

AN ABSTRACT OF THE THESIS OF

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Nutritional ecology of un hunted and sympatric populations of Roosevelt elk, Cervus elaphus roosevelti, and Columbian black-tailed deer, Odocoileus hemionus columbianus, was investigated in old-growth forests of the Hoh Valley in Olympic National Park, Washington, from September 1979 to November 1981. Seasonal diets of both cervids generally were comprised of common forages; relative availabilities of other preferred forages minimized their contributions to the diet of either ungulate. Hemlock, swordfern, oxalis, and alder were the most common dietary components on an average annual basis. Levels of crude protein, dry matter digestibility and phosphorus in important forages varied with phenology, but seasonal trends were more pronounced for shrubs and grasses than forbs and trees. Dietary levels of those nutritional attributes for both elk and deer varied seasonally in the following ascending order: winter, fall, summer, spring. Protein and phosphorus appeared to be adequate in diets, but low in vitro digestibilities suggested that digestible energy may be limited. Levels of sodium and selenium were low in most forages and suggested

that dietary levels also were low. No significant differences in seasonal diet quality were demonstrated between deer and elk. Fecal nitrogen of both cervids was correlated with dietary protein and provided an index to seasonal changes in nitrogen intake. Sympatry of elk and deer was typified by 1) a high degree of dietary overlap, 2) diets that seemed to afford little opportunity for partitioning plant parts, 3) a similar pattern of food acquisition in major forest-types, and 4) heavy use of the forage base to the point of restricting distributions of preferred forages and influencing the physiognomy of the shrub layer in some forest communities. Those observations suggested that one cervid should competitively exclude the other. It was speculated that sympatry was enhanced by the spatial heterogeneity of the old-growth forest, in that large numbers of downed trees created areas only accessible to and used by deer. Cervids probably were limited by undernutrition and low reproduction, both consequences of maximum density and theoretically low forage availability and quality.

NUTRITIONAL ECOLOGY OF CERVIDS IN OLD-GROWTH FORESTS
IN OLYMPIC NATIONAL PARK, WASHINGTON

by

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INTRODUCTION

Roosevelt elk, Cervus elaphus roosevelti, and Columbian black-tailed deer, Odocoileus hemionus columbianus, belong to the family Cervidae, which is typified by cloven-hooved ruminants that grow antlers annually (Walker 1975). Members of both genera are presumed to have evolved in Eurasia and spread into North America during the late Pleistocene via the Bering Land Bridge. Presently, both subspecies are restricted to coastal forests of the northwestern part of the United States from northern California to Washington and extreme southwestern Canada, including Vancouver Island, British Columbia (Bryant and Maser 1982, Wallmo 1981b).

Subspecific designations of both species are determined in part by geographic distributions; however, different habitats may have contributed to basic ecological and physical divergences (McCullough 1969, Starkey et al., in press). Related subspecies of Rocky Mountain elk, C. e. nelsoni, and mule deer, O. h. hemionus, are far more abundant and widespread than Roosevelt elk and Columbian black-tailed deer; therefore, more basic ecological data have been obtained on the former subspecies (e.g., Thomas and Toweill 1982, Wallmo 1981a).

Roosevelt elk and Columbian black-tailed deer do not always coexist. Areas with high densities of elk may have few or no deer, and vice-versa. It is difficult to ascertain if those general

patterns are a result of evolutionary and ecological constraints (e.g., interspecific relationships or habitat affinities), or human perturbations (e.g., intense forest management or hunting), or some combination of both. There is a paucity of information on sympatric populations of these subspecies (Mackie 1981, Nelson 1982); additional insight is needed.

The rapid liquidation of mature climax forests in the Pacific Northwest necessitates research on forest-wildlife interactions (Meslow et al. 1981). A vestige of primeval coastal forests was protected in the early 1900s in Olympic National Park. It provides one of the remaining opportunities to examine the ecologies of Roosevelt elk and Columbian black-tailed deer under pristine and sympatric conditions. Until recently, cervids in the park had received only sporadic research by Park and Forest Service biologists. Results of those investigations have not been readily available, but persist largely in the form of unpublished manuscripts on file at Park Headquarters, Port Angeles, Washington (Murie 1934, Newman 1958, Schwartz 1939, Sumner 1938). Therefore, research on cervid-habitat interactions in Olympic National Park has been initiated to obtain information that will allow assessment of future trends and to enhance our understanding of the natural regulation of ungulate populations under "unmanaged" conditions.

In 1976, radio-telemetry studies of elk began in lowland forests of the Hoh Valley to determine size of home range, habitat use patterns, and grouping behavior (Jenkins 1979, Jenkins and Starkey 1982). The Hoh Valley is typical of westside drainages on the Olympic

Peninsula, and densities of elk are higher in these valleys than elsewhere in the park. For the past 50 years, little has been done to manipulate cervids or plants in Olympic National Park, and little has changed from early descriptions (cf. Schwartz 1939 and Jenkins 1981). Population size appears stable for elk with annual cow/calf ratios typically low (Jenkins 1981). Effects of predation on population size are probably minimal, because sightings and sign of extant predators are rare. Forest composition is affected directly by herbivory, yet the habitat is pristine and stable relative to man-induced alterations. Therefore, the collective cervid population in the Hoh Valley within Olympic National Park is probably at its maximum density, or ecological carrying capacity, as defined by Caughley (1976), and therefore, resource limited. In theory, a dynamic equilibrium of plant and herbivore (Caughley 1976) exists in the Hoh Valley.

The overall objective of this research was to examine foraging ecology and nutritional constraints of elk and deer in old-growth, maritime forests on the westside of Olympic National Park. Specific objectives were to 1) determine seasonal food habits of cervids, 2) determine levels of important macro- and micronutrients in forages that were consumed by cervids, 3) establish seasonal dietary levels of crude protein, dry matter digestibility and phosphorus and examine the interrelationships of each, 4) provide information on productivity and availability of important forage species, and 5) examine the nature of sympatry of the 2 cervids.

STUDY AREA

Location and Physiography

The study area was located in lowland forests of the Hoh Valley (47°50'N, 124°00'W), and was completely within Olympic National Park, which encompasses 3,600 km² in the center of the Olympic Peninsula, Washington (Fig. 1). Physiography of drainages on the westside of the Olympic Peninsula resulted from Pleistocene glaciation (Tabor 1975). The Hoh Valley is characteristically broad and U-shaped; elevations vary from 150 m on the valley floor to 910 m on surrounding ridges. Width of the valley floor is 1-2 km and consists of an irregular sequence of river terraces that resulted from glacial and alluvial depositions, as well as present fluvial processes (Fonda 1974, Swanson and Lienkaemper 1980).

Climate

Copious rainfall typifies lower elevations of the westside of the Olympic Peninsula, and some consider the vegetation representative of a temperate "rain forest" (Franklin and Dyrness 1973:64-67). Unlike tropical rain forests, however, seasonal patterns of precipitation are pronounced. Winter months receive about 130-140 cm, and summers are relatively dry. Precipitation at the Hoh River Ranger Station averages about 350 cm annually. Most precipitation below 600 m is rain, but sporadic and ephemeral snowfall usually occurs each winter below this elevation.

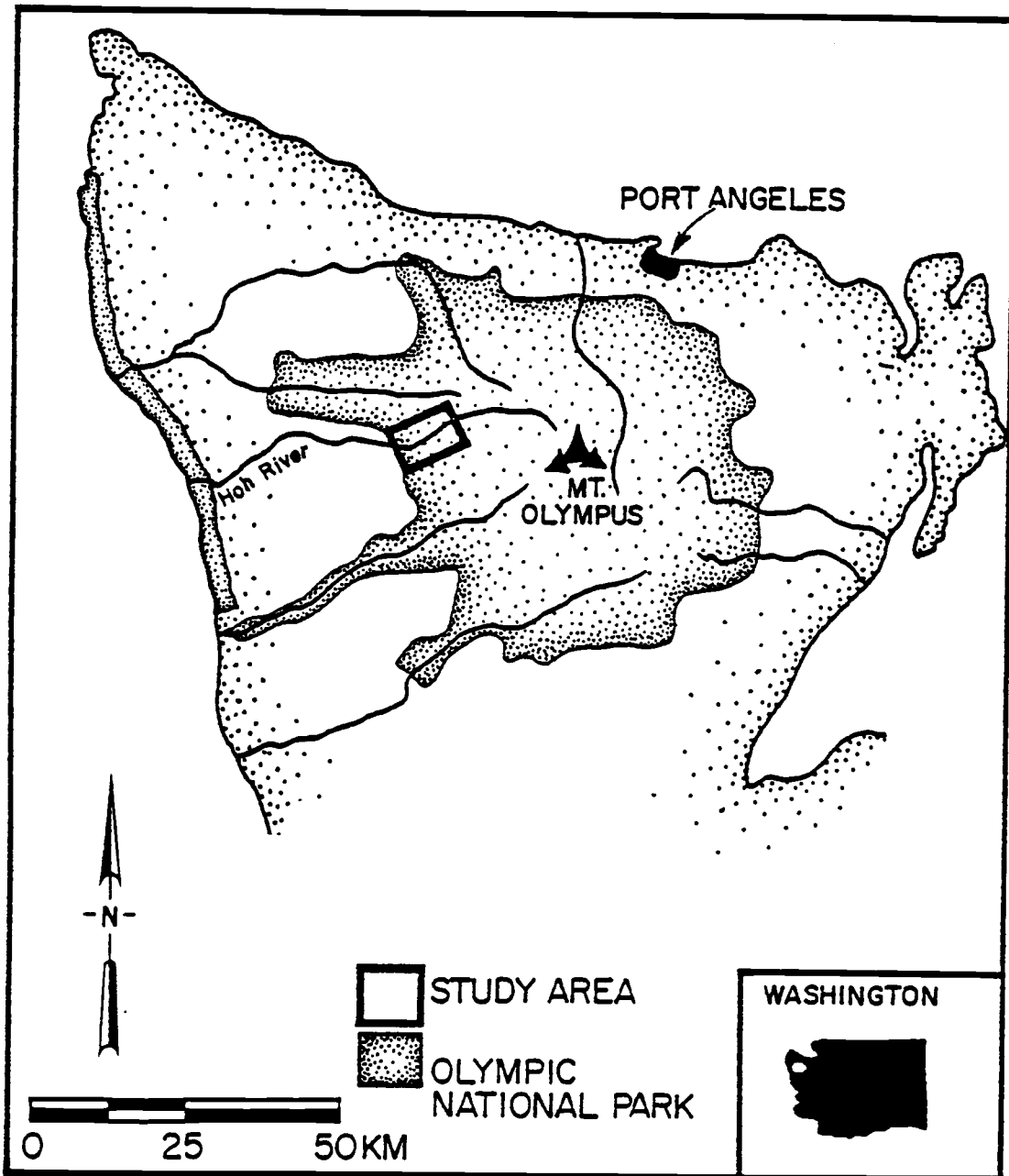


Figure 1. Location of the Hoh Valley study area in Olympic National Park, Washington.

Temperatures are mild and reflect the maritime influence of the Pacific Ocean. For example, daytime temperatures in January 1980 averaged about 4°C, and in July 1980, they averaged 23°C.

Vegetation

Vegetation in old-growth forests on the Olympic Peninsula is very heterogeneous; interpretation and delineation of communities are complex (Fonda 1974, Franklin and Dyrness 1973, Franklin et al. 1980, Jenkins 1979, Smith and Henderson, in prep.). Franklin and Dyrness (1973:58, 64) considered these forests variants of the Picea sitchensis Zone, which can be considered a variant of the Tsuga heterophylla Zone; the climax species in either case tends to be western hemlock, T. heterophylla (Raf.) Sarg. Fonda (1974) described a sere that was comprised of 4 stages from red alder, Alnus rubra Bong., and willow, Salix spp. L., dominated gravel bars near the river to climax stands of hemlock. Groves of bigleaf maple, Acer macrophyllum Pursh, developed on unique edaphic substrates but were not considered part of the sere. Fonda (1974) associated each seral community with a chronosequence of river terraces and argued that given enough time, each would progress toward a hemlock climax. That model may be overly simplistic as ages of river terraces and of forest stands do not always follow in sequence and suggest more complexity in stand development and replacement (McKee et al. 1980). Franklin and Dyrness (1973) suggested that herbivory by elk might maintain a disclimax of Sitka spruce, P. sitchensis (Bong.) Carr., and hemlock; the final step to a hemlock climax may be thwarted by selective

consumption of that conifer by elk. Smith and Henderson (in prep.) recognized 8-10 forest communities in the Hoh Valley but did not observe a consistent chronosequence of forest development on river terraces. Rather, a mosaic of geomorphic terraces and resulting forest stands typified the valley. Apparently a sere exists, but its specific characteristics have been difficult to define.

For practical purposes, Jenkins (1979) delineated "habitat units" of vegetation that were discernable largely from aerial photographs. They were defined as "mappable, distinctive land areas with vegetation and thermal characteristics that were believed to be ecologically significant to elk" (Jenkins 1979:18). Habitat units provided a means of assessing movements of elk but did not require a botanical description of the sere or a geomorphic description of river terraces. Jenkins' (1979) classification is therefore time-specific, but it is useful in establishing relative availabilities of "habitat units," and thus forage, to cervids. His classification was used to establish the sampling scheme in this study.

Jenkins (1979) recognized the following habitat units: 1) Gravel Bar, typified by young alder and willow and a sparse cover of grasses and forbs, 2) Alder Flat, dominated by alder and a dense cover of herbaceous vegetation, 3) Spruce-Cottonwood Terrace, indicated by black cottonwood, Populus trichocarpa Torr. & Ray, but including bigleaf maple and spruce, 5) Spruce-Hemlock, dominated by those conifers, typified by a well-developed "shrub" layer of huckleberries, Vaccinium spp. L., and swordfern, Polystichum munitum (Kaulf.) Presl,

and a copious cover of cryptogams (i.e., the mature conifer forest),
5) Vine maple, Acer circinatum Pursh, dominated by that species and including salmonberry, Rubus spectabilis Pursh, and assorted forbs,
6) Bigleaf Maple, typified by maples and a well-developed herbaceous layer of grasses and forbs, and 7) Valley Wall, dominated by hemlock, Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, and western redcedar, Thuja plicata Donn., including a diverse shrub layer of huckleberries, salmonberry and salal, Gaultheria shallon Pursh, and a sparse cover of forbs. Additionally, willow clearings among alder flats were recognized and sampled in this study. Affinities of common species for various habitat units are given in Table 1.

