest successional patterns and forage availability. We make no attempt to simulate actual carrying capacities (i.e., potential numbers of elk) of the MORA ecosystem; rather, this model simulates changes in forage values of habitats resulting from past and present logging activities. It is tempting to equate variations of forage values caused by forest management activities with corresponding changes in carrying capacity of elk ranges. Carrying capacity, however, is defined by complex interactions among availability of high quality forages, availability of forested cover used for energy conservation, human disturbance factors, and interspersion of required habitat components. Changes in forage values, therefore, would influence carrying capacity only if forage were limiting. Other important limiting factors, including cover, winter weather, and hunting will be discussed qualitatively. The model is deterministic in the sense that winter severity is held constant to allow the user to compare influences of several forest management scenarios without the confounding influence of variable winter severity. We have, however, added an optional stochastic element in the model to also permit an assessment of potential effects of winter weather.

The model was developed for assessing forage values on specific winter and spring home ranges used by migratory elk in the White River drainage (Fig. 1.2-1.3). The first step in model construction, therefore, was to describe site-specific patterns of forest succession found within the home ranges of elk. We identified two broadly different successional pathways along the White River, one describing a mesic sere in bottomlands on the valley floor, and another describing a xeric sere on elevated river terraces and uplands (Fig. 3.2). For both seres, two stages of clearcuts were recognized; 0-10 year-old clearcuts, which corresponded to grass-, forb- and shrub-dominated stages of early succession, and 11-20 year-old clearcuts,

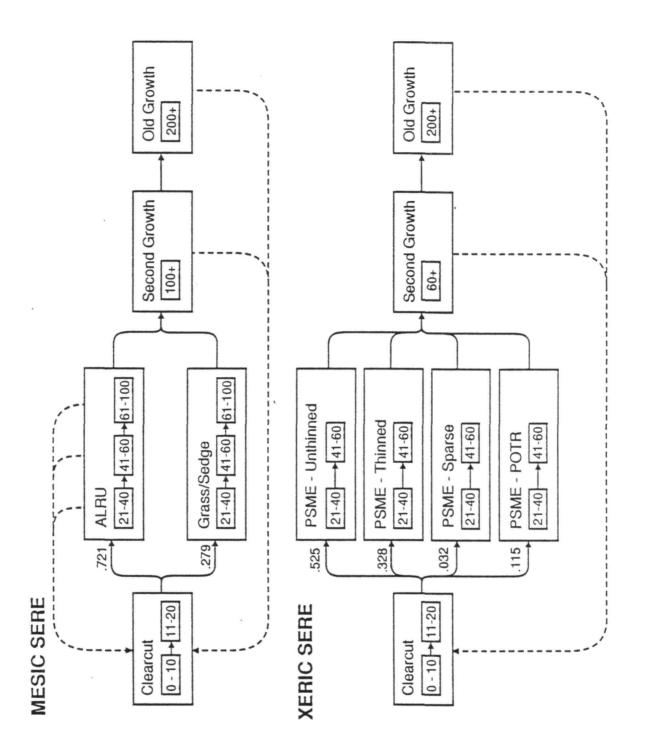


Fig. 3.2 Post-logging successional pathways for mesic and xeric seres along the White River, Washington. Solid lines represent forest successional pathways and dashed lines represent timber harvesting options in the model. Transition probabilities shown for 20-year-old forests were determined from aerial photographs and thinning records.

which corresponded to shrub— and conifer—dominated stages that occur before complete crown closure is reached. Successional pathways were variable after age 20 in both seres. Mesic stands developed closed canopies of red alder (AIRU, Fig. 3.2) on mesic to hydric soils of the <u>Tsuga heterophylla—Polystichum munitum</u> and <u>Thuja plicata</u> habitat types (Henderson and Peter 1984). Grass/sedge stands formed on hydric soils on <u>Thuja plicata</u> habitat types. Mid—seral stages of succession in xeric seres included thinned and unthinned Douglas—fir stands (PSME, Fig. 3.2), sparse PSME stands on xeric, shallow soils, and PSME—Black Cottonwood (POTR, Fig. 3.2) stands on shallow alluvium.

System feed-backs were incorporated in the model by allowing rotation-aged stands to be converted to clearcuts as a result of timber harvesting activities (Fig. 3.2). Rotation lengths of 60 and 100 years were assumed for xeric and mesic seres, respectively. Longer rotation periods in the mesic sere simulate the effects of approximately 40-60 years of competition between regenerating conifers and either red alder overstories or grass-sedge understories.

Forest successional patterns observed along the White River were simulated using a compartment-based model similar to that described by Shugart et al. (1973) and applied to elk habitats by Hett et al. (1978). modeling algorithm treats each vegetation class as an environmental compartment and land-area as a variable that flows between compartments. The rate of flow of land between compartments during each simulated time-step is controlled by a series of transition probabilities. In this model we used a time increment of 5 years, and during each iteration we allowed 100% of area within each 5-year age-compartment to flow to the next older compartment. Following each iteration, land areas contained within each of the vegetation and age-classes shown in Fig. 3.2 were determined by summing land areas within the appropriate 5-year intervals. Flow of land-areas among various mid-successional pathways were governed by transition probabilities determined from aerial photographs. Rotation-aged stands were allowed to remain in the same cover class during an iteration or they were converted to clearcuts at a user-defined transition rate. From an ecological viewpoint, transition probabilities allowed seral communities to age five years during each iteration, and they allowed rotation-aged stands to either remain the same, or to be harvested and converted to a clearcut.

The successional model was used to simulate future patterns of forest succession. To provide a complete record of past and future habitat composition, historical patterns were reconstructed from logging records of each land-ownership in the study area. Historical patterns linked with future projections provided a continuous record of past and future vegetational composition of elk winter and spring ranges in the White River drainage.

The successional model was developed for making projections of elk forage values on winter and spring ranges in the White River drainage. This was accomplished by estimating a forage value index (FVI) for each vegetation class and weighting these indices by acreages of each vegetation class after each model iteration. As discussed in chapter 2, FVI was defined as the sum

of digestible dry matter of forage classes in each vegetation class weighted by relative forage preferences of elk (see Fig. 2.5). An examination of Fig. 2.5 reveals that FVI of each vegetation class varies seasonally in response to changing snow depths and forage availabilities. Therefore, it was necessary to derive mean estimates of FVI that described relative forage values of vegetation classes averaged over winter. Mean FVIs were computed as the mean of weekly estimates of FVI obtained between 1 November 1986-15 April 1987 (Fig. 2.5). Those indices reflected average forage values for a winter that received approximately 12" of snow for a two-week period. In actuality, however, FVIs vary between years in relation to depth and duration of snowpacks. Therefore, we also estimated mean FVIs of each vegetation class for a variety of snowpacks possible in winter (Table 3.1). Mean FVIs were estimated for variable snowpacks based upon known height distributions of twigs in each vegetation class (K. Jenkins, unpublished data). Unless otherwise specified, all simulations of forage values were based on snowfree winter conditions. An optional stochastic feature permitted evaluation of influences of random snowpacks on forage values. To simulate the effects of stochastic snowfalls, a sub-routine was used to randomly select (equal probabilities) one column vector of FVIs corresponding to a specific combination of depth and duration of snowpacks.

Simulation of FVI as a function of successional change required the use of several simplifying assumptions. First, it was assumed that rates of forest succession were constant during the simulation. Secondly, it was assumed that forage values were constant within each vegetation class and throughout the simulation period, and there was no interaction between elk and their food supplies.

## Model Applications

The forage succession model was used to simulate changes in elk forage values resulting from past and future forest management activities in the White River watershed. Forage values were simulated separately for winter and spring ranges of the White River elk herd. Results of the model, therefore, apply only to these specific ranges and may not reflect regional trends.

Reconstruction of past logging histories indicated that forest management activities have influenced forage values profoundly for both the winter and spring ranges of elk in the White River (Fig. 3.3). Forage values increased sharply on winter ranges during the 1960's, reflecting the rapid liquidation of low-elevation old-growth forests during the late 1950's and 1960's (Table 1.3). Forage values of winter ranges peaked in the late 1960's and declined from the 1970's to the present. Declining forage values have resulted primarily from development of complete crown closure in dense regenerating stands of Douglas-fir.

Forage values on spring ranges also increased in response to forest harvesting during the 1950's and 1960's (Fig. 3.3). Forest harvesting, however, occurred more gradually on higher elevation spring ranges than on low-elevation winter ranges. Consequently, the increase in forage values seen on spring ranges occurred more gradually than on winter ranges and has

Table 3.1. Mean seasonal Forage Value Indices (FVIs) of 13 plant community/age class combinations estimated for various combinations of snow depth (cm) and snow duration (weeks) in the White River. Mean values were compiled as the mean of weekly estimates of FVI between 1 Nov. - 15 Apr.

Community/age class			Sn	ow depth	(cm)	snow du	ration(w	ks) <u>b</u>		
2, 3	0/0	25/4	25/8	25/12	50/2	50/6	50/10	75/4	75/10	100/12
Mesic Bottomlands										
0-10 yrs	16.2	12.8	10.6	8.5	13.4	11.2	9.0	12.0	8.6	7.3
10-20 yrs	18.6	16.0	14.2	12.5	16.4	14.6	12.8	15.0	12.1	10.8
20-40 yrs/ALRU	11.0	9.5	7.9	6.4	10.2	8.6	7.0	9.3	6.8	5.9
20-40 yrs/Grass-sedge	15.5	13.8	11.4	9.1	14.5	12.2	9.8	13.2	9.7	8.3
200+ yrs/THPL <sup>a</sup>	8.9	6.2	5.2	4.4	6.5	5.6	4.7	6.0	4.6	4.0
Xeric Uplands						,				
0-10 yrs	7.5	5.9	4.9	4.0	6.1	5.1	4.1	5.4	3.9	3.2
10-20 yrs	17.9	14.8	13.5	12.1	14.9	13.5	11.9	13.8	11.4	9.9
20-40 yrs/Unthinned PSME	6.4	4.0	3.3	2.7	4.2	3.5	2.9	3.8	2.7	2.4
20-40 yrs/Thinned PSME	7.7	5.0	4.3	3.6	5.1	4.4	3.7	4.6	3.5	3.1
20-40 yrs/Sparse PSME	12.1	8.7	7.7	6.7	9.0	7.9	6.9	8.4	6.8	6.1
	5.8	4.7	3.9	3.1	4.9	4.2	3.4	4.5	3.3	2.8
20-40 yrs/PSME-POTR	5.0									
	2.8	1.7	1.4	1.2	1.6	1.4	1.1	1.4	1.1	0.9

<sup>&</sup>lt;sup>a</sup> FVIs of 14 plant community/age classes were presented in Fig. 2.5. Mesic old-growth PSME stands were omitted from this analysis. Rather, FVIs of THPL stands were employed in the successional models.

b Snow depth measured in open plant communities where adjusted for forested communities based on measurements of snow depths in the study area.

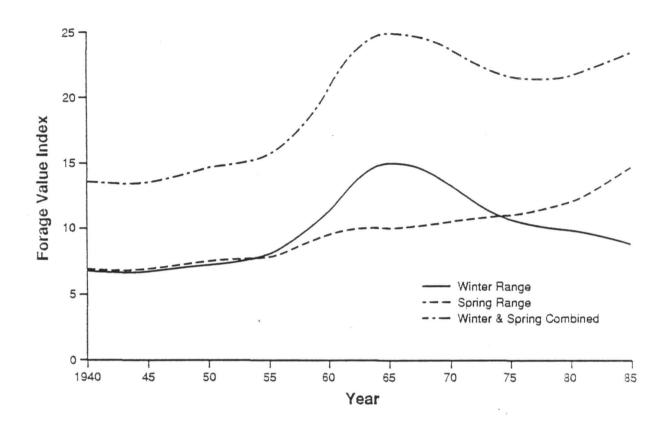


Fig. 3.3. Simulated response of Forage Value Indices (FVI) to past forest harvesting activities and forest succession on winter range, spring range and combined range in the White River watershed. Combined FVI is the sum of FVIs for winter and spring ranges.

been more persistent. Forage values on spring ranges appear to have increased steadily from the time logging was initiated until the present.

Four different forest management activities were simulated using the forest transition matrices, the 1985 plant community composition, and forage value indices. The first set of simulations examined the influence of different rates of forest harvesting on winter and spring ranges. Harvest rates referred to the percentage of rotation-aged stands that were cut every five years. Computationally, these are the transfer rates governing the flow of land area from second-growth and old-growth model compartments to the clearcut compartment during each model iteration (Fig. 3.2).

Three harvest levels, corresponding to 0%, 20%, and 40%, were simulated on elk winter ranges along the White River (Fig. 3.4). Predicted forage values declined steadily from 1985 levels until approximately 2015 in each simulation. Declining forage values reflected overstory development and shading in areas clearcut during the 1950's and 1960's. Different harvest rates had very little effect on forage values before 2015 because only a few stands came of rotation age before then. Beyond that date, forage values increased at a rate depending upon cutting intensity. Simulation of a no-harvest option produced a pattern of declining forage values well into the next century.

Two harvest levels were simulated on elk spring ranges, corresponding to 20% and 40% five-year harvest rates (Fig. 3.5). As on winter ranges, estimated forage values of spring ranges declined until the existing second-growth stands reached rotation age. Simulated forage values decreased rapidly during the 1990's as the extensive areas harvested in the early 1970's developed a closed canopy. Stands that were harvested in the 1940's reached rotation-age in the early 2000's. Simulated harvest of those stands helped stabilize forage values of spring range during the early 21st century.

A second set of simulations examined the influence of precommercial thinning on forage values in 20-40 year-old Douglas-fir stands. Two thinning scenarios were compared on elk winter ranges: 0% thinning rate in which no stands were thinned, and 100% thinning in which all stands were thinned every five years. Variable thinning rates were simulated by varying the transition probabilities which governed the flow of land area into thinned versus unthinned model compartments (Fig. 3.2).

Simulated thinning activities had little influence on forage values of elk winter ranges in the White River (Fig. 3.6). The small influence of thinning reflected narrow differences of forage values between thinned versus unthinned stands (Table 3.1).

A third set of simulations compared forage values resulting from various harvesting rates of second-growth alder communities. We simulated 0%, 20% and 60% five-year harvest rates in alder communities by adjusting transition probabilities governing flow of land between alder and clearcut model compartments.

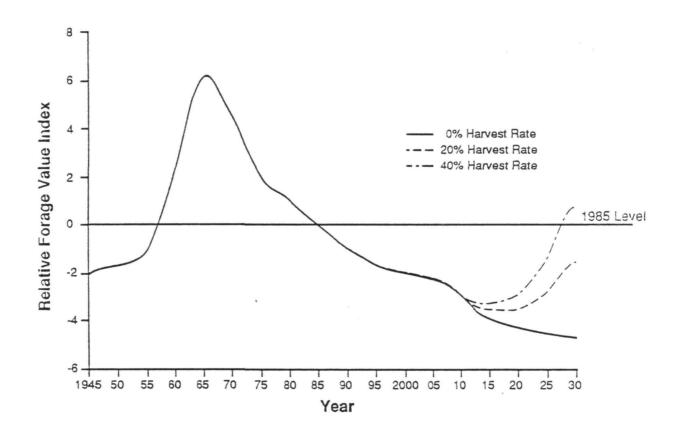


Fig. 3.4 Simulated response of Forage Value Indices (FVI) to three levels of forest harvesting on elk winter range in the White River watershed. FVIs are scaled relative to baseline 1985 levels.