Fauna

The mammalian fauna in coastal forests can be diverse (Maser et al. 1981); as many as 44 species of mammals may occur in the Hoh Valley (Franklin et al. 1972). Elk and deer are the most conspicuous herbivores, but slugs, Ariolimax spp., snowshoe hare, Lepus americanus, and mountain beaver, Aplodontia rufa, no doubt contribute to the overall use of the flora. Populations of predators in Olympic National Park were reduced greatly in the early 1900s, and little is known of their specific ecologies today. Wolves, Canis lupus, were extirpated from the Olympic Peninsula by the 1920s. Extant predators include cougar, Felis concolor, coyote, Canis latrans, black bear, Ursus americanus, and bobcat, Lynx rufus.

Table 1. Common plant species in the Hoh Valley. Acronyms are used in subsequent tables and figures.

Forage Class ^a Species ^b	Acronym Used Below ^c	Common Name	Habitat Unit Affinity
Tree			
<u>Acer macrophyllum</u>	Acma	Bigleaf maple	3,6
<u>Alnus rubra</u>	Alru	Red alder	1,2
<u>Picea sitchensis</u>	Pisi	Sitka spruce	3,4
<u>Populus trichocarpa</u>	Potr	Black cottonwood	3
<u>Pseudotsuga menziesii</u>	Psme	Douglas-fir	4,7
<u>Thuja plicata</u>	Thpl	Western redcedar	4,7
<u>Tsuga heterophylla</u>	Tshe	Western hemlock	4,7
Shrub			
<u>Acer circinatum</u>	Acci	Vine maple	4,5
<u>Rubus spectabilis</u>	Rusp	Salmonberry	3,4,5,6,7
<u>Salix spp.</u>	Sa	Willow	1,2
<u>Vaccinium spp.</u>	Va	Huckleberry	4,7
Forb			
<u>Cornus canadensis</u>	Coca	Bunchberry dogwood	4
<u>Fragaria vesca</u>	Frve	Wild strawberry	1
<u>Hypochoeris radiata</u>	Hyra	Cats-ear	1,2
<u>Oxalis oregana</u>	Oxor	Oxalis	3,4,5,6,7
<u>Rubus ursinus</u>	Ruur	Trailing blackberry	2,4,6,
<u>Tiarella trifoliata</u>	Titr	Coolwort	4,7
<u>Tolmiea menziesii</u>	Tome	Youth-on-age	2,3,4
<u>Stachys cooleyae</u>	Stco	Hedge nettle	2
Fern			
<u>Athyrium filix-femina</u>	Atfi	Lady fern	2,4,6
<u>Blechnum spicant</u>	Blsp	Deer fern	4
<u>Polystichum munitum</u>	Pomu	Swordfern	3,4,7
<u>Pteridium aquilinum</u>	Ptaq	Bracken fern	4
Grass or Grass-like			
<u>Agrostis gigantea</u>	Aggi	Bent grass	2,6
<u>Carex deweyana</u>	Cade	Dewey's sedge	2,3,4,6
<u>Carex spp.</u>	Carex	Elk sedge	2,3,4,6
<u>Dactylis glomerata</u>	Dagl	Orchard-grass	4,6
<u>Deschampsia atrophurpurea</u>	Deat	Hairgrass	4,6
<u>Elymus glaucus</u>	Elgl	Ryegrass	1,2
<u>Phleum pratensis</u>	Phpr	Timothy grass	1,2
<u>Poa spp.</u>	Poa	Bluegrass	2,6
Moss			
<u>Hylocomium splendens</u>	Hysp	Fern moss	3,4,6

^a Species grouped into forage classes as defined by growth form and importance to cervids, not strictly taxonomic.

^b Nomenclature follows Hitchcock and Cronquist (1973).

^c Most acronyms follow Garrison et al. (1976), except where species designation is lacking. In those cases, a number of very similar species were treated as one in subsequent analyses: Salix spp. included S. scouleriana and S. sitchensis; Vaccinium spp. included V. parvifolium and V. ovalifolium, to a lesser extent V. alaskense; Carex spp. was primarily C. deweyana; Poa spp. included P. pratensis and P. trivialis, to a lesser extent P. marcida.

^d Habitat units after Jenkins (1979): 1 = Gravel Bar, 2 = Alder Flat, 3 = Spruce-Cottonwood Terrace, 4 = Spruce-Hemlock, 5 = Vine maple, 6 = Bigleaf Maple, 7 = Valley Wall.

METHODS

Unless otherwise indicated, all statistical tests were deemed significant if $P < 0.05$. Statistical Package for the Social Sciences (Nie et al. 1975) was used for some statistical procedures.

Botanical Nomenclature

Species and common names follow Hitchcock and Cronquist (1973); acronyms for various species generally follow Garrison et al. (1976). Important species in the study area, along with their common names and acronyms are listed in Table 1; the latter are used in all figures and tables.

Delineation of Sampling Blocks

Elk in the lower portions of the Hoh Valley are not migratory and occupy limited home ranges throughout the year (Jenkins and Starkey 1982). With the aid of radio telemetry, Jenkins (1979) found that 4 home range groups of elk inhabited a 10 km stretch of the valley from the Park boundary to the Hoh Ranger Station. Those groups were relatively disjunct socially and occupied fairly distinct home ranges. Two of those home range groups limited their activity to undisturbed habitats within the National Park. Those home ranges were used to delineate 4 sampling blocks, each approximately 6 km², 2 corresponding to each home range. Each pair of blocks was separated by the Hoh River, which bisected the center of the study area.

Therefore, study blocks were delineated based on known activities of elk and enabled an evaluation of important habitat components of a group's home range. It was assumed that black-tailed deer occupied similar areas; however, no telemetric data on their activities were available.

Delineation of Sampling Periods

Major sampling periods were delineated based on the cycle of reproduction of elk and deer. Spring samples were collected from 15 April to 15 May during the third trimester of gestation of both elk and deer. Summer samples were collected from 15 July to 15 August during the probable peak in lactation for both cervids. Fall samples were collected from 15 October to 15 November during the late rut of elk and early rut of deer. Winter samples were collected from 15 January to 15 February during a presumed low in nutritional levels of forages.

Food Habits

Microscopic analyses of fecal material were used to determine seasonal diets of elk and deer, following the procedures of Sparks and Malechek (1968) and Vavra and Holechek (1980). Laboratory work was conducted at the Eastern Oregon Agricultural Research Center, Union, Oregon. Generally, 1 composite fecal sample was collected from each of the 4 blocks seasonally from Fall 1979 to Spring 1981. Initially, a composite sample consisted of 5-g of fresh fecal material from 10-15 individual pellet groups. For deer, that sampling rate remained unchanged throughout the study, as obtaining fresh material was

difficult due to lush herbaceous vegetation and low numbers of deer. For elk, the sampling rate was increased to a minimum of 25 5-g subsamples in a composite sample beginning Summer 1980.

Fecal material was frozen until a collection was complete; it then was oven-dried to a constant weight and stored in air-tight containers. Three slides were prepared from each composite sample and 20 randomly selected fields were examined at a magnification of 100X (Vavra et al. 1978). A reference collection of 120 plant species from the study area was established for histological identification of epidermal fragments. Identified fragments consisted of stems, leaves, flowers, and in several cases, hairs of known reference samples and were tabulated on a frequency basis and converted to relative density (Sparks and Malechek 1968).

Results from fecal analyses can be biased by differential digestibility of forages as they pass through the digestive system of a ruminant (Dearden et al. 1975, McInnis 1976, Pulliam and Nelson 1979, Slater and Jones 1971, Stewart 1970), yet the technique can be useful in describing major dietary patterns of large herbivores (Anthony and Smith 1974, 1977; Free et al. 1970, Hansen and Martin 1973, Hansen et al. 1973, Owaga 1977, Stewart 1967, Stewart and Stewart 1970, Todd and Hansen 1973, and others). Frequently, fecal analysis is the only practical method available (Vavra et al. 1978), particularly when lush vegetation and wariness of the animals preclude direct feeding observations and protection from hunting eliminates the possibility of collecting ruminal samples (the case in this study).

Dearden et al. (1975) showed that the accuracy of fecal analysis was improved if results were corrected for differential digestibility of food items. Therefore, correction factors were determined for most plant species in seasonal diets of elk and deer. Each plant species was part of 5 hand-mixed diets and occurred in various known densities in those mixtures. Each mix was digested in vitro (Tilley and Terry 1963) and analyzed microscopically. The observed density of each species (X_i) was correlated with the known density in the hand-mixed diet (Y_i) using a least-squares regression with the line forced through the origin (Neter and Wasserman 1974:156). The estimate of β was $b = \Sigma X_i Y_i / \Sigma X_i^2$ and represented the degree of over- or underestimation of a plant species in the microscopic analyses of fecal material (Dearden et al. 1975). It was assumed that single correction factors were applicable to both deer and elk, despite possible differences in digestive capabilities (Hungate et al. 1959, Mould and Robbins 1982).

Dietary Overlap

Two indices of dietary overlap were used to compare the mean seasonal diets of elk and deer. Following Anthony and Smith (1977), the percent overlap (Y) was calculated as:

$$Y = \sum_{i=1}^n y_i$$

where y_i was the overlap in use of the i th species in the diets of 2 animals and n was the total number of plants used by both animals.

The probability (\hat{C}_λ) that any randomly selected forage item occurred in both elk and deer diets was calculated after Horn (1966), modified from Morisita (1959):

$$\hat{C}_\lambda = \frac{\sum_{i=1}^s X_i Y_i}{\sum_{i=1}^s X_i^2 + \sum_{i=1}^s Y_i^2}$$

where s was the total number of plant species and X_i and Y_i were the proportions of the total diets of elk (X) and deer (Y) taken from the i th plant species. The index varied from zero to 1.0; the latter indicated total similarity between diets.

Nutritional Studies

Plant samples were collected simultaneously with fecal material. Procedures of Radwan and Crouch (1974) generally were followed, and those parts of a plant thought to be selected by cervids were collected. Composite samples of forage species that were thought to be important dietary constituents of elk and deer from previous studies (elk: Batchelor 1965, Harper 1967, 1971; Lemos and Hines 1974; Schwartz and Mitchell 1945, Skinner 1936, Troyer 1960; deer: Brown 1961, Cowan 1945, Crouch 1968, Hines 1973, Miller 1968) and from preliminary observations in the Hoh Valley (Jenkins, pers. comm.) were collected in each block from Fall 1979 to Spring 1981, yielding 4 samples per species per season. In each season, a minimum of 10 forage species was analyzed for nutritional attributes.

Determination of the variability of nutritional quality of forage species from one year to the next was not a specific objective of this

study. If 1 species was an important component of a cervid diet in Fall 1979 and 1980, for example, it was not necessarily sampled in both years. Seasonal replicates between years were made for some species in some seasons but not all dietary components. The main objective was to assess the nutritional adequacy of as many individual forage species during as many seasons as possible (within budgetary constraints).

Fresh plant material was weighed and dried at 50°C to a constant weight (in most cases, 48 hrs) for determination of percent dry matter. Samples were ground through a 1 mm mesh screen in a macro-Wiley mill and stored for subsequent analyses.

Dry matter digestibility (DMD) and percent crude protein (CP = percent total nitrogen x 6.25) were selected as the most meaningful nutritional attributes to be assessed regularly in important forage species. The digestible fraction of a forage is an important measure of the relative value of a food to a ruminant (e.g., Bissell et al. 1955, Blaxter et al. 1956, Holechek et al. 1982, Robbins et al. 1975, Short and Reagor 1970, Smith 1952, Van Soest 1964). DMD bears a 1:1 relationship with digestible energy (Fonnesbeck et al. 1981, Milchunas et al. 1978, Moir 1961, Rittenhouse et al. 1971, Robbins et al. 1975) and reflects levels of undigestible plant constituents, such as lignin (Colburn et al. 1968, Hjeljord et al. 1982, Mautz et al. 1974). Because gross energies of forages tend to vary little between 4.0 - 4.8 Mcal/Kg (Mereszczak 1978, Milchunas et al. 1978), DMD allows a relative assessment of the value of forages at a particular season for meeting energy requirements of the ruminant (e.g., Moen 1973). Levels

of CP in feeds allow assessment of nitrogen intake. Also, CP may be correlated with other desirable nutritional attributes (Glover et al. 1960, Kothmann 1980, Lewis et al. 1975, Rochelle 1980).

In vitro DMD was determined following the procedures of Tilley and Terry (1963) at the Eastern Oregon Agricultural Research Center. That in vitro technique, as opposed to in vivo methods, may underestimate (Person et al. 1980) or overestimate (Milchunas et al. 1978) actual digestibilities attained by a wild ruminant, but the values from various forages provide a relative index to the nutritional adequacy of the forage base (Scales et al. 1974). Inoculum source was a fistulated steer that was maintained on an alfalfa diet. It may have been preferable to have rumen liquor from elk and deer; however, such samples were not available from the protected populations in the park.

Percent nitrogen (N) of all plant samples was determined using the standard Kjeldahl digest for total N (Bradstreet 1965, AOAC 1980) at the Forage Analysis Laboratory, Department of Soil Science, Oregon State University. Digested samples were analyzed for N and phosphorus (P) with an autoanalyzer and tabulated on a percent dry matter basis. Spot checks for various other elements also were conducted on important dietary components. A total of 40 forage species from all sampling periods between Summer 1980 and Spring 1981 was analyzed, after a standard perchloric acid digest (AOAC 1980), for P, calcium (Ca), potassium (K), sodium (Na), magnesium (Mg) and copper (Cu) at the above laboratory, and 24 forages were analyzed for selenium (Se)

(Brown and Watkinson 1977) by the Department of Agricultural Chemistry, Oregon State University.