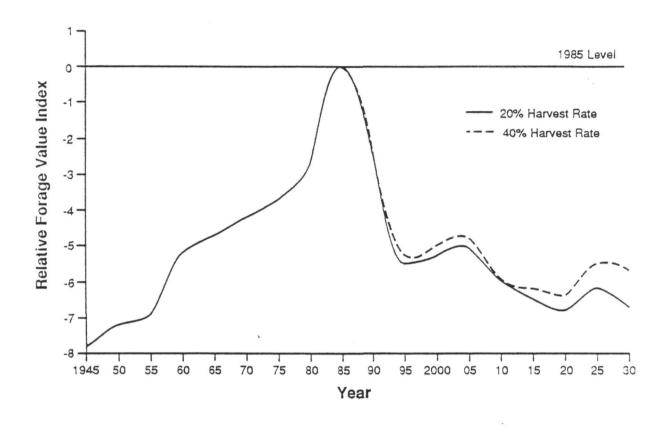


Fig. 3.5 Simulated response of Forage Value Indices (FVI) to two levels of forest harvesting on elk spring range in the White River watershed. FVIs are scaled relative to baseline 1985 levels.

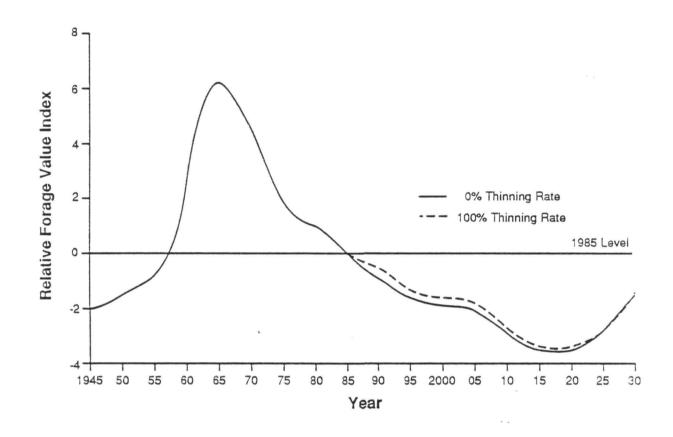


Fig. 3.6 Simulated response of Forage Value Indices (FVI) to two levels of precommercial thinning of 20 year-old Douglas-fir forests on elk winter range in the White River watershed. FVIs are scaled relative to baseline 1985 levels.

Simulated harvest of alder communities produced a minor influence on forage values of elk winter range (Fig. 3.7). Even under very intensive harvesting, forage values generated from logging were insufficient to offset declining forage values overall. Although forage values increased following logging in alder communities, land area was too small compared to that of Douglas-fir communities for logging in alder stands to have a strong influence on forage values overall.

A fourth simulation examined the influence of rotation-length on forage values. A shortened rotation length of 45 years was simulated by adjusting transition probabilities of 45-55 year-old stands to allow 20% harvest every five years.

Shortened rotation length produced an appreciable increase in forage values of winter range after the year 2010 (Fig. 3.8). Increased forage production due to shortened rotation was sufficient to increase forage values to approximately the 1985 level by 2020.

Each of the above simulations assumed a constant, negligible influence of snow, which seemed desirable for the sake of making comparisons among forest management activities. In an additional simulation, however, forest management activities were held constant and severity of winter snowpack was adjusted randomly during each model iteration. Incorporating stochastic snowfall in the model permitted an assessment of the influences of winter severity on forage values.

Influences of stochastic snowfall are demonstrated in Fig. 3.9. Forage values for random snow depths were always less than the baseline values because the baseline represented snowfree conditions. The annual percentage change in forage value due to snowfall averaged 29%, compared to 9% due to forest succession in the base run, indicating that stochastic variation in snowfall would have an appreciable influence on forage values. The influence of random winter severity did not obscure underlying successional patterns, but it added a high level of annual variability.

### Discussion

Our model required the use of several simplifying assumptions. The primary assumption was that forage production and successional trends remained constant during the simulation period. Forage production and successional trends appear to have been constant in the recent past. Successional pathways and forage values, however, may change appreciably in the future due to modern forest management practices. Forage seeding and new thinning practices in clearcuts are just two examples of management practices that could enhance forage values of regenerating forests. Because we were unable to anticipate and model these and other possible management activities, results of our simulations are most useful for evaluating immediate or short-term influences of selected management activities.

Simulation results suggest that forage values of elk winter and spring ranges have been altered appreciably by recent forest management activities. There is little question that logging practices have improved forage

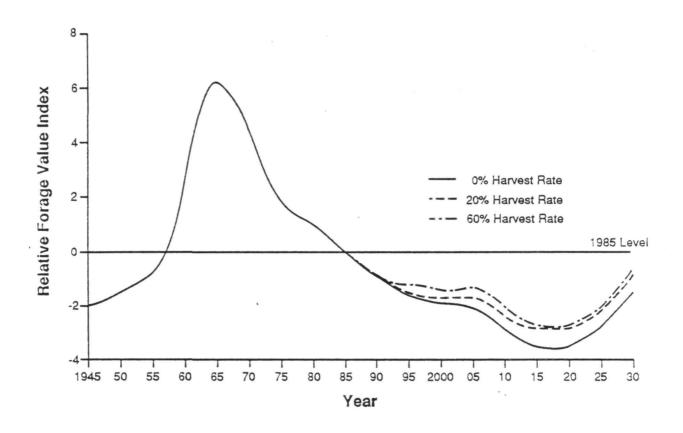


Fig. 3.7 Simulated response of Forage Value Indices (FVI) to three levels of forest harvesting of 30-year-old red alder stands on elk winter range in the White River watershed. FVIs are scaled realtive to baseline 1985 levels.

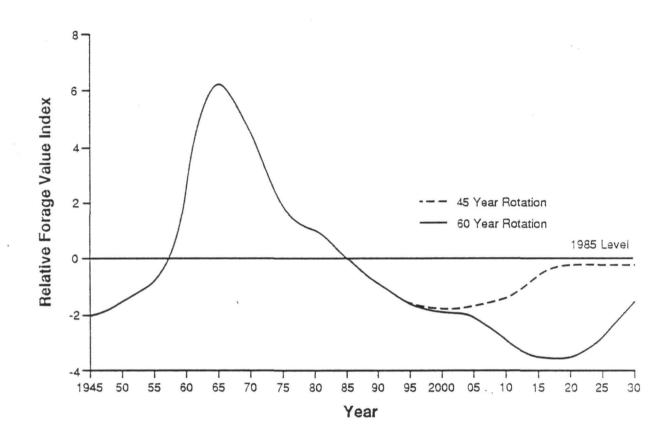


Fig. 3.8. Simulated response of Forage Value Indices (FVI) to two harvest rotation lengths on elk winter range in the White River. FVIs are scaled relative to baseline 1985 levels.

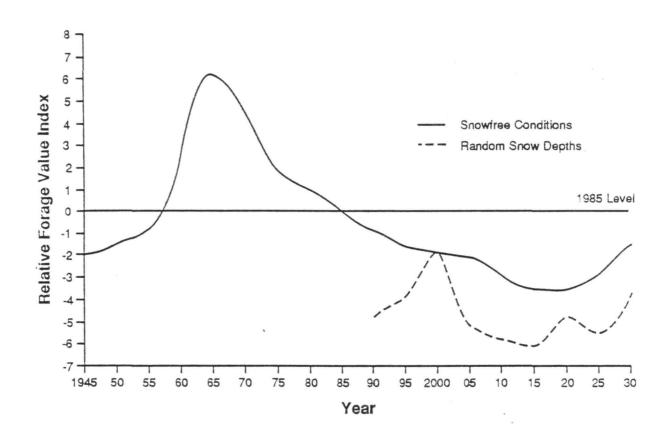


Fig. 3.9. Simulated response of Forage Value Indices (FVI) to snowfree conditions versus random snow depths on elk winter range in the White River watershed. FVIs are scaled relative to baseline 1985 levels.

conditions on both the spring and winter ranges of elk that migrate from MORA, but that forage conditions are now declining on both ranges as a result of forest succession and overstory closure. It is important to recognize that the anticipated decline on managed lands is due largely to the <u>rapid rate</u> with which old-age stands in this drainage were converted. The population increase that this brought about in recent years, aided by mild winters, simply cannot be sustained. Long-lived seral communities in bottomlands, such as red alder and grass/sedge communities, have prolongd forage benefits derived from logging somewhat, but they are not extensive enough to offset declining forage values on the winter range overall.

Our simulations also suggest that opportunities are limited at the present for improving forage conditions in the near future through normal silvicultural practices. The majority of stands are approximately 30 years old on the primary winter range. Thus they will require an additional 15-30 years until they reach harvestable age. There are opportunities for harvesting red alder at present, however, forage values of existing red alder communities are already high, and harvestable alder stands are scarce compared to Douglas-fir, so harvesting alder communities will have little effect on forage values. Lastly, accumulation of slash and low forage production in thinned stands appear to limit possibilities of improving forage values appreciably through extensive thinning.

Changes in forage values of an elk range would produce changes in carrying capacity only when forage is limiting. Primevally, elk populations west of the Cascades appeared to be limited largely by the availability of forage in seral and old-growth riparian corridors along the major river systems (Raedeke and Taber 1979, Starkey et al. 1982). It is likely, therefore, that improved foraging conditions due to logging would have increased elk carrying capacities during the early phases of logging in the White River. At present, following extensive logging of bottomland forests, cover used for energy conservation during severe winters and security from harassment may be more limiting than forage. Elk populations limited by cover may be expected to exhibit rapid growth during successive mild winters and to exhibit large density-dependent and -independent winter mortality during periodic severe winters. Under present circumstances, therefore, we consider forage to be an unreliable indicator of elk population trends.

Simulation models presented above, based on site-specific data, improve upon the previously existing, more speculative models. Results of our simulation models support the notion that increased densities of elk within Mount Rainier National Park during the 1970's may be related to increased availability of forage resulting from intensive logging outside the park. Based on the current stand age-structures and successional patterns, however, we anticipate that forage values of winter and spring ranges outside MORA will decline until the next century. Future reductions of available forage, together with reductions of mature forested cover, will reduce potential carrying capacities of winter and spring ranges adjoining the park. Reductions of mature forested cover, as suggested above, may also increase density-dependent and -independent winter mortality of elk and could destabilize population numbers.

In concluding, we offer two qualifiers for the above predictions. Reliability of these predictions depends upon, first, the distribution patterns of elk, and secondly, forest management activities remaining constant in the future. The model is based on age structure and forage production of forests on specific winter and spring ranges used by elk that migrate from MORA. If elk in the White River were to alter movement and distribution patterns in response to declining habitat quality, they may be able to improve nutritional qualities of winter and spring diets. Clearly, therefore, distributional shifts of elk could compensate for declining habitat values on presently used ranges. Secondly, the model employed forage values measured under existing silvicultural practices. Several innovative management activities, however, may be used in the future to increase forage values of regenerating forests. For example, seeding clearcuts with mixtures of legumes and grasses has been used to increase forage abundance in clearcuts. Additionally, thinning regenerating stands of Douglas-fir at an early age (e.g. 5-10 years after cutting) may reduce accumulation of slash and promote understory production in thinned stands. We suggest that monitoring distribution of elk and land-use activities outside MORA would be useful every 10 years to detect these or other developments that would influence elk populations in the White River.

### CONCLUSIONS

Recent forest management activities on land adjacent to MORA appear to have benefited elk populations wintering outside the park. During the mild winter of this study, high-quality winter forages were more abundant in early seral than in old-age forest communities, which resulted in improved dietary quality for elk wintering outside MORA. High soil moisture, intensive browsing pressure by elk, and competition with productive understories all appear to have hindered conifer regeneration in cutover bottomland forests along the White River, and to have prolonged the beneficial influences of logging on elk forage resources. Presumably, below-average winter severity which prevailed during much of the last 10-15 years, coupled with enhanced forage production resulting from logging, has contributed to improved winter nutrition, survival rates and reproductive rates of cow elk, and population growth observed in the 1970's and early 1980's.

As described above, our results leave little question that clearcutting improved forage resources available to elk during a mild winter. Old-age forest communities, however, also provided important forage during a short critical period following one 12" snowstorm. These findings, together with abundant supportive evidence from other similar studies, suggest that mature coniferous forests are critical winter habitats of elk during winters when snow covers forage resources in clearcuts and other open areas. Mature coniferous forests are important both because of forage resources available within them and reduced energetic costs of foraging associated with low snow depths. Clearly, the optimum ratios of seral vs. old-age communities in the managed forest will depend upon prevailing winter severity, forage production trends, and elk management objectives for the region.

We offer the following interpretation of influences of forest harvesting on population growth and regulation of elk populations in seasonally variable winter environments. First, from the viewpoint of elk habitat management, we define the optimum level of forest harvesting as that which produces a balance between forage used by elk in mature forests during critical winter periods and forage used on the remaining winter range during mild periods (Scharp et al. 1985). The more mild the prevailing winter weather, the less forage is needed in old-age forest communities to sustain elk through an average winter. Therefore, clearcutting old-age forests will increase carrying capacities of elk winter ranges until forage produced in old-growth becomes limiting during snowy winter periods. Further reduction of mature coniferous forests below this optimum may increase carrying capacity during mild winters, permitting continued population growth, but forage limitations in old-age forests may promote increased density-dependent and -independent mortality of elk herds during periodic severe winters. We suggest, therefore, that in the absence of intensive management of elk harvests, excessive reduction of old-age forests will increase the amplitude of population fluctuations over time due to increased population growth during mild winters and increased mortality of elk during periodic severe winters.

Intensive forest harvesting on elk winter-spring ranges in the White River, although providing a short-term boom of forage resources for elk, now has resulted in declining forage values. Future reductions of available

forage, together with reductions of mature forested cover used by elk for foraging and energy conservation during severe winters, will probably reduce carrying capacities of seasonal elk ranges adjoining the park, and may increase density-dependent and density-independent winter mortality of elk. Increased human disturbance on elk winter ranges may further reduce carrying capacity of elk winter ranges adjoining MORA. Furthermore, increased harvest of antlerless elk is anticipated in the region, which in addition to helping stabilize population fluctuations may also further reduce population numbers.

In conclusion, we anticipate that in the absence of innovative new forage enhancement activities, past logging activities and continued forest succession will reduce and destabilize elk populations summering within MORA. We foresee little improvement in winter ranges adjoining MORA that will permit elk populations to continue to grow in the White River in the 1990's.