Analyses of Nutritional Attributes and Dietary Levels

An overall analysis of variance (ANOVA) was not performed on nutritional data, because not all plant species were examined at all seasons, which rendered some 'treatments' void of data. The sampling scheme was chosen in an attempt to mimic seasonal forage selection by cervids and was not designed to fit into a predetermined statistical design. Yet, 4 replicates per species in a given season generally were available so analyses of variances were possible within forage classes. A standard two-factor analysis of variance (Neter and Wasserman 1974:549) and in cases of unequal sample size, an approximate analysis of variance (Neter and Wasserman 1974:614) were conducted to examine the general effects of species and season on nutritional attributes within forage classes. Arcsin transformations were used as recommended for proportional data (Snedecor and Cochran 1967:327).

The seasonal and species-specific variability of nutritional quality of forages relative to cervid use was examined by calculating the percent CP, DMD and P of seasonal diets after Westoby (1974):

$$N_{i\cdot} = \sum_{i=1}^n X_i Y_{ij}$$

where X_i was the proportion of the i th forage species in the diet, Y_{ij} was the j th nutrient content (in this case, CP, DMD, or P) of the i th plant species, and $N_{i\cdot}$ was the diet content of a specific nutrient

Mean nutritional levels (Y_{ij}) for seasons were used to calculate N_i . When nutrient values were available from a specific season in 2 different years, the mean of the means was used for Y_{ij} .

In most cases, greater than 90 percent of the total diet was accounted for by mean nutritional levels (CP, DMD, and P) of particular forages in given seasons. However, only about 80 percent of fall and summer diets of elk could be accounted for by specific nutrient values of forages. The following procedures were used to account for the remaining percentage of the diet:

- 1) if nutritional levels were not measured for the season in question, but for the preceeding and succeeding season, a linear extrapolation was made and that value used as Y_{ij} ;
- 2) if no nutritional information was available, the nutritional value of a closely related species from the same forage class was used and,
- 3) average nutritional levels for all grasses and for all browse-forbs that were found in the diet in a given season were used to account for material that could not be identified beyond those classes.

Simple regression analyses (Neter and Wasserman 1974) were used to test these hypotheses:

- 1) as dietary CP (X) increased so did dietary DMD (Y),
- 2) as dietary CP (X) increased so did dietary P (Y), and
- 3) dietary quality varied seasonally in the following ascending order: winter, fall, summer, spring.

If significant relationships existed, regressions for each cervid were tested for significant differences (Neter and Wasserman 1974:160). It was hypothesized that deer obtained diets higher in all nutritional attributes than elk at all seasons by virtue of their smaller size (Moen 1973, Robbins 1973).

Each composite fecal sample was also analyzed for percent N following the Kjeldahl procedure (AOAC 1980) by the Forage Analysis Laboratory, Department of Soil Science, Oregon State University. Two-factor analysis of variance (Neter and Wasserman 1974:569) was used to test effects of cervid and season. Dietary levels of CP and DMD were correlated with percent fecal nitrogen using simple regression to assess the value of fecal nitrogen as an index to dietary quality of cervids in the study area.

Forage Availability and Use

Herbs

Estimates of herbaceous yield were obtained at approximately 6-week intervals from December 1979 to November 1981. Twenty-five 0.2m² circular plots were distributed at random in each of 5 major habitat units of known importance to cervids (Jenkins 1979): mature alder, willow clearings, cottonwood terrace, mature forest, and big leaf maple clearings. Additionally, a young alder stand and a vine maple-dominated clearing were sampled with less intensity for comparative information. In each plot, ocular estimates of total biomass were made, as well as estimates of the percent grass, forb-fern, moss, lichen and fungi. A double-sampling approach (Wilm

et al. 1944, cited by Pieper 1978) was used, whereby every fifth plot was clipped, weighed to the nearest gram and oven-dried to a constant weight. Actual weight of a clipped plot (Y_i) and estimated weight from the same plot (X_i) were used to develop a regression based, correction equation for the estimated mean yield in each habitat unit during a particular sampling period.

The percent of the biomass that was green (or living) also was estimated. To check the accuracy of that estimate, 12 plots were collected in Fall 1980 and were separated into dead and living categories. The relationship between the actual percent green biomass and the estimate was examined using simple regression; departure from a 1:1 relationship, which would indicate over- or underestimation of biomass, was tested by constructing 95 percent confidence intervals around the regression relationship (Neter and Wasserman 1974). The ocular estimate did not depart significantly ($P < 0.05$) from the actual green biomass in a plot (Fig. 2).

Analysis of variance and a series of orthogonal contrasts (Neter and Wasserman 1974:470) were used to test the following hypotheses regarding biomass production in various habitat units:

- 1) deciduous habitat units and forest clearings consistently provided more herbaceous biomass for cervids during growing periods than the mature forest, and
- 2) all cover-types provided equal biomass during the non-growing period, although species composition might vary between areas.

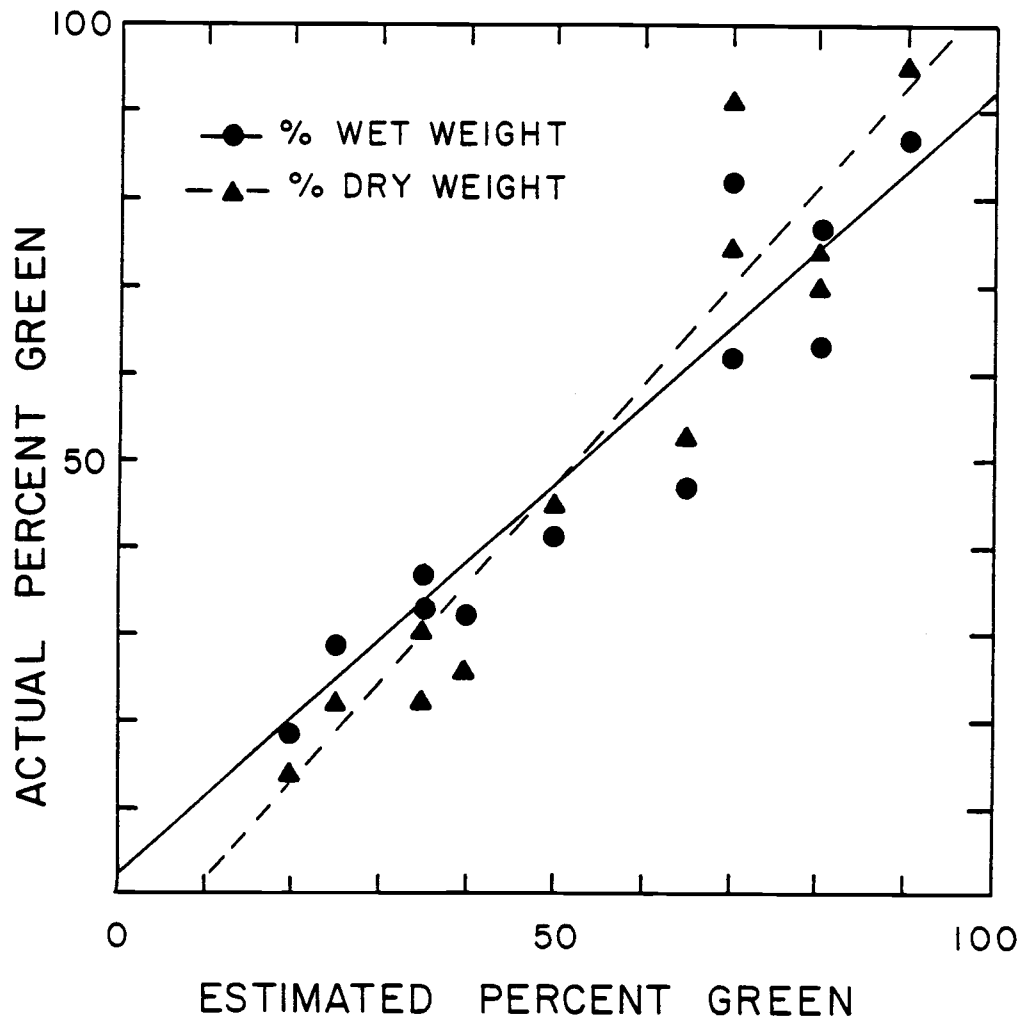


Figure 2. Relationship of ocular estimates of percent green biomass in 12 0.2 m² herbaceous plots to actual percent green biomass. Regressions do not depart significantly ($P < 0.05$) from 1:1 relationship.

Those hypotheses suggest that non-growing periods provide a more homogenous forage base of herbaceous vegetation than growing periods and are consistent with observations by Jenkins (1979) that demonstrated high selectivity of elk for certain habitat units during the growing season and less selectivity during non-growing phases.

Shrubs

The majority of annual production of shrubs in the study area occurred in spring and early summer, but a short elongation of current year's growth (CYG) also was apparent in early fall. Estimates of shrub production were calculated following Wetzel et al. (1975) and were made after fall growth terminated, but before leaf drop. Estimates were made only in Fall 1980, so annual variability was not examined.

Twenty individuals of salmonberry, willow and huckleberry were selected at random in each block, and the number of twigs per rooted stem enumerated. A minimum of 75 twigs of current year's growth was clipped from each species in a stratified-random manner (Basile and Hutchings 1966, Lyon 1970), weighed and oven-dried to a constant weight. Density estimates for each shrub species (i.e., rooted stems/m²) were obtained from 1,000 plots that were distributed simultaneously with measurements of shrub utilization. Dry matter production (g/m²) for each shrub was calculated as:

$$\text{stems/m}^2 \times \text{twigs/stem} \times \text{grams/twig},$$

and converted to kg/ha for comparison with herbaceous yield.

Swordfern was an abundant species, and its growth form, biomass and general availability resembled a browse species. Individual

fronds persisted for a year and a half, before they drooped to the forest floor and were replaced by new growth. Biomass availability was relatively stable throughout the year. Thus, it was treated as a browse species. Production of swordfern was estimated in March 1981 (just before new fronds began to emerge) by counting the number of fronds on a random selection of 50 individuals in all habitat units in which it occurred. A total of 120 fronds in 6 length classes was collected at random and oven-dried to a constant weight. Density was obtained as above, and production (g/m^2) estimated as:

$$\text{ferns}/\text{m}^2 \times \text{new fronds}/\text{fern} \times \text{grams}/\text{new frond},$$

and converted to kg/ha for comparison with herbaceous yield.

In April and May 1981, 200 forest sites were measured for shrub use. At each site, a plot was delineated by 2 15-m line transects (Canfield 1941) that were placed perpendicular to one another and oriented along the cardinal directions. Percent shrub use was estimated for 20 individuals of a given species nearest the center of each plot, using Hormay's (1943) method that was originally developed for bitterbrush, Purshia tridentata (Pursh) DC. Shrub use at a site was weighted by an estimate of the biomass contribution of each individual relative to its use. The method required an estimate of the average length of unbrowsed CYG and the percent of CYG that has been removed, and a measurement of the elliptical canopy area of the individual from diameter lengths. Weighted shrub use (WSU) for a site was then calculated as:

$$WSU = \frac{\sum_{i=1}^n (P_i R_i)}{\sum_{i=1}^n P_i} \times 100,$$

where $n = 20$, P_i = the species production index (canopy area x average length of unbrowsed twig) for the i th individual shrub, and R_i = the percent of CYG that was removed from the i th individual. The broader application of Hormay's method to shrubs in the Hoh Valley was appropriate because production (i.e., biomass) and canopy area are highly correlated in a wide range of species (Alabeck, in press; Gholz et al. 1979, Peek 1970).

Additionally, each individual was assigned to a form class (modified after Cole 1959), which reflected past herbivore use: (1) zero use, (2) 0.1-10%, (3) 10-25%, (4) 25-50%, (5) 50-75%, (6) 75-90%, (7) 90-99.9%, (8) 100% or greater (if more than CYG was removed).

Cervid Preferences

Forage Preference

Data on herbaceous and shrub production and information on conifer production from the literature were used to rank forage species as to their seasonal availability in the composite home range. The difference of each forage species' rank order of occurrence in the diet and its rank-order availability provided an index to dietary preference (Johnson 1980). That difference was defined as:

$$t_{ij} = r_{ij} - s_i,$$

where r_{ij} was the rank of the i th forage species in the j th diet and s_i was the rank of the i th forage species' availability in the composite home range. The averages of the t_{ij} 's across all seasonal diets (generally, 4 per cervid per season) were ranked in order of increasing \bar{t}_i and indicated the relative preference for dietary components (Johnson 1980).

The statistical procedures and program described by Johnson (1980) could not be used due to sample size constraints. The application of his method, therefore, provided only an index to the ranking of preferred forages, but not a test of significance between species. Preference ranks were evaluated relative to nutritional characteristics of forages with Spearman's rank-correlation, using Kendall's significance levels of r_s for small sample size (Snedecor and Cochran 1967:194).

The Sere

Vegetation data that were collected in a concurrent study were examined by Smith and Henderson (in prep.) using detrended correspondence analysis (Gauch 1982). The ordination procedure was similar to reciprocal averaging (Hill 1973, Pimentel 1979), and examined the percent cover of 161 plant species in 86 standard forest plots that were measured in the lower portions of the Hoh Valley in the summers 1978 and 1979 (Smith and Henderson, in prep.). Ordination scores of individual plant species gave a quantitative index to their distributional affinities along the sere. The score was envisioned as

the center of a species distribution along the ordination axes (B.G. Smith, pers. comm.).

Seasonal diets for both cervids and ordination scores for each forage species were used to calculate mean dietary scores that allowed a visual placement of a cervid diet along the sere. Dietary scores were calculated using the procedure already presented (Westoby 1974), where N_i equalled the dietary ordination scores, X_i equalled the proportion of the i th forage species in the diet, and Y_{ij} equalled the ordination score of the i th plant species. It was hypothesized that dietary scores for deer would possess more affinity to young seral communities than scores for elk.