#### LITERATURE CITED

- Bradley, W. P. 1982. History, ecology and management of an introduced wapiti population in Mt. Rainier National Park, Washington. Ph.D. Dissertation, Univ. Washington, Seattle. 274pp.
- Bradley, W. P., and C. H. Driver. 1981. Elk ecology and management perspectives at Mount Rainier National Park. Cooperative Park Studies Unit Report CPSU/UW 81-2. Univ. Washington, Seattle. 27pp.
- Bunnell, F. L. 1985. Forestry and black-tailed deer: conflicts, crises, or cooperation. For. Chron. 61:180-184.
- Bunnell, F. L., and G. W. Jones. 1984. Black-tailed deer and old-growth forests—a synthesis. Pp 411-420 in W. R. Meehan, T. R. Merrell, and T. A. Hanley, eds. Fish and Wildlife Relationships in old-growth forests: Proceedings of a Symposium. Amer. Inst. Fish. Res. Biol.
- Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Pp 183-246 <u>in</u> T. H. Coaker, ed. Applied Biology Vol. 1, Academic Press, London.
- Cook, C. W. 1972. Comparative nutritive value of forbs, grasses, and shrubs. Pp 303-310 in C. M. McKell, J. P. Blaisdell, and J. R. Goodin, eds. Wildland shrubs—their biology, and utilization. USDA For. Serv. Gen. Tech. Rep. INT-1.
- Cooper, K. C. 1987. Seasonal movements and habitat use of migratory elk in Mount Rainier National Park. M.S. Thesis, Oregon State Univ., Corvallis. 84pp.
- Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54:57-69.
- Fracker, S. B., and J. A. Brischle. 1944. Measuring the local distribution of Ribes. Ecology 25:283-303.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.
- Franklin, J. F., W. H. Moir, M. A. Hemstrom, and S. Greene. In prep. Forest ecosystems of Mount Rainier National Park.
- Goering, H. K., and P. J. Van Soest. 1970. Forage fiber analysis: apparatus, reagents, procedures, and some applications. U.S. Dep. Agric. Handb. 379. 20pp.
- Hanley, T. A., R. G. Cates, B. Van Horne, and J. D. McKendrick. 1987.

  Forest stand-age-related differences in apparent nutritional quality of forage for deer in southeastern Alaska. Pp 9-17 in F. D. Provenza, J. T. Flinders, and E. D. McArthur, eds. Proceedings—Symposium on Plant-

- Herbivore Interactions. USDA For. Serv. Gen. Tech. Rep. INT-222. 179pp.
- Hanley, T. A. 1984. Habitat patches and their selection by wapiti and black-tailed deer in a coastal montane coniferous forest. J. Appl. Ecol. 21:423-436.
- Happe, P. J., K. J. Jenkins, E. E. Starkey, and S. H. Sharrow. In Prep. Nutritional quality and tannin astringency of browse in clearcuts and old-growth forests.
- Harestad, A. S., J. A. Rochelle, and F. L. Bunnell. 1982. Old-growth forests and black-tailed deer on Vancouver Island. Trans. N. Am. Wildl. Conf. 47:343-352.
- Harper, J. A. 1985. Ecology and management of Roosevelt elk in Oregon. Oregon Dept. Fish and Wildl., Portland, OR 70pp.
- Henderson, J. A., and D. Peters. 1984. Preliminary plant associations and habitat types of the Mt. Baker-Snoqualmie National Forest. U.S.D.A. For. Serv. Pacific Northwest Region, Portland.
- Hett, J., R. Taber, J. Long, and J. Schoen. 1978. Forest management policies and summer carrying capacity in the <u>Abies amabilis</u> forest, western Washington. Environ. Manage. 2:561-566.
- Hobbs, N. T., D. L. Baker, J. E. Ellis, D. M. Swift, and R. A. Green. 1982. Energy- and nitrogen-based estimates of elk winter range carrying capacity. J. Wildl. Manage. 46:12-21.
- Horowitz, W. (editor) 1980. Official methods of analysis of the Association of Official Analytical Chemists. Thirteenth edition. Assoc. Off. Anal. Chem., Washington, D.C. 1018pp.
- Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press.
- Janz, D. W. 1983. Seasonal composition and quality of Roosevelt elk diets on Vancouver Island. M.S. Thesis, Univ. British Columbia, Vancouver. 68pp.
- Jenkins, K. J., and R. G. Wright. 1987. Simulating succession of riparian spruce forests and white-tailed deer carrying capacity in northwestern Montana. West. J. Appl. For. 2:80-83.
- Jenkins, K. J., P. J. Happe, and R. G. Wright. 1990. Evaluating above—snow browse availability using non-linear regressions. Wildl. Soc. Bull. 18:54-61.
- Leslie, D. M. Jr., E. E. Starkey, and M. Vavra. 1984. Elk and deer diets in old-growth forests of western Washington. J. Wildl. Manage. 48:762-775.

- Long, J. N., and J. Turner. 1975. Above-ground biomass of understory in an age sequence of four Douglas-fir stands. J. Appl. Ecol. 12:179-188.
- Merrill, E., K. Raedeke, and R. Taber. 1987. Population dynamics and habitat ecology of elk in the Mount St. Helens blast zone. Wildlife Sciences Group, College of Forest Resources, Univ. Washington, Seattle. 186pp.
- Milchunas, D. G., and D. L. Baker. 1982. In vitro digestion—sources of within and between trial variability. J. Range Manage. 35:199-203.
- Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. J. Wildl. Manage. 48:474-488.
- Raedeke, K. J., and J. F. Lemkuhl. 1985. A simulation procedure for modeling the relationships between wildlife and forest management.

  Pages 377-382 in J. Verner, M. Morrison, and C. J. Ralph (eds.) Wildlife 2000: Modeling habitat relationship of terrestrial vertebrates. Univ. Wisconsin Press, Madison.
- Raedeke, K. J., and J. Lemkuhl. 1984. Elk populations of Mount Rainier National Park: status of range outside of the park. Final Report, Cooperative Park Studies Unit, Univ. Washington, Seattle. 69pp.
- Raedeke, K. J., and R. D. Taber. 1979. Mechanisms of population regulation in western Washington forests for <u>Cervus</u> and <u>Odocoileus</u>. Proc. Int. Congr. Game Biol. 14:69-80.
- Ripple, W. J., E. E. Starkey, and B. J. Schrumpf. 1988. Assessing elk trail and wallow impacts in Mount Rainier National Park. Final Report (Cooperative Agreement CA-9000-3-0003, Subagreement 16).
- Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, New York. 343pp.
- Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, C. C. Schwartz, and W. W. Mautz. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecol. 68:98-107.
- Scharpf, R. W., M. P. Kuttel, R. J. Anderson, E. R. Brown, E. P. Harshman, and J. A. Rochelle. 1985. Forage/cover model: deer and elk habitat management. USDA For. Serv., Pacific Northwest Region, Portland, OR.
- Schoen, J. W., O. C. Wallmo, and M. D. Kirchoff. 1981. Wildlife-forest relationships: is a reevaluation of old-growth necessary? Trans. N. Am. Wildl. Nat. Res. Conf. 46:
- Schoen, J. W. 1977. The ecological distribution and biology of wapiti (<u>Cervus elaphus nelsoni</u>) in the Cedar River Watershed, Washington. Ph.D. Dissertation, Univ. Washington, Seattle. 406pp.

- Sharrow, S. H., and D. E. Kuntz. 1989. Plant response to elk grazing in subalpine dry meadow communities of Mount Rainier National Park. Oregon Cooperative Park Studies Unit Report 89-5. 18pp.
- Shugart, H. H., Jr., T. R. Crow, and J. M. Hett. 1973. Forest succession models: a rationale and methodology for modeling forest succession over large regions. Forest Sci. 19:203-212.
- Spalinger, D. E., C. T. Robbins, and T. A. Hanley. 1986. The assessment of handling time in ruminants: the effect of plant chemical and physical structure on the rate of breakdown of plant particles in the rumen of mule deer and elk. Can. J. Zool. 64:312-321.
- Sparks, D. R., and J. C. Malechek. 1968. Estimating percentage dry weights in diets using a microscopic technique. J. Range Manage. 21:264-265.
- Starkey, E. E., D. S. deCalesta, and G. W. Witmer. 1982. Management of Roosevelt elk habitat and harvest. Trans. N. Am. Wildl. Nat. Res. Conf. 47:353-362.
- Stevenson, S. K., and J. A. Rochelle. 1984. Lichen Litterfall—its availability and utilization. Pp 391-396 in W. R. Meehan, T. R. Merrell, and T. A. Hanley, eds. Fish and wildlife relationships in old-growth forests: Proceedings of a symposium. Amer. Inst. Fish. Res. Biol.
- Swanson, D. O. 1970. Roosevelt elk-forest relationships in the Douglas fir region of the southern Oregon Coast Range. Ph.D. Thesis, Univ. Michigan, Ann Arbor. 173pp.
- Thorne, E. T., R. E. Dean, and W. G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. J. Wildl. Manage. 40:330-335.
- Trainer, C. E. 1971. The relationship of physical condition and fertility of female Roosevelt elk (<u>Cervus canadensis roosevelti</u>) in Oregon. M.S. Thesis, Oregon State Univ., Corvallis. 93pp.
- Wallmo, O. C., and J. W. Schoen. 1980. Response of deer to secondary forest succession in southeast Alaska. For. Sci. 26:448-462.
- Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108:290-304.