Correspondence analysis assumes a linear model (Pimentel 1979:146). Additionally, by using a single ordination from summer data only (Smith and Henderson, in prep.), it was assumed that the affinity and relative availability of any forage species, as expressed by cover remained the same at all seasons. Although biomass of herbaceous vegetation can change dramatically during various seasons, that assumption was probably reasonable for perennial species.

RESULTS AND DISCUSSION

Food HabitsUncorrected vs. Corrected Diets

Fecal analysis can be improved by correction factors that compensate for differential digestibility of ingested plant species (Dearden et al. 1975, Fitzgerald and Waddington 1979, Pulliam and Nelson 1979, Vavra and Holechek 1980, Voth and Black 1973). Forbs are usually highly digestible and underestimated by fecal analyses (McInnis 1976, Vavra and Holechek 1980). Some grasses and browse species are overestimated, while others are underestimated (Dearden et al. 1975, Vavra and Holechek 1980). However, these relationships have not been described for forages in coastal ranges of the Pacific Northwest.

A total of 26 correction factors was determined for 16 forages that were used by elk and deer (Table 2). Two ferns, a moss, and a sedge were overestimated (i.e., $b < 1.0$) in all seasons, while forbs, shrubs and a grass were consistently underestimated (i.e., $b > 1.0$). Trees were less consistent, but only 4 determinations were made. Phenology probably influenced digestibility (e.g., Laycock and Price 1970) and thus, correction factors. Values for salmonberry and bluegrasses, were highest in spring and decreased through summer and fall. Other species, such as swordfern and oxalis, displayed the opposite trend. The least digestible forage, and the 1 overestimated to the greatest extent was fern moss, Hylocomium splendens (Hedw.)

Table 2. Correction factors (b) and correlation coefficients (r) for common forages in the Hoh Valley to improve estimates of relative density from fecal analyses.

Species Acronyms ^a	Spring		Summer		Fall		Winter	
	b ^b	r	b ^b	r	b ^b	r	b ^b	r
Tree: Tshe	0.854	0.966	- ^c	-	-	-	0.759	0.925
	-	-	- ^d	-	-	-	2.780	0.924
	-	-	- ^d	-	1.359	0.911	-	-
Shrub: Rusp	4.263	0.912	2.687 ^d	0.946	-	-	-	-
	-	-	- ^d	-	2.131	0.962	-	-
	- ^e	-	1.702	0.965	-	-	-	-
	- ^e	-	1.921	0.985	-	-	-	-
Fern: Pomu	0.293	0.904	0.664	0.985	-	-	0.663	0.937
	-	-	-	-	0.684	0.902	0.664	0.997
Forb: Oxor _f	1.086	0.991	- ^c	-	2.161	0.988	-	-
	-	-	-	-	1.418	0.801	-	-
	-	-	-	-	6.120	0.910	-	-
	-	-	-	-	1.012	0.931	-	-
Grass: Poa	3.720	0.950	1.232	0.941	1.124	0.952	2.264	0.948
	0.782	0.953	- ^c	-	-	-	0.602	0.999
Moss: Hysp	0.240	0.971	0.208	0.963	-	-	0.200	0.786

a) Acronyms identified in Table 1.

b) b is the slope of the regression $Y = bX$, and represents the degree of over- or underestimation.

c) Spring correction factor used to correct fecal analyses.

d) Fall correction factor used to correct fecal analyses.

e) Summer correction factor used to correct fecal analyses.

f) Species could not be differentiated microhistologically; average correction factor was used.

B.S.G. Changes in estimates of relative densities of various forage classes (Table 3) therefore reflected those species-specific corrections.

The strong interseasonal variability of correction factors for most species suggested that they should have been determined for each period in which a diet was considered. However, correction factors were not determined for all species in all seasons; therefore, when necessary, the value from the most closely related phenological period was used (Table 2). For huckleberry and vine maple, use of summer correction factors for spring may have underestimated relative densities in diets, because in vitro dry matter digestibilities for both species were higher in spring than in summer (Appendix 1). Interseasonal similarity of in vitro digestibilities for other species (hemlock, alder, trailing blackberry, Rubus ursinus Cham. & Schlecht) suggested that 1 correction factor was applicable to other seasons. Nevertheless, the magnitude of change for some species was noticeably greater than has been reported for other forages (Dearden et al. 1975, Vavra and Holechek 1980), and substantially altered estimates of relative densities of various plants in the diet (Table 3).

Cervid Diets

Across their range, Roosevelt elk and black-tailed deer select a wide variety of forages (e.g., Crouch 1981, Nelson and LEEGE 1982), which reflect many endogenous and exogenous conditions, such as availability, genotypic variation in chemical content, habitat alterations, experience and preference. Most dietary comparisons of

Table 3. Relative proportions of forage classes in seasonal cervid diets, showing changes (i.e., uncorrected vs. corrected) that resulted from use of correction factors.

Season		Forage Classes						
		Grass	Forb	Fern	Shrub	Tree	Moss	Unk.
ELK								
Fall 1979	Uncor.	18.4	8.4	9.9	5.9	45.1	11.4	0.9
	Cor.	17.2	13.4	6.5	8.5	51.4	2.2	0.8
Winter 1980	Uncor.	10.6	0.0	28.5	4.6	29.6	24.3	2.4
	Cor.	9.6	0.0	24.7	7.0	47.5	5.7	5.5
Spring 1980	Uncor.	7.8	8.7	48.8	5.4	3.5	23.3	2.5
	Cor.	14.3	18.6	27.4	17.6	6.2	10.8	5.1
Summer 1980	Uncor.	13.5	25.5	16.2	3.8	5.9	26.2	8.9
	Cor.	16.4	36.5	16.3	8.8	7.0	6.5	8.5
Fall 1980	Uncor.	29.3	10.0	7.6	11.9	25.5	14.5	1.2
	Cor.	28.0	18.4	5.3	15.3	29.0	3.1	0.9
Winter 1981	Uncor.	5.3	0.2	28.3	4.3	39.9	20.9	1.1
	Cor.	7.6	0.3	27.1	10.4	46.3	6.5	1.8
Spring 1981	Uncor.	5.7	10.0	60.6	2.8	2.3	16.1	2.8
	Cor.	13.4	22.9	37.1	8.7	4.2	8.0	5.7
DEER								
Fall 1979	Uncor.	4.7	30.0	2.8	2.8	55.8	3.1	0.8
	Cor.	3.1	39.2	1.3	3.1	52.4	0.5	0.4
Winter 1980	Uncor.	1.5	4.4	23.6	2.8	54.6	12.4	0.7
	Cor.	3.1	7.5	19.1	4.9	60.8	3.5	1.1
Spring 1980	Uncor.	2.1	16.5	63.8	4.8	2.4	8.4	1.4
	Cor.	7.1	29.0	29.6	25.8	3.2	3.2	2.1
Summer 1980	Uncor.	7.8	41.6	5.2	7.9	22.3	8.8	6.4
	Cor.	6.6	49.5	3.1	9.2	24.8	1.4	5.4
Fall 1980	Uncor.	3.5	31.5	3.0	3.8	51.5	4.4	2.3
	Cor.	3.5	40.9	1.3	3.8	49.3	0.6	0.6
Winter 1981	Uncor.	2.0	3.7	14.4	3.4	56.9	18.2	1.4
	Cor.	3.8	7.6	13.2	8.2	59.9	5.1	2.2
Spring 1981	Uncor.	3.0	14.5	59.0	12.6	1.6	7.2	2.7
	Cor.	5.6	21.1	23.3	42.8	1.8	2.4	3.1

the 2 cervids have been general and compared allopatric populations that were studied independently. Hanley (1980) described monthly diets (May-October) of sympatric black-tailed deer and introduced Rocky Mountain elk that inhabited intensively logged habitats east of Seattle, Washington. However, no published accounts exist on dietary selection of sympatric cervids in old-growth forests of western Washington.

Elk Diets

All forages that were used by elk in this study (Table 4) have been previously documented (Packee 1975, Nelson and Leege 1982), but heavier use of some species in some seasons was noted (e.g., oxalis in spring and summer, alder in fall, hemlock in winter, fern moss in all seasons). Throughout the year, elk generally used grasses and forbs inversely to shrubs and trees (Fig. 3A). Use of grasses and sedges was notably less in seasons of abundance than reported for Rocky Mountain elk (Nelson and Leege 1982), or for some populations of Roosevelt elk (Harper 1967, Janz 1980). Schwartz (1939) also noted that grasses did not constitute a major part of any seasonal diet of elk on the Olympic Peninsula. In most previous accounts, shrubs and some deciduous trees were used to a greater extent than coniferous species (Batchelor 1965, Harper 1971, Troyer 19670, Schwartz and Mitchell 1945). In the Hoh Valley, swordfern (17.9%), hemlock (13.3%), oxalis, Oxalis oregana Nutt., (12.7%), and alder (9.0%) were the most abundant dietary items, on an average annual basis.

Table 4. Mean seasonal diets of elk and deer, expressed as percent relative density (\pm S.E.), and corrected for differential digestibility of predominant forages, from Fall 1979 to Spring 1981, Hoh Valley. Values in () following cervid species indicates the number of composite fecal samples analysed in each season.

Forage Class Species Acronyms ^a	Fall 1979 ^b		Winter 1980		Spring 1980		Summer 1980	
	Elk (4)	Deer (4)	Elk (4)	Deer (5)	Elk (2)	Deer (1)	Elk (4)	Deer (4)
Total Grasses	17.2	3.1	12.0	3.9	14.4	7.1	16.4	6.6
Aggl	9.1 (3.28)	0.9 (0.47)	2.4 (1.55)	1.0 (0.53)	1.8	-	11.3 (1.90)	3.2 (1.86)
Carex	1.3 (0.24)	0.2 (0.13)	2.9 (1.40)	-	8.6	1.1	2.9 (0.80)	0.8 (0.50)
Dagl	-	0.2 (0.22)	-	-	-	1.1	-	-
Dear	-	-	-	-	-	-	-	-
Elgl	0.3 (0.33)	-	-	-	-	-	-	-
Phpr	-	0.5 (0.26)	-	-	0.2	-	-	-
Poa	4.5 (1.13)	0.5 (0.26)	4.3 (4.30)	2.9 (2.55)	2.8	3.8	1.5 (0.71)	1.8 (0.64)
Unk. Grass	2.0 (0.54)	0.8 (0.33)	2.4 (0.83)	-	1.0	1.1	0.7 (0.38)	0.8 (0.44)
Total Forbs	13.4	39.2	0.0	7.5	18.6	29.0	36.5	49.5
Coca	0.3 (0.30)	-	-	1.0 (1.04)	-	-	-	-
Frve	-	0.8 (0.29)	-	-	-	-	0.3 (0.28)	4.5 (1.31)
Hyca	-	0.2 (0.23)	-	-	-	-	-	0.6 (0.58)
Oroc	9.1 (3.59)	12.1 (4.10)	-	-	17.6	26.9	26.7 (3.02)	16.8 (2.07)
Ruar ^b	1.7 (1.00)	20.4 (3.62)	-	-	-	-	4.9 (1.61)	22.9 (4.12)
Stco	-	0.7 (0.32)	-	-	-	-	-	-
Tome/Titr ^c	2.3 (0.93)	5.0 (0.91)	-	6.5 (3.26)	1.0	2.1	4.6 (1.24)	4.7 (2.79)
Total Ferns	6.5	1.3	24.7	19.1	27.4	29.6	16.3	3.1
Atfi	-	-	-	-	-	-	0.3 (0.28)	-
Blsp	5.4 (1.62)	0.8 (0.32)	1.7 (1.01)	-	-	-	0.2 (0.20)	0.3 (0.30)
Pomu	0.5 (0.31)	0.3 (0.09)	23.0 (7.79)	19.1 (6.16)	27.4	29.6	10.3 (2.10)	2.5 (1.06)
Praq	0.6 (0.55)	0.2 (0.23)	-	-	-	-	5.5 (1.30)	0.3 (0.25)
Total Shrubs	8.5	3.1	7.0	4.9	17.9	25.8	8.8	9.2
Acci	1.7 (1.68)	0.3 (0.30)	-	-	0.9	-	2.5 (1.46)	1.9 (0.66)
Rusp	0.9 (0.90)	1.6 (0.75)	-	0.6 (0.60)	0.9	23.1	4.9 (0.92)	2.1 (1.42)
Sa	2.2 (1.30)	1.0 (0.50)	2.6 (0.91)	0.4 (0.42)	0.5	1.1	0.8 (0.47)	4.8 (0.81)
Va	3.7 (1.77)	0.2 (0.20)	4.4 (1.66)	3.9 (2.01)	15.6	1.6	0.6 (0.63)	0.4 (0.43)
Total Trees	31.4	52.4	47.5	60.8	6.2	3.2	7.0	24.8
Alru	37.1 (6.97)	50.3 (7.16)	0.8 (0.78)	1.0 (0.64)	1.1	-	1.9 (0.79)	22.2 (2.36)
Psum	-	-	-	-	-	-	-	-
Thpl	4.7 (1.84)	1.2 (0.71)	27.9 (9.08)	14.9 (10.27)	0.7	-	-	0.9 (0.88)
Tshe	9.6 (3.63)	0.9 (0.09)	18.8 (4.91)	44.9 (8.40)	4.4	3.2	5.1 (1.02)	1.7 (0.22)
Total Browse	59.9	55.5	54.5	65.7	24.1	29.0	15.8	34.0
Total Moss-Hypp	2.2 (0.44)	0.5 (0.23)	5.7 (0.81)	3.5 (0.96)	10.8	3.2	6.5 (1.08)	1.4 (0.27)
Unk. Browse-Forb	0.8	0.4	5.5	1.1	5.3	2.2	8.7	5.4

^aAcronyms identified in Table 1.

^b*Rubus ursinus* is taxonomically considered a trailing shrub; however, its growth form, phenology and availability from a cervid's standpoint resembled a forb.

^c*Tolmiea menziesii* and *Thlasella trifoliata* could not be distinguished between each other histologically; therefore, it had to be considered a common forage here and below. Average nutrient levels of the two species were used in analyses below.