Appendix I. Regression equations used to predict standing crop biomass (SCB, g DM/1  $\rm m^2$ ) of herbs, grasses and evergreen shrub species from plant cover (COV, %) in 1  $\rm m^2$  frames. Equations are of the form SCB =  $\rm b \cdot COV.^1$ 

Species	N	b	S.E.	$r^2$
•				
Alnus rubra lvs.	12	0.959	0.029	0.99
Anaphalis margaritaceae	12	1.685	0.144	0.93
Arctostaphylos uva-ursi	12	4.357	0.135	0.99
Berberis nervosa	12	1.756	0.108	0.96
Carex spp.	12	0.980	0.059	0.92
Chimophila umbellata	12	0.541	0.024	0.98
Circium spp.	12	0.892	0.056	0.96
Epilobium spp.	12	2.471	0.166	0.95
Fragaria spp.	12	0.196	0.021	0.89
Galium spp.	11	0.255	0.015	0.96
Gaultheria shallon	12	1.572	0.020	0.99
Grassa	30	0.87 (COV)	0.110	0.86
		0.62 (HT)	0.189	
Hypochaeris radicata	. 12	0.861	0.058	0.95
Lactuca muralis	12	0.851	0.070	0.93
Linnaea borealis	12	0.417	0.012	0.99
Lotus corniculatus	12	2.223	0.170	0.94
Lupinus latifolius	12	1.284	0.060	0.98
Lysichitum americana	12	0.256	0.018	0.95
Montia sibirica	12	0.324	0.019	0.96
Oenanthe sarmentosa	12	0.176	0.008	0.98
Plantago spp.	12	0.674	0.114	0.76
Populus trichocarpa (lvs.)	12	0.800	0.041	0.97
Pyrola spp.	12	0.535	0.024	0.98
Ranunculus radicata	12	0.261	0.008	0.99
Stachys spp.	12	0.607	0.027	0.98
Taraxacum spp.	12	0.789	0.043	0.97
Tiarella spp.	12	0.179	0.003	0.99
Tolmiea menziesii	12	0.411	0.018	0.98
Trifolium spp.	12	1.863	0.174	0.91
Veronica americana	12	0.614	0.052	0.93
Veronica officinale	12	1.945	0.056	0.99
Viola spp.	12	0.274	0.009	0.99
		*****		

<sup>&</sup>lt;sup>a</sup> Equation for grass is of the form  $SCB = (b1 \cdot COV) + (b2 \cdot HEIGHT)$ 

Appendix II. Average twig weights used to estimate standing crop biomass of deciduous shrub, fern and conifer species.

Species	Canopy <sup>a</sup> Class	N	Average Weight (g)
Abies spp.	-	46	0.52
Acer circinatum	Open	41	1.40
Acer circinatum	Closed	100	0.30
Alnus rubra		20	4.00
Athyrium filix-femina		51	0.45
Blechnum spicant		48	0.40
Cornus stolonifera	Open	54	0.98
Cornus stolionifera	Closed	101	0.26
Equisetum arvense		29	1.26
Lonicera involucrata		29	1.35
Oplopanax horridum		30	1.63
Pinus contorta		20	4.17
Picea sitchensis		43	0.45
Polystichum munitum		20	2.41
Populus trichocarpa		26	0.89
Psuedotsuga menziesii		41	0.95
Ribes spp.		99	0.94
Rosa spp.		125	0.18
Rubus leucodermis		20	9.60
Rubus parviflorus		21	1.64
Rubus spectabilis		25	1.09
Rubus ursinus	Open	20	1.96
Rubus ursinus	Closed	21	0.44
Salix spp.		30	1.87
Sambucus racemosa		20	7.02
Spiraea spp.		126	0.15
Symphoricarpus spp.		284	0.06
Taxus brevifolia		78	0.20
Thuja plicata		82	0.20
Tsuga heterophylla		101	0.20
Vaccinium spp.	Open	191	0.14
Vaccinium spp.	Closed	100	0.20

a Open = canopy < 25% Closed = canopy > 25%

Appendix III. Mean percentages (x, n = 4) and SD of plant species in the seasonal diets of elk inhabiting old-growth and managed forest ecosystems in the White River drainage, November 1986-April 1987. Species names are listed in Appendix IV.

				(	Old-gro	wth			Managed Forest								
		Nov		Jan		Feb		Apr		Nov		Jan		Feb		Apr	
Species	х	SD	x	SD	x	SD	x	SD	x	SD	x	SD	x	SD	x	SI	
Shrubs																	
ACCI	1.0	0.7	0.2	0.1	0.4	0.2	0.3	0.1	-0.6	0.2	0.2	0.2	0.3	0.3	1.1	0.9	
ALRU	10.2	2.2	2.0	1.5	7.9	3.6	4.4	0.8	3.3	1.9	1.0	0.2	3.4	0.8	1.4	1.0	
AMAL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
COST	0.2	0.1	0.2	0.2	0.1	0.1	0.3	0.1	0.1	0.1	0.4	0.1	0.4	0.3	0.6	0.6	
LOIN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
ОРНО	0.4	0.6	0.1	0.0	0.3	0.3	0.0	0.0	1.0	1.6	0.1	0.0	0.3	0.2	0.0	0.0	
OSCE	0.0	0.0	0.1	0.1	0.1	0.1	0.5	0.3	0.0	0.0	0.2	0.1	0.3	0.2	0.1	0.0	
POTR	2.5	2.8	0.5	0.3	0.3	0.2	0.4	0.2	2.2	1.2	0.9	0.5	0.3	0.2	0.8	0.3	
RISP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
ROSP	0.3	0.2	1.1	0.7	0.6	0.3	1.3	0.9	0.4	0.3	1.2	0.6	1.0	0.7	0.8	0.7	
RUID	0.2	0.1	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	
RULE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
RUPA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	
RUSP	2.3	1.8	0.9	0.4	2.1	0.3	2.2	0.3	1.7	2.0	1.0	0.8	1.8	0.8	3.1	1.1	
RUUR	1.1	0.6	0.7	0.3	0.9	0.1	1.6	1.0	2.4	0.5	1.2	0.8	1.1	0.9	1.4	0.6	
SASP	2.5	0.5	1.3	0.7	0.9	0.5	1.5	0.2	10.4	6.1	1.1	0.3	2.1	0.6	3.1	1.4	
SARA	0.1	0.1	0.0	0.0	0.0	0.0	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	
SPDO	0.0	0.0	0.4	0.1	0.2	0.2	0.5	0.2	2.0	2.6	0.3	0.2	0.5	0.3	0.3	0.1	
SYSP	0.6	0.6	0.1	0.1	0.2	0.2	0.2	0.2	0.8	0.5	0.4	0.2	0.7	0.6	0.1	0.0	
VASP	5.7	2.0	1.2	0.4	0.6	0.3	1.3	0.7	0.9	0.6	0.5	0.5	0.1	0.0	0.3	0.2	
UNIDENT	10.9	1.0	9.4	0.7	7.9	1.0	8.5	2.2	7.3	0.8	9.8	2.7	7.7	2.1	6.9	1.4	
TOTAL	38.0	7.5	18.2	2.9	22.3	5.2	23.0	4.3	33.2	6.1	18.2	5.7	19.9	4.1	19.9	1.3	