Table 4. Continued

Forage Class Species Acronyms ^a	Fall 1980		Winter 1981		Spring 1981	
	Elk (5)	Deer (4)	Elk (7)	Deer (4)	Elk (5)	Deer (4)
Total Grasses	28.0	3.5	7.6	3.8	13.4	5.6
Aggl	15.0 (2.35)	0.4 (0.38)	2.1 (0.55)	0.5 (0.48)	1.9 (0.87)	0.5 (0.45)
Carex	2.8 (0.88)	-	2.2 (0.59)	0.3 (0.25)	5.9 (1.35)	1.1 (0.83)
Dagl	-	0.3 (0.25)	-	-	-	0.3 (0.60)
Deat	1.3 (0.35)	-	-	-	-	-
Elgl	-	-	-	-	-	-
Phpr	-	-	-	-	-	0.2 (0.23)
Poa	7.2 (2.11)	1.0 (0.69)	2.6 (0.89)	2.7 (1.52)	5.0 (2.06)	2.4 (1.54)
Unk. Grass	1.7 (0.51)	1.8 (0.34)	0.7 (0.18)	0.3 (0.25)	0.6 (0.40)	1.1 (0.09)
Total Forbs	18.4	40.9	0.3	7.6	22.9	21.1
Coca	-	-	-	-	-	-
Frve	-	0.6 (0.30)	-	-	-	1.0 (0.69)
Hyra	-	-	-	-	-	-
Oxor ^b	13.2 (2.83)	17.7 (2.23)	0.2 (0.22)	1.5 (1.50)	22.1 (2.15)	18.0 (1.31)
Ruar ^b	2.4 (1.21)	15.1 (5.28)	-	0.6 (0.60)	0.6 (0.36)	0.5 (0.45)
Stco	0.8 (0.49)	-	-	-	-	-
Tom/Titr ^c	2.0 (0.54)	7.5 (2.31)	0.1 (0.13)	5.5 (1.10)	0.2 (0.16)	1.6 (0.66)
Total Ferns	5.3	1.3	27.1	13.2	37.1	23.3
Arfi	-	-	-	-	-	-
Blsp	3.0 (0.71)	1.1 (0.24)	0.6 (0.22)	0.3 (0.25)	0.2 (0.16)	0.2 (0.23)
Pomu	0.7 (0.18)	0.2 (0.15)	26.5 (2.09)	12.6 (5.50)	36.9 (2.34)	23.1 (2.61)
Ptaq	1.6 (0.46)	-	-	0.3 (0.25)	-	-
Total Shrubs	15.3	3.8	10.4	8.2	8.7	42.8
Acci	2.5 (1.90)	0.7 (0.73)	-	2.3 (1.41)	0.3 (0.34)	0.7 (0.68)
Rusp	1.6 (1.56)	1.2 (0.75)	-	-	-	26.3 (7.93)
Sa	8.1 (1.99)	1.9 (0.92)	-	-	0.2 (0.18)	0.9 (0.31)
Va	3.1 (1.58)	-	10.4 (1.66)	5.9 (1.64)	8.2 (1.33)	14.9 (4.20)
Total Trees	29.0	49.3	46.3	59.9	4.2	1.8
Alru	21.9 (4.79)	45.2 (3.09)	-	1.8 (1.05)	-	-
Pame	-	1.0 (0.95)	-	-	-	-
Thpl	-	2.2 (2.20)	2.5 (1.32)	1.3 (1.25)	-	-
Tshe	7.1 (2.01)	0.9 (0.60)	43.8 (3.79)	56.8 (6.48)	4.2 (1.06)	1.8 (0.33)
Total Browse	44.3	53.1	56.7	68.1	12.9	44.6
Total Moss-Hypp	3.1 (0.32)	0.6 (0.17)	6.5 (0.79)	5.1 (0.77)	8.0 (0.65)	2.4 (0.68)
Unk. Browse-Forb	0.9	0.6	1.8	2.6	5.8	3.1

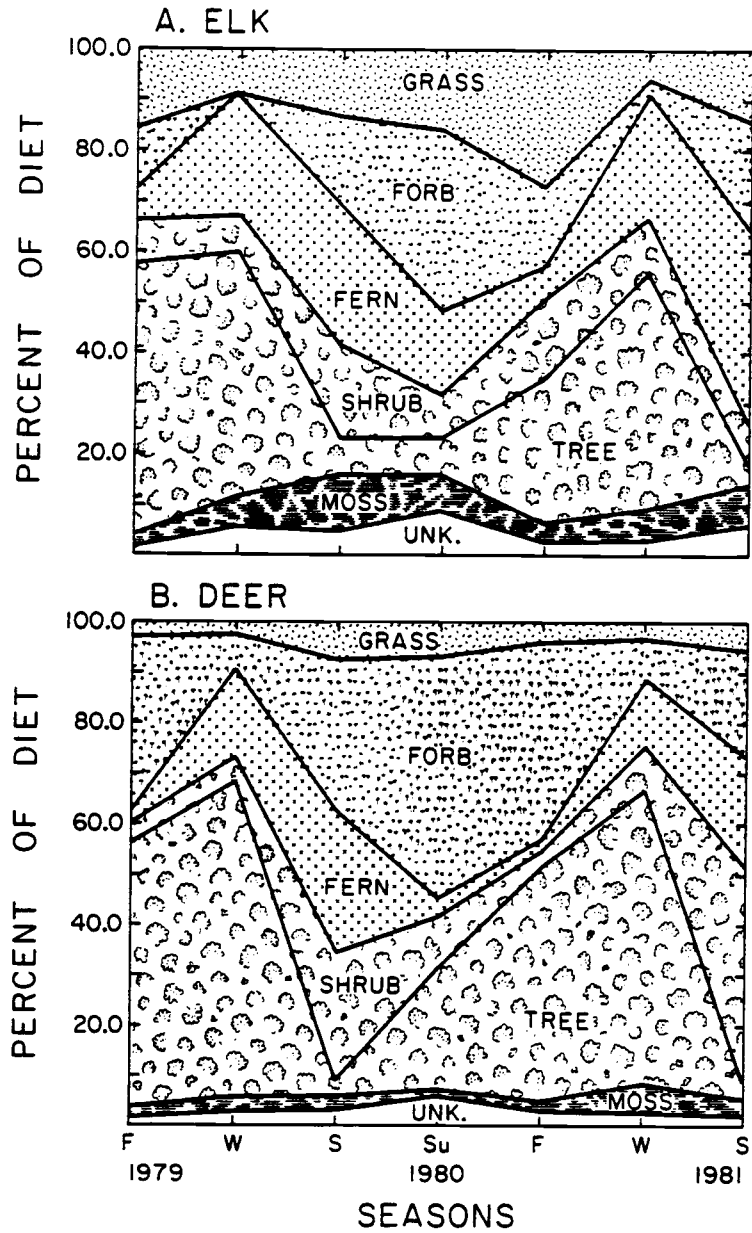


Figure 3. Average seasonal use of forage classes by elk (A) and deer (B) in the Hoh Valley, 1979-1981.

Deer Diets

Diets of both cervids displayed similar seasonal trends, but generally, deer used more browse than elk, particularly in winter and fall (Fig. 3B). Similarly, deer used forbs to a greater extent than elk in spring and summer. Browse use by deer in this study was not as high as that reported by Brown (1961), but comparable to Cowan (1945) and Rochelle (1980). However, previous studies generally indicated heavier use of shrubs than conifers, which was not the case for either cervid in this study (Table 4). Grasses and mosses were consistent in their seasonal occurrence, but represented a relatively small percentage of the annual diet. On an annual basis, the same 4 forages that were most abundant in elk diets were also most abundant in deer diets; however, proportions differed (alder 17.2%, hemlock 15.7%, oxalis 13.3%, swordfern 12.5%).

Dietary Overlap

Similar taxa were used by both deer and elk, although the extent of use of an individual plant varied between cervids (Table 4). Two indices of dietary overlap indicated a high degree of similarity in the mean proportions of food items that were selected by cervids (Fig. 4). Both indices indicated that diets were most similar in Winter 1981 and most dissimilar in either Summer or Fall 1980, depending on the index. The probability of co-occurrence of a plant (Horn 1966) in cervid diets was always higher than the proportion of plants that were common to both diets (Fig. 4). Both indices were higher than those reported from other multi-species assemblages of ungulates (Anthony and Smith 1977, Schwartz and Ellis 1981, Skovlin and Vavra 1979).

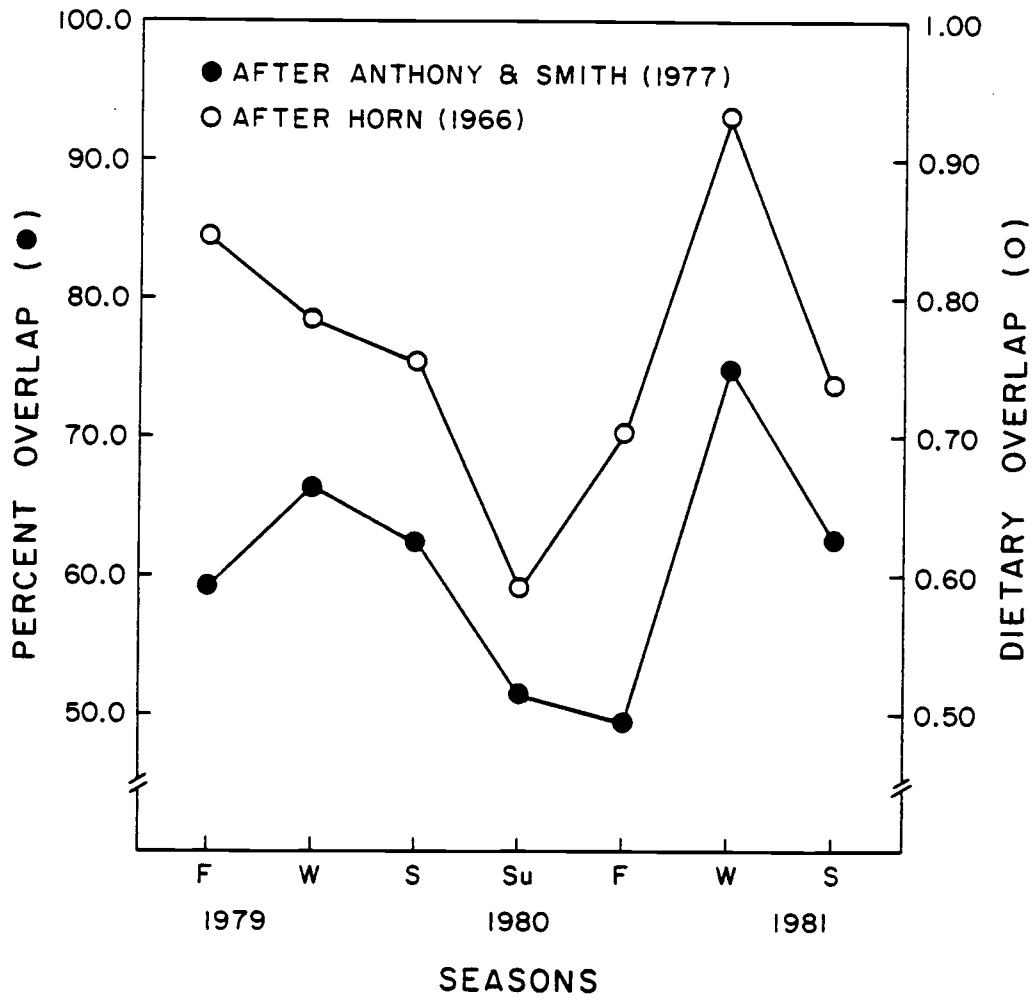


Figure 4. Two indices of seasonal dietary overlap of elk and deer in the Hoh Valley, 1979-1981.

With the exception of shrub use in spring and summer, general feeding observations of both cervids indicated similar selection of plant parts. For example, fall use of alder by both cervids was restricted to abscissing leaves; swordfern fronds and hemlock twigs were rarely stripped of their foliage, but rather tips were consumed completely by both cervids; most forbs, and importantly, oxalis, were too small to permit selection of only leaves.

Dietary overlap of sympatric ungulates is common in a wide variety of species and habitats (Anthony and Smith 1977, Constan 1972, Cowan 1947, Crawford et al. 1968, Field 1968, Gwynne and Bell 1968, Hansen and Reid 1975, Hansen and Clark 1977, Lamprey 1963, Mackie 1970, Morris and Schwartz 1957, Olsen and Hansen 1977, Peden et al. 1974, Schwartz and Nagy 1976, Schwartz and Ellis 1981, Skovlin and Vavra 1979). However, the dietary niche is only 1 facet in a complex array of characteristics and behaviors that define a species place in a community (e.g., Pianka 1978), and an index of dietary similarity alone does not measure the degree to which species may compete for a common food source. In multispecies assemblages of African ungulates, for example, dietary divergence can occur on the level of plant parts (Bell 1970, 1971; Gwynne and Bell 1968, Ducan 1975, cited by Jarman and Sinclair 1979); morphological (Hanley 1982) and anatomical differences (Giesecke and Van Gylswyk 1975, Hofmann 1968) also occur. Even if the same plant parts were selected, as appeared to be the case in this study, the degree of interspecific competition would depend on the abundance of the food source, relative to the needs of the

populations. Therefore, a measure of food abundance is required to infer possible competitive interactions from indices of dietary overlap.

Nutrition of the Forage Base

Plant Nutrients

Percent crude protein (CP) and percent dry matter digestibility (DMD) displayed similar seasonal trends in individual forage species (Fig. 5, 6; Appendix 1), while percent dry matter displayed an inverse pattern (Fig. 7). Generally, trends were similar within species in 4 forage classes (Figs. 5, 6, 7). The greatest seasonal change in CP was among shrubs (Fig. 5A); trees and forb-ferns displayed notably less seasonal change in CP, but in the latter case, interspecific variability was high (Fig. 5D). Alder and black cottonwood were consistently higher in CP than conifers (Fig. 5B), but that relationship was not as apparent for DMD (Fig. 6B).

Winter samples were collected from 15 January to 15 February, which was believed to represent the period when nutritional levels in forages were lowest and therefore, the most critical point in the nutritional ecology of cervids. Shrubs and trees were consistently low in CP and DMD in fall and winter, whereas grasses and forbs were relatively high in both (Fig. 5 and 6). Winter samples from the latter 2 classes were green regrowth. The mild climate in the Hoh Valley apparently promoted nutritious regrowth of some herbaceous species in winter, although overall biomass production was relatively low (see Fig. 17 and 18).

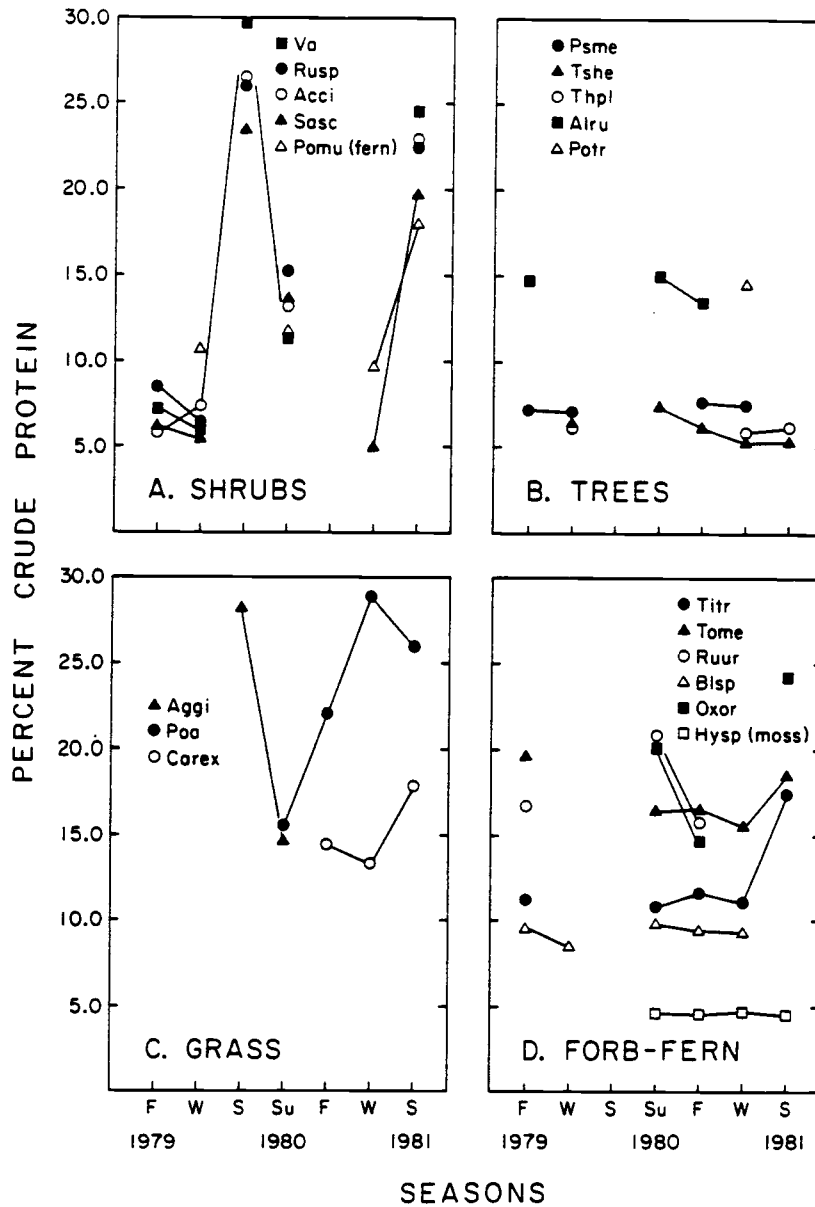


Figure 5. Seasonal mean levels ($n = 4$) of crude protein in selected forages in 4 major forage classes: shrubs (A), trees (B), grass (C), and forb-fern (D). Note that some species are included in forage classes based on their physical properties relative to cervid use, not taxonomic affinities.

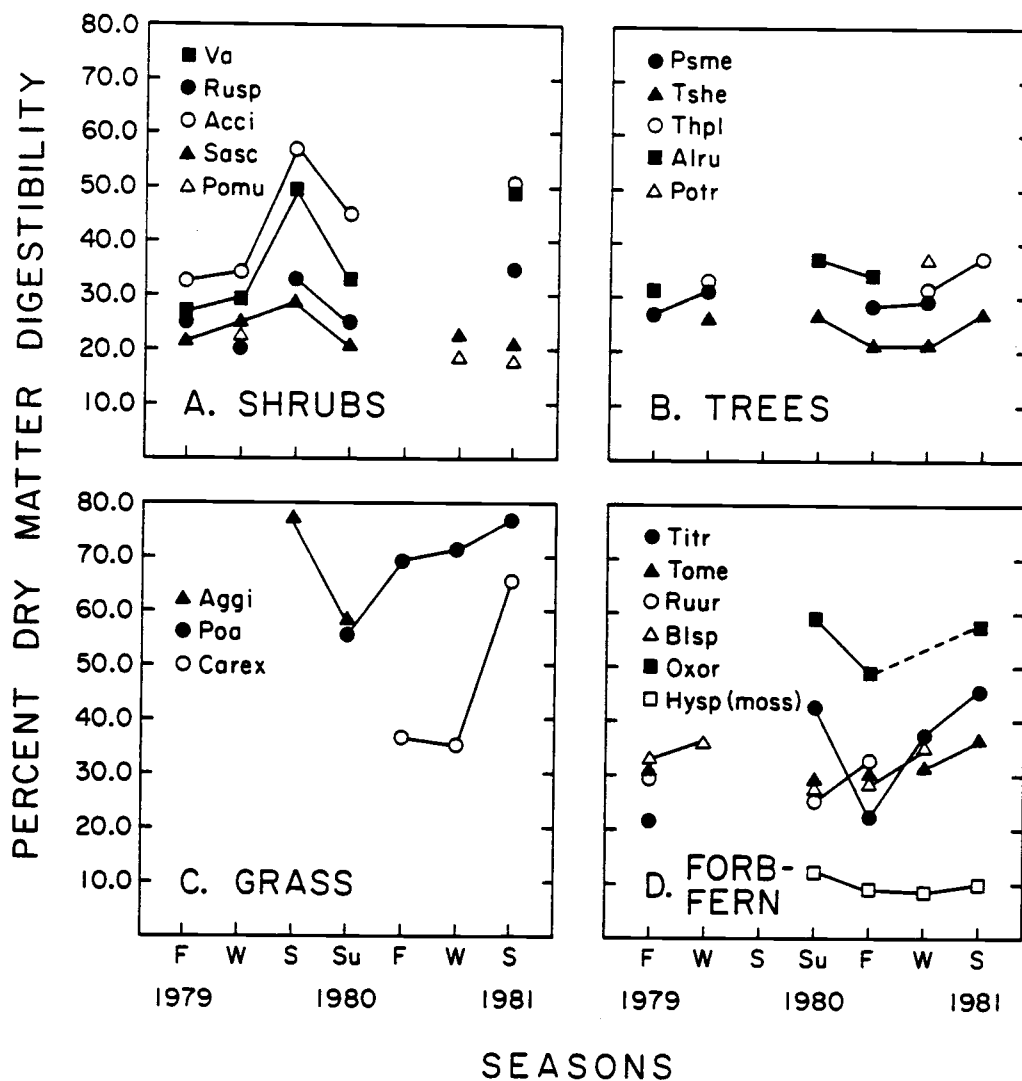


Figure 6. Seasonal mean levels ($n = 4$) of dry matter digestibility in selected forages in 4 major forage classes: shrubs (A), trees (B), grass (C), and forb-fern (D). Note that some species are included in forage classes based on their physical properties relative to cervid use, not taxonomic affinities.

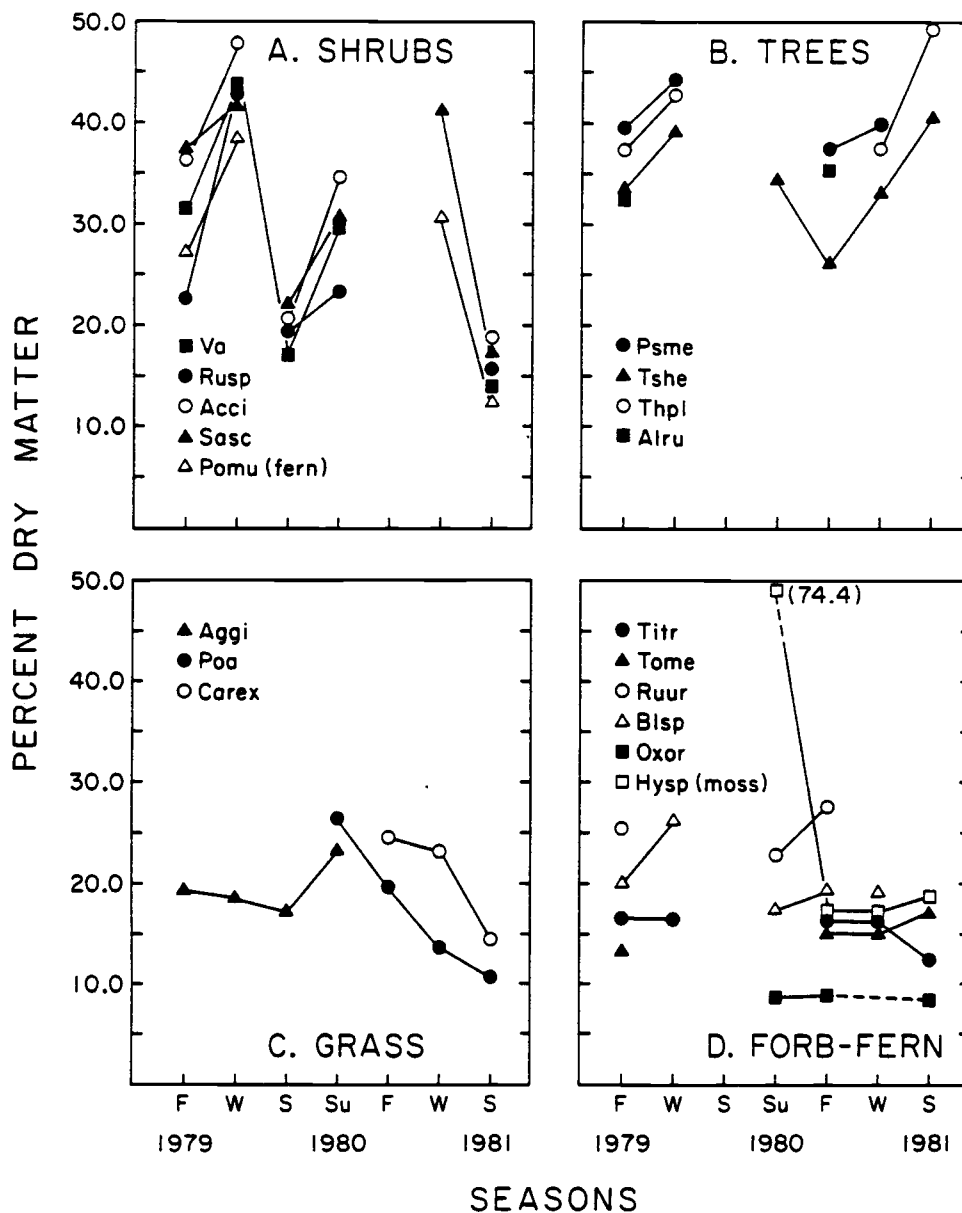


Figure 7. Seasonal mean levels (n = 4) of dry matter in selected forages in 4 major forage classes: shrubs (A), trees (B), grass (C), and forb-fern (D). Note that some species are included in forage classes based on their physical properties relative to cervid use, not taxonomic affinities.

If maintenance requirements of cervids for CP were roughly 7 percent (Moen 1973, Robbins 1973), forage quality appeared adequate. With the exception of fern moss, virtually all species provided CP in excess of 5 percent and many in excess of 7 percent, even in winter (Fig. 5). Estimates of CP in this study were not significantly different from those determined by Rochelle (1980) for 13 of the same forages on Vancouver Island, nor did they depart from estimates that were made by Sharrow and Rhodes (1981) for many of the same forages in western Oregon. They also were in agreement with other general observations (Beaton et al. 1964, 1965; Brown 1961, Edmunds 1980, Einarsen 1945, Hines 1973, Minore 1979, Murie 1952, Radwan and Crouch 1974, Tarrant et al. 1951).

The digestibilities (DMD) of certain forages, particularly shrubs and trees, were low in all seasons (Fig. 6). For some species, such as willow, swordfern, and salmonberry, that may have been attributable to secondary metabolites, such as phenolics or monoterpenes (Bryant 1981, Hergert 1960, Li 1974, Maruzzella and Lichtenstein 1956, Sakai et al. 1967, von Rudloff 1975). Those compounds can significantly depress fungal and microbial activities in forest ecosystems (e.g., Benoit et al. 1968, Swain 1977, 1979), as well as inhibit ruminal microbes (e.g., Bryant and Kuropat 1980, McLeod 1974, Mould and Robbins 1981, Nagy et al. 1964, Oh et al. 1968, 1970; Radwan 1974, Radwan and Crouch 1974, Schwartz et al. 1980a). Grasses and some shrubs in spring provided the most digestible forage, although several forbs had relatively high DMD values (Fig. 6).

There are few data in the literature concerning DMD of forages in maritime forests of the Northwest. However, estimates of DMD that were determined by Rochelle (1980) were significantly higher than those reported here (Fig. 8) and those reported by Sharrow and Rhodes (1981). All 3 studies used the two-stage in vitro method of Tilley and Terry (1963); however, inoculum source differed. Rochelle (1980) obtained rumen liquor from wild black-tailed deer, Sharrow and Rhodes (1981) used alfalfa-fed sheep as inoculum sources, and an alfalfa-fed steer was used in this study.