Appendix III. Continued.

					old-gro	wth			Managed Forest							
	_	Nov		Jan		Feb		Apr		Nov		Jan		Feb		Apr
Species	х	SD	x	SD	x	SD	x	SD	x	SD	x	SD	x	SD	x	SE
FORBS																
АММА	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CISP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
EPSP	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.1	0.1	0.0	0.0	0.0	0.0	1.0	1.1
FRSP	1.3	0.7	0.4	0.2	0.5	0.2	0.7	0.2	- 1.6	0.8	0.4	0.2	0.4	0.1	2.0	0.9
GASP	0.2	0.2	0.4	0.3	0.1	0.1	0.7	0.3	0.2	0.2	0.4	0.3	0.1	0.0	0.4	0.2
HYRA	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.2	0.1	0.1	0.0	0.0	0.5	0.3	2.2	0.4
LAMU	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LOSP	0.1	0.1	0.1	0.1	0.2	0.2	1.0	0.6	1.1	0.6	0.3	0.1	0.3	0.2	1.2	0.6
LUSP	0.2	0.2	0.1	0.1	0.2	0.3	0.1	0.1	0.2	0.1	0.2	0.2	0.1	0.0	0.0	0.0
LYAM	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2
MESP	0.0	0.0	0.3	0.4	0.9	0.4	1.3	1.2	0.0	0.0	0.0	0.0	0.9	0.4	0.5	0.6
MOSI	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
DESA	0.8	0.8	0.5	0.3	0.4	0.4	0.4	0.4	1.4	0.7	0.7	0.4	1.6	1.6	2.0	1.0
PLSP	0.1	0.1	0.0	0.0	0.0	0.0	0.4	0.2	0.8	0.8	0.1	0.1	0.3	0.3	0.4	0.0
PRVU	0.0	0.1	0.1	0.2	0.0	0.0	0.1	0.1	0.9	0.9	0.1	0.1	0.3	0.3	0.3	0.2
RASP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
SMST	0.0	0.0	0.0	0.0	0.3	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1
STCO	0.1	0.1	0.1	0.1	0.1	0.0	0.3	0.2	0.5	0.5	0.3	0.3	0.4	0.4	0.9	0.3
TASP	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.1	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.7
TITR	0.0	0.0	0.0	0.0	0.3	0.3	0.1	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
POME	0.0	0.0	0.4	0.3	0.0	0.0	0.7	0.2	0.3	0.2	0.1	0.1	0.2	0.1	0.6	0.3
rrs p	0.4	0.4	0.4	0.4	0.8	0.8	2.8	0.2	1.8	0.5	0.2	0.1	0.6	0.2	1.8	0.2
VEOF	0.1	0.1	0.1	0.1	0.1	0.1	0.5	0.3	1.9	0.3	0.6	0.6	0.5	0.2	0.6	0.2
VISP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
JNK	1.3	1.5	0.3	0.3	0.3	0.3	0.4	0.1	0.9	0.4	0.7	0.4	0.8	0.6	1.9	1.2
UNIDENT	3.0	0.2	1.3	1.0	1.9	0.4	5.2	1.7	8.0	2.0	3.1	1.2	5.9	1.8	7.3	2.2
TOTAL	7.5	2.3	4.4	2.1	6.1	1.7	16.9	3.7	19.8	2.4	7.2	2.7	12.8	4.9	24.2	4.2

Appendix III. Continued.

					Old-gro	owth						Manag	ed Fore	est		
		Nov		Jan		Feb		Apr		Nov		Jan		Feb		Apr
Species	×	SD	x	SD	x	SD	x	SD	x	SD	x	SD	x	SD	×	SI
FERNS																
ATFI	0.1	0.1	0.6	0.7	0.1	0.1	0.1	0.1	0.4	0.3	0.8	0.5	1.1	0.3	0.3	0.2
BLSP	0.1	0.1	0.3	0.6	0.3	0.2	0.5	0.4	0.3	0.2	0.1	0.0	0.2	0.2	0.2	0.1
EQSP	0.2	0.1	0.1	0.0	0.1	0.1	0.2	0.1	5.1	2.7	1.9	1.4	1.6	2.3	1.2	0.8
POMU	0.7	0.6	1.0	0.7	0.8	0.6	0.6	0.2	0.4	0.2	2.3	1.3	3.7	1.4	0.4	0.3
TOTAL	1.1	0.5	1.9	1.4	1.2	0.5	1.3	0.4	6.1	2.5	5.0	1.2	6.5	3.2	2.0	1.0
CONIFERS	S															
ABGR	1.4	0.9	0.8	0.5	1.2	0.3	0.9	0.6	0.2	0.2	0.2	0.1	0.5	0.4	0.0	0.0
ABPR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PISI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PICO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PIMO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PSME	0.7	0.2	3.1	1.1	3.9	0.7	6.4	0.6	0.1	0.2	1.5	1.1	2.2	0.6	0.9	0.3
TABR	12.4	4.5	15.5	7.7	9.0	4.0	5.3	1.7	1.0	0.6	11.1	9.3	0.7	0.6	1.0	1.3
THPL	5.2	1.1	17.7	6.2	13.9	2.9	15.4	5.2	0.7	0.3	6.7	1.2	6.2	3.3	2.8	2.5
TSHE	1.4	0.9	7.2	4.1	4.3	2.2	3.5	2.8	0.8	0.8	2.6	1.9	3.2	1.0	2.5	1.1
UNIDENT	3.9	0.5	6.5	2.0	1.9	0.7	2.0	0.7	1.1	0.4	3.2	1.1	1.1	0.6	0.3	0.1
TOTAL	24.7	6.3	50.8	5.8	34.1	5.7	33.4	7.8	3.9	1.0	25.3	12.7	13.7	4.8	7.4	4.4
EVERGRE	EN SHR	UB														
ARUV	2.2	0.9	1.1	0.6	0.7	0.3	0.4	0.1	0.7	0.2	0.4	0.1	0.2	0.1	0.1	0.1
BENE	0.1	0.1	7.7	8.4	8.7	2.9	3.6	2.8	0.2	0.1	1.0	0.5	0.9	0.5	0.4	0.1
CHUM	1.6	0.3	0.9	0.6	0.6	0.4	0.2	0.1	0.6	0.4	1.1	0.4	0.1	0.0	0.2	0.2
COCA	0.0	0.0	0.0	0.0	1.0	0.7	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
GASH	0.6	0.3	3.4	2.5	2.6	1.0	1.0	0.4	1.5	1.6	4.9	2.4	2.9	0.9	2.5	0.9
LIBO	2.4	2.0	8.7	3.6	13.8	5.9	7.3	0.7	3.4	3.2	10.1	2.9	9.9	1.0	9.9	4.2
PYSP	0.0	0.0	0.2	0.3	0.2	0.2	0.2	0.3	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0
UNIDENT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOTAL	6.9	2.2	22.0	8.5	27.5	6.8	12.8	3.0	6.4	2.3	17.5	5.4	14.1	2.1	13.1	5.0