Many studies have found that the source of inoculum is not as important for in vitro methods as is the diet of the donor (e.g., Holechek et al. 1982). N.T. Hobbs (pers. comm.) and others recommend that nitrogen and fiber characteristics of the diet of donor approximate levels expected in the diet of the study animal. Inoculum in this study was obtained from an alfalfa-fed steer, i.e., a diet of approximately 10 percent CP and 55 percent DMD. Rumen microbes maintained on that diet are expected to be efficient at digestion (M. Vavra, pers. comm.). The ability of the microbes from the steer and cervids should be comparable in spring and summer. Winter and fall estimates could be overestimated, if vigorous microbes from steer inoculum were capable of digesting forages to a greater extent than nutritionally depleted microbes of elk or deer. Increased digestion of various roughages by cattle following protein supplementation (e.g., Crampton and Harris 1969, Church 1980) supports that contention.

Year to year changes in nutritional quality were evident for some species. Although testing for such effects was not a specific

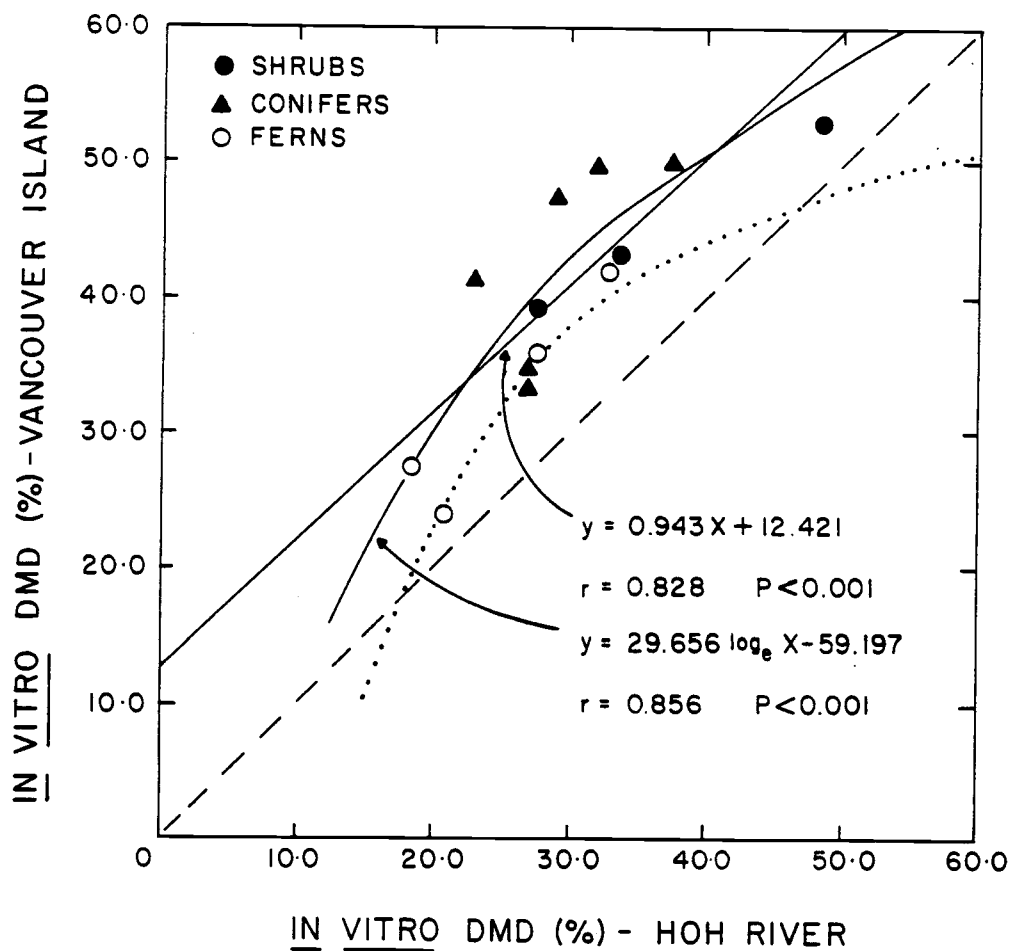


Figure 8. Comparison of estimates of dry matter digestibilities for 13 common forages from Vancouver Island (Rochelle 1980) and from the Hoh Valley. Stipled line indicates lower 95 percent confidence interval for the curvilinear function.

objective of this study, spring values of CP of shrub species were significantly higher in 1980 than 1981 ($F_{1,15} = 35.079$, $P < 0.001$). Similar relationships were not demonstrated in the other forage classes. Since annual trends in CP were most pronounced in the shrub class, phenology at the time of sampling probably accounted for that difference. Annual variability in timing of bud-burst, leaf development, and twig elongation was an important determinant in the nutritional balance of moose, Alces alces, in Saskatchewan (Stewart et al. 1977) and may be important in the Hoh Valley in some years. On the average, however, mild weather conditions probably allow early growth of shrubs to occur somewhat consistently from year to year.

Within forage classes, differences among species were evident at certain seasons. For example, a significant effect of species occurred among forb-ferns in fall ($F_{3,24} = 121.452$; $P < 0.001$), as well as among shrubs in spring ($F_{3,15} = 9.631$; $P < 0.001$). No effect among conifers could be detected.

Nutritional Interrelationships

CP frequently is assumed to reflect other nutritional attributes of forages (e.g., Cowan et al. 1970, Crampton and Harris 1969, Kothmann 1980), such as digestible protein, DMD, P and carotene. Some forage classes may show stronger relationships than others. For example, Lewis et al. (1975) contended that CP was useful in predicting digestibility of grasses, but not forbs or shrubs. To ascertain if it provided a index to other nutritional attributes in this study, CP (X) was correlated with DMD (Y_1) and P (Y_2) for paired

observations of forage samples that were collected in each block during various seasons.

CP and DMD were significantly correlated in 6 species that represented all forage classes except trees (Table 5; Fig. 9); relationships were significantly different for each species. Rochelle (1980) also demonstrated positive correlations for 2 species of huckleberry (V. alaskaense Howell and V. parvifolium Smith) but a negative relationship for deer fern. The slope for deer fern was also negative in this study, but a significant relationship could not be demonstrated. Similarly, CP and P were significantly correlated in 7 species (Table 5; Fig. 10). All species displayed similar slopes, but levels of P were lower in graminoids than in browse species (Fig. 10). Several species (willow, oxalis, and swordfern) showed only a relationship of CP to either DMD or P (Table 5). Antiherbivore strategies, (i.e., secondary compounds, silica or lignin) may maintain digestibility of swordfern and willow at low levels throughout the year, while CP and P fluctuate in response to season and phenology.

CP provided an index to DMD and P in only 5 of 18 forages. For a significant part of the forage base such relationships could not be demonstrated. That did not necessarily reflect nutritional inadequacies of those forages, but rather seasonal stability of some nutritional attributes. The seasonal mean values of CP and DMD graphically illustrated that some forages changed little, while others changed dramatically (Fig. 11). With the exception of spring values for shrubs and 2 deciduous trees, browse contained substantially less

Table 5. Correlations of crude protein (X) to dry matter digestibility (Y_1) and phosphorus (Y_2) in 8 forages of importance to cervids in the Hoh Valley.

Forage Class	Species Acronyms ^a	Sample Size	Dry Matter Digestibility				Phosphorus			
			b_0	b_1	r^2	$\underline{P} <$	b_0	b_1	r^2	$\underline{P} <$
Shrub:	Rsup	19	16.064	0.754	0.830	0.05	0.001	0.019	0.846	0.05
	Sa	22	-	-	-	-	-0.059	0.029	0.945	0.001
	Va	17	21.004	1.060	0.945	0.001	-0.039	0.023	0.945	0.001
	Acci	18	27.161	1.015	0.918	0.001	-0.009	0.025	0.862	0.001
Forb-Fern:	Oxor	7	34.946	0.933	0.891	0.05	-	-	-	-
	Pomu	10	-	-	-	-	-0.038	0.025	0.898	0.05
Grass:	Poa	16	35.722	1.447	0.786	0.05	-0.146	0.025	0.857	0.05
	Cade	11	-46.764	6.082	0.821	0.05	-0.114	0.023	0.878	0.05

^aAcronyms identified in Table 1.

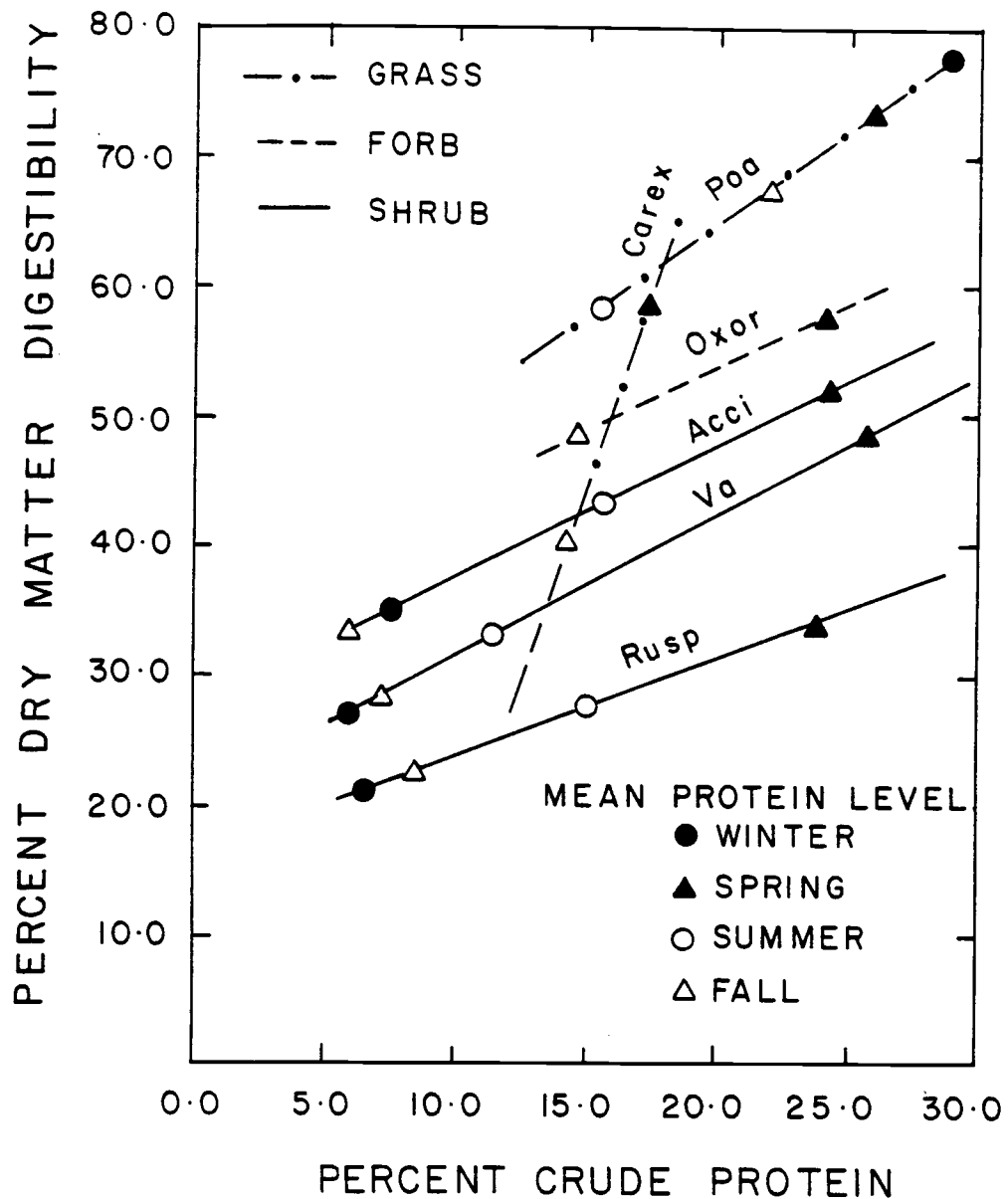


Figure 9. Summary of all significant regression relationships of crude protein and dry matter digestibility in common forages in the Hoh Valley. Length of each line indicates the range of observations for each species.

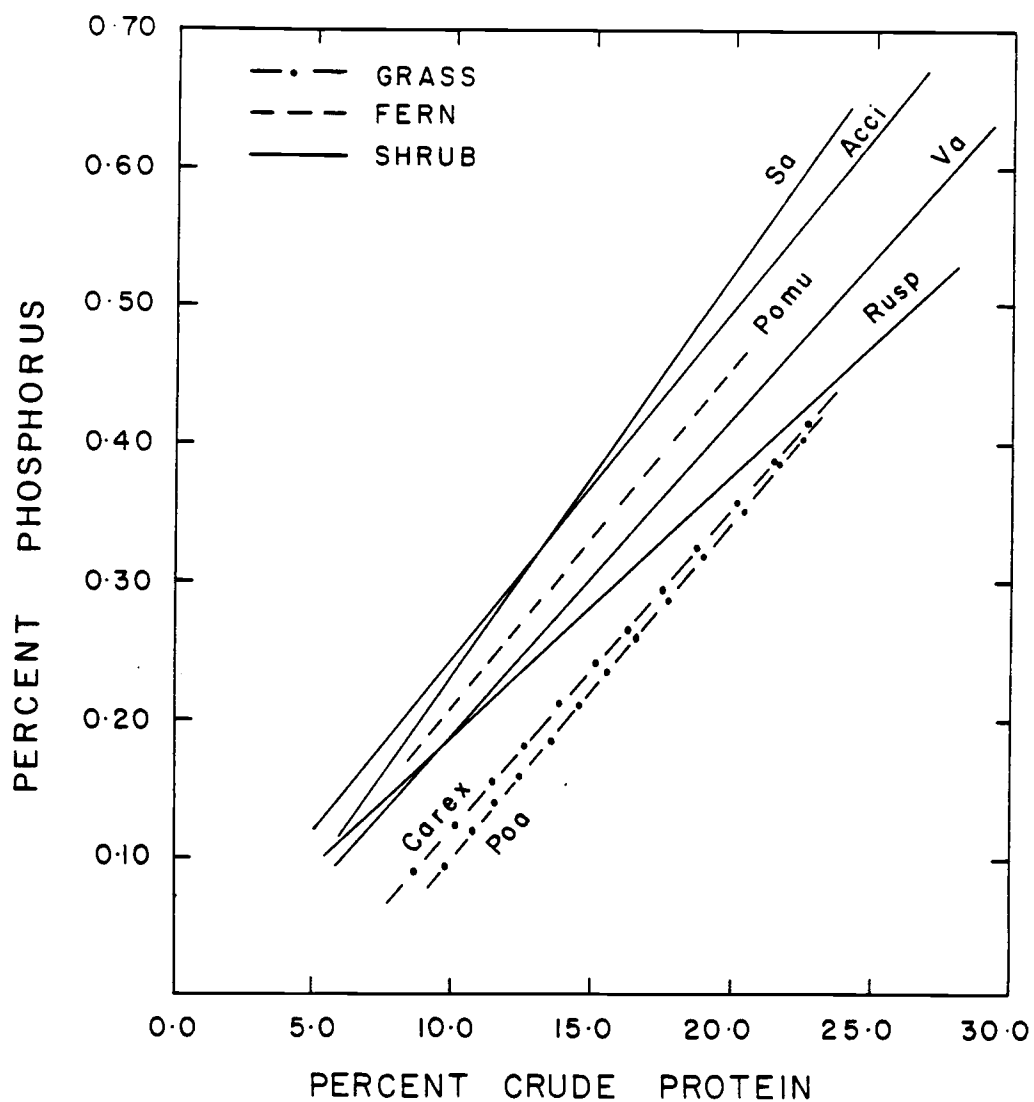


Figure 10. Summary of all regression relationships of crude protein and phosphorus in common forages in the Hoh Valley. Length of each line indicates the range of observations for each species.