Appendix 3. Continued

					Old-gro	wth						Manag	ed Fore	est		
		Nov		Jan		Feb		Apr		Nov		Jan		Feb		Apr
Species	х	SD	×	SD	x	SD	×	SD	x	SD	x	SD	x	SD	×	SD
GRASSES																
AGSP	1.6	1.3	0.2	0.1	0.8	0.4	1.3	0.6	2.1	1.0	1.9	0.6	3.0	1.8	3.1	1.1
BRSP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
CASP	0.4	0.4	0.0	0.0	0.1	0.1	0.4	0.1	0.8	0.3	0.3	0.2	1.0	0.3	1.7	1.2
DAGL	1.1	0.7	0.0	0.1	0.4	0.5	0.4	0.2	1.4	0.6	0.6	0.2	0.2	0.1	0.5	0.3
DESP	0.6	0.7	0.3	0.4	0.9	0.6	0.7	0.4	0.6	0.5	0.8	0.2	1.0	0.4	0.3	0.1
ELGL	1.5	1.0	0.3	0.4	0.3	0.1	0.5	0.4	2.0	1.5	1.7	1.4	0.5	0.5	0.5	0.1
FEAR	1.4	0.4	0.3	0.3	0.8	0.2	0.8	0.4	2.0	1.1	2.1	1.1	2.0	0.7	1.9	0.5
FESP	2.6	1.1	0.4	0.4	1.2	0.8	1.4	1.0	3.0	3.1	2.9	0.7	2.0	0.7	1.7	0.5
HOLA	0.2	0.2	0.0	0.0	0.1	0.1	0.1	0.1	1.7	1.4	2.9	2.7	2.1	1.2	1.2	0.7
JUSP	4.1	3.7	0.1	0.1	1.0	1.0	2.2	0.7	3.0	2.4	4.7	2.1	10.7	2.0	12.2	2.2
LOSP	1.0	0.8	0.0	0.0	0.6	0.5	0.8	0.3	1.1	1.4	0.1	0.1	0.5	0.5	0.7	0.3
LUDI	0.1	0.1	0.0	0.0	0.1	0.1	0.2	0.1	0.5	0.2	0.1	0.1	0.4	0.4	0.7	0.3
PHPR	1.9	1.3	0.4	0.4	1.2	0.9	1.2	0.3	4.6	1.4	2.9	0.4	2.5	1.4	1.8	1.1
POSP	1.4	0.7	0.2	0.2	0.8	0.2	1.2	0.7	1.7	0.9	2.0	0.7	2.6	1.9	2.8	0.6
TRSP	0.1	0.2	0.0	0.0	0.1	0.1	0.2	0.1	0.0	0.0	0.1	0.1	0.3	0.2	0.1	0.0
UNIDENT	3.2	0.9	0.5	0.5	0.7	0.6	1.6	0.3	4.5	0.7	3.8	1.0	4.4	1.0	4.3	1.3
TOTAL	21.0	3.8	2.8	2.7	8.7	3.9	12.7	3.7	28.7	5.0	26.9	7.8	33.1	7.6	33.5	4.3
GRANTOT	99.1	0.2	100.1	0.3	100.0	0.2	100.0	0.0	98.1	2.1	100.0	0.1	99.9	0.3	100.1	0.2

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Appendix IV. Acronyms and names of principal forage species

Acronym	Latin Name	Common Name
Shrubs		
ACCI	Acer circinatum	Vine maple
ALRU	Alnus rubra	Red alder
AMAL	Amelanchier alnifolia	Western serviceberry
COST	Cornus stolonifera	Red-osier dogwood
LOIN	Lonicera involucrata	Bearberry
OPHO	Oplopanax horridum	Devil's club
OSCE	Osmaronia cerasiformis	Indian plum
POTR	Populus trichocarpa	Cottonwood
RISP	Ribes spp.	Gooseberry
ROSP	Rosa spp.	Wildrose
RUID	Rubus ideaus	Red raspberry
RULE	Rubus leucodermis	Blackcap
RUPA	Rubus parviflorus	Thimbleberry
RUSP	Rubus spectabilis	Salmonberry
RUUR	Rubus ursinus	Trailing blackberry
SASP	Salix spp.	Willow
SARA	Sambucus racemosa	Red elderberry
SPDO	Spiraea douglasii	Spiraea
SYSP	Symphoricarpos spp.	Snowberry
VASP	Vaccinium spp.	Huckleberry
FORBS		
ANMA	Anaphalis margaritacea	Pearly everlasting
CISP	Circium spp.	Thistle
EPSP	Epilobium spp.	Fireweed
FRSP	Fragaria spp.	Strawberry
GASP	Galium spp.	Bedstraw
HYRA	Hypochaeris radicata	Hairy Catsear
LAMU	Lactuca muralis	Wild lettuce
LOSP	Lotus spp.	Deervetch
LUSP	Lupinus spp.	Lupine
LYAM	Lysichitum americanum	Skunkcabbage
MESP	Medicago spp.	Alfalfa
MOSI	Montia sibirica	Western springbeauty
OESA	Oenanthe sarmentosa	Water parsley
PLSP	Plantago spp.	Plaintain
		(Cont.)

Appendix IV. Cont.

Acronym	Latin Name	Common Name
PRVU RHSP SMST STCO TASP TITR TOME TRSP VEOF VISP FERNS	Prunella vulgaris Ranunculus spp. Smilacina stellata Stachys cooleyae Taraxacum spp. Tiarella trifoliata Tolmiea menziesii Trifolium spp. Veronica officionale Viola spp.	Selfheal Buttercup Solomon's seal Hedge nettle Dandelion Foam flower Youth-on-age Clover Veronica Violet
ATFI BLSP EQSP POMU CONIFERS	Athyrium filix-femina Blechnum spicant Equisetum spp. Polystichum munitum	Ladyfern Deerfern Horsetail rush Swordfern
ABAM ABGR ABPR PISI PICO PIMO PSME TABR THPL TSHE	Abies amabilis Abies grandis Abies procera Picea sitchensis Pinus contorta Pinus monticola Psuedotsuga menziesii Taxus brevifolia Thuja plicata Tsuga heterophylla	Pacific silver fir Grand fir Noble fir Sitka spruce Lodgepole pine Western white pine Douglas-fir Western yew Western redcedar Western hemlock
EVERGREEN S	HRUB	
ARUV BENE CHUM COCA GASH LIBO PYSP	Arctostaphylos uva-ursi Berberis nervosa Chimaphila umbellata Cornus canadensis Gaultheria shallon Linnaea borealis Pyrola spp.	Bearberry Oregongrape Pipsissewa Bunchberry dogwood Salal Twinflower Pyrola

Appendix V. Mapping codes and selected characteristics of mapped land cover types contained in Appendix VI.

Map Code	Vegetation Cover	Canopy <sup>1</sup>	Moisture <sup>1</sup>	Age <sup>1</sup>
1	Young Clearcut	1	2	1
2	Young Clearcut	1	3	1
3	Mid Clearcut	1	2	2
4	Mid Clearcut	ī	3	2
5	Old Clearcut/PSME Regeneration	3	2	3
6	Old Clearcut/PSME Regeneration	2	1	3
7	Old Clearcut/PSME Thinned Regenerati	on 2-	3 2	3 3 3 3
8	Old Clearcut/ALRU Regeneration	2-	3 3	3
10	Old Clearcut/PSME-POTR Regeneration	2-	3 2	3
11	Seral Riparian Forest/PISI-ABGR	3	3	4
12	Old Clearcut/Grass-sedge	1	3-4	
13	Old Clearcut/Brushfield	2	3	3 5
20	Old-Growth Forest/THPL	3	3	5
21	Old-Growth Forest/PSME-ACTR	3	1	5
22	Old-Growth Forest/PSME-GASH	3	1	5
25	Wetland	1	4	-
28	Riparian Deciduous Forest	3	3	-
30	Rock/Scree/Other	1	1	-
31	Select Cut/PSME	2	2	-
15	Second Growth/PSME	3	2	4
1 Key to	Canopy (%) 0-30	<u>3</u> 60 <b>-</b> 90	4 90+	5

1 Key to Codes:		_1_	_2_	3	4	5
-	Canopy (%)	0-30	30-60	60-90	90+	
	Moisture	Xeric	Xeric-mesic	mesic	hydric	
	Age (vrs)	0-5	6-18	18-32	60-150	>150

Appendix VI. Map of vegetation cover in and adjoining the study area.