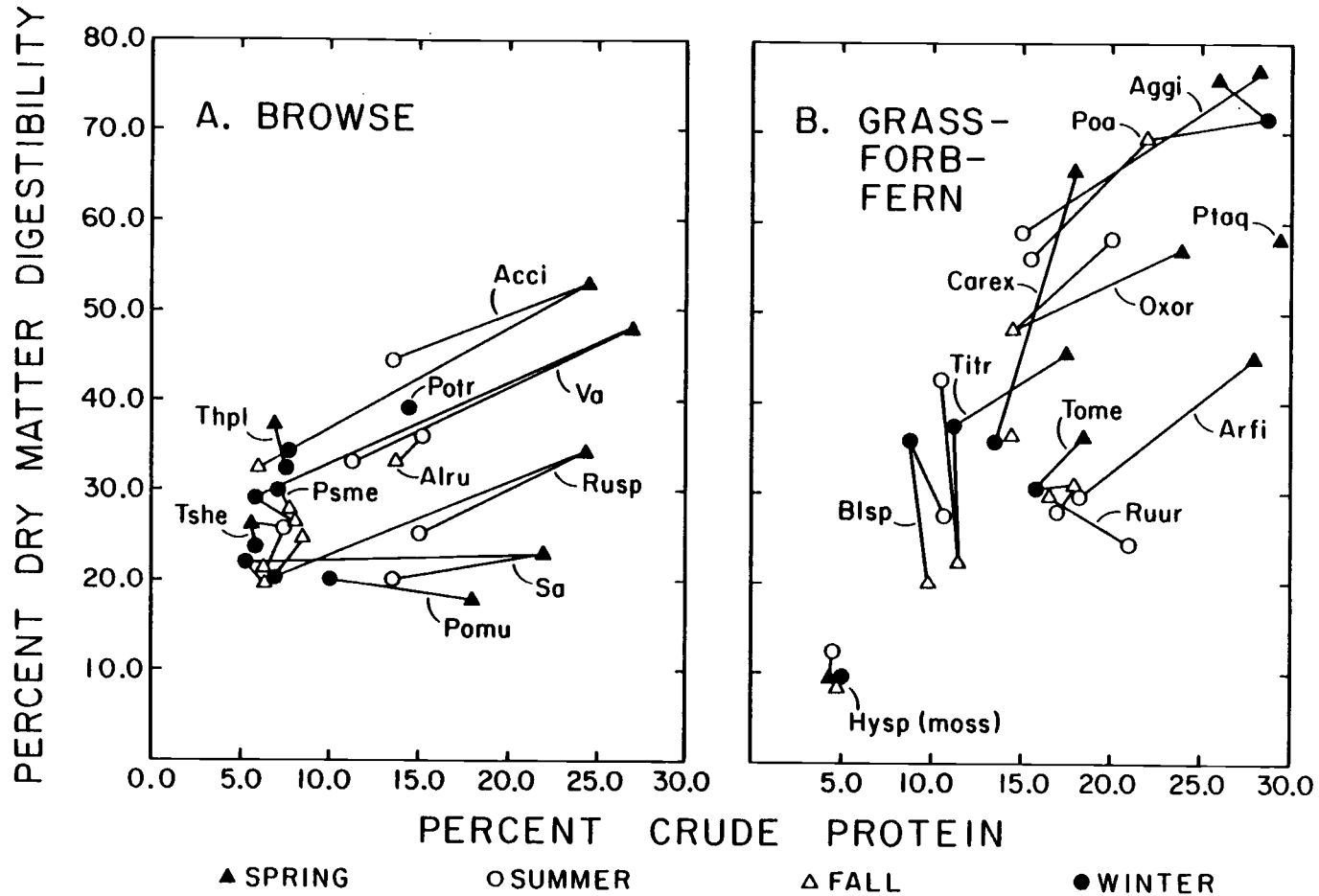


Figure 11. Overall summary of crude protein and dry matter digestibility for all forages sampled in the Hoh Valley, 1979-1981. Each point is a mean of 4 replicates in a given season; in some cases, it represents a mean of 2 seasonal means (see Appendix 1 for species that were sampled in the same season in different years).

CP and DMD (on a percentage basis) throughout the year than did most grasses and forbs. However, browse provided more dry matter (Fig. 7A and 7B) and biomass.

Additional Elements

Other macro- and micro-nutrients are essential. At least 17 are known to be required by some species (Church and Pond 1974, Scott 1972), including Mg, Cu, Ca, Na, K, Se, iron (Fe), zinc (Zn), and molybdenum (Mo). Reproduction demands high nutrient levels of various elements and "may be the most vulnerable physiological aspect sensitive to transient (or persistent) inadequacies or imbalances of trace elements" (Egan 1975:373).

Data specific to requirements of wild cervids for various elements are limited, so minimum levels for domestic livestock (NRC 1975, 1976, 1978) were used as indices (Table 6). Because of similarities in body size, requirements of domestic sheep and cattle were used as indices to the requirements of deer and elk, respectively. However, conclusions are tentative, because wild ruminants may have evolved efficient means of sequestering limited nutrients.

Phosphorus (P) and Calcium (Ca)

Concentrations of P and Ca in most forages exceeded minimum maintenance requirements of about 0.20 percent (Table 7). Ca concentrations generally exceeded established levels for normal development of white-tailed deer, O. virginianus, fawns (Ullrey et al. 1973), and because requirements of young animals are usually highest

Table 6. Requirements of domestic livestock for various elements (NRC 1975, 1976, 1978).

Species	Percent Dry Matter					PPM	
	P	Ca	Na	K	Mg	Cu ^a	Se ^b
Sheep (General)	0.16-0.37	0.21-0.52	0.04-0.10	0.50	0.04-0.08	5.0	0.10
Beef Cattle (General)	-	-	0.05-0.10	0.60-0.80	0.18-0.20	-	0.10
Dairy Cattle							
Gestation	0.26	0.37	0.10	0.80	0.16	10.0	0.10
Lactation	0.38	0.54	0.18	0.80	0.20	10.0	0.10

^a8-25 ppm considered toxic for sheep.

^b> 2.0 ppm considered toxic

Table 7. Levels of various elements in selected forages used by cervids in the Hoh Valley (n=1).

Season Species Acronyms ^a	Percent Dry Matter						PPM	
	p ^b	Ca	Ca/P	Na	K	Mg	Cu	Se
Summer 1980								
Shrub: Rusp	0.20	1.01	5.0/1	0.279	1.18	0.47	16	0.074
Tree: Tshe	0.20	0.29	1.5/1	0.014	0.78	0.11	7	0.038
Forb: Tome	-	-	-	-	-	-	-	0.029
Oxor	-	-	-	-	-	-	-	0.017
Fern: Pomu	-	-	-	-	-	-	-	0.013
Blsp	0.26	0.37	1.4/1	0.210	2.73	0.51	9	-
Arfi	0.42	0.49	1.2/1	0.067	3.26	0.44	13	0.062
Moss: Hysp	0.14	0.23	1.6/1	0.034	0.86	0.13	8	-
Fall 1980								
Shrub: Ruur	0.22	1.05	4.8/1	0.014	1.22	0.49	11	-
Tree: Psme	0.21	0.51	2.4/1	0.012	0.68	0.13	7	-
Tshe	0.24	0.28	1.2/1	0.018	0.79	0.12	7	0.030
Alru	0.12	1.05	8.8/1	0.020	0.78	0.17	12	-
Forb: Titr	0.41	1.59	3.9/1	0.084	2.61	0.53	7	-
Tome	0.22	1.65	7.5/1	0.031	1.98	0.60	8	0.033
Oxor	0.49	0.92	1.9/1	0.191	2.32	0.56	8	0.026
Fern: Blsp	0.30	0.58	1.9/1	0.280	1.85	0.60	10	-
Grass: Poa	0.41	0.30	0.7/1	0.026	2.60	0.22	13	0.034
Cade	0.18	0.49	2.7/1	0.027	2.51	0.28	9	0.027
Moss: Hysp	0.16	0.31	1.9/1	0.046	0.45	0.15	6	-
Winter 1981								
Shrub: Sa	0.13	0.76	5.8/1	0.010	0.44	0.09	11	0.020
Tree: Psme	0.21	0.48	2.3/1	0.006	0.54	0.14	7	-
Tshe	0.18	0.33	1.8/1	0.015	0.47	0.12	6	0.030
Thpl	0.13	1.19	9.2/1	0.009	0.50	0.11	6	0.024
Potr	0.34	1.06	3.1/1	0.009	1.02	0.15	18	-
Forb: Titr	0.45	1.72	3.8/1	0.105	2.60	0.60	8	-
Tome	0.27	1.80	6.7/1	0.052	2.27	0.57	9	-
Fern: Pomu	0.23	0.34	1.5/1	0.027	1.29	0.31	8	0.026
Blsp	0.29	0.56	1.9/1	0.201	1.66	0.58	9	-
Grass: Poa	0.52	0.37	0.7/1	0.048	3.84	0.30	19	0.042
Cade	0.20	0.37	1.9/1	0.021	1.88	0.20	7	0.028
Moss: Hysp	0.16	0.39	2.4/1	0.037	0.55	0.16	6	-
Spring 1981								
Shrub: Rusp	0.48	0.51	1.1/1	0.056	1.67	0.39	23	-
Sa	0.54	0.70	1.3/1	0.021	1.83	0.22	19	0.071
Va	0.60	0.31	0.5/1	0.022	2.07	0.22	24	0.027
Acci	0.62	0.22	0.4/1	0.007	1.84	0.18	15	0.027
Tree: Tshe	0.20	0.35	1.8/1	0.016	0.37	0.12	5	-
Forb: Titr	0.42	1.26	3.0/1	0.076	2.76	0.44	8	0.035
Tome	0.30	1.15	3.8/1	0.033	2.04	0.50	12	-
Oxor	0.54	0.41	0.8/1	0.051	3.06	0.35	10	-
Fern: Arfi	0.64	0.26	0.4/1	0.033	4.39	0.36	18	-
Pomu	-	-	-	-	-	-	-	0.063
Grass: Poa	0.54	0.46	0.9/1	0.060	5.12	0.33	15	-
Cade	0.34	0.31	0.9/1	0.016	3.39	0.21	12	0.030
Moss: Hysp	0.12	0.48	4.0/1	0.026	0.38	0.17	5	-

^a Acronyms identified in Table 1.

^b Independent samples and analyses from those in Appendix C; these values were not used to establish dietary levels.

(Moen 1973), they were considered adequate for the cervid population in general. Both elements displayed a seasonal trend similar to CP (see Fig. 5) and reached their lowest levels in winter (Table 7).

Excessive levels of Ca in the diet can reduce availability of P (Wasserman 1960), as well as Mg, Fe, Zn, Cu, and Mn (Chicco et al. 1973, Church and Pond 1974, Suttle 1975). Ratios of Ca:P greater than 2:1 may produce fibrous osteodystrophy in some domestic species (Church and Pond 1974), and levels above 3:1 allow the formation of insoluble tricalcium phosphate, which may reduce availability of dietary P (Wasserman 1960). None of those synergistic relationships have been demonstrated in wild ruminants, whose forages frequently contain Ca:P ratios greater than 3:1, particularly in desert ranges. In this study, some major dietary constituents (e.g., alder and trailing blackberry in fall diets or salmonberry in summer diets; see Table 4) had Ca:P ratios in excess of 3:1 (Table 7). However, outward signs of P deficiency (Church and Pond 1974) were not observed in either elk or deer.

Magnesium (Mg)

Levels of Mg in this study were quite variable seasonally and between forage classes (Table 7). Throughout the year, Mg concentrations in tree species were low (below critical level in winter; Table 7), whereas levels in forb-fern species were adequate. Brown (1961) reported Mg levels for browse species in western Washington that were notably higher than those reported here. Brown's samples were collected from second-growth forests, which may be the

reason for that discrepancy (Turner et al. 1978); however, variations in laboratory procedures cannot be ruled out.

Deficiency of Mg most commonly occurs in lactating cattle that have been restricted to a diet of primarily young grasses and results in a malady known as grass tetany (Grunes et al. 1970, Kubota et al. 1980). That malady has not been documented in wild ruminants. In this study, Mg levels appeared adequate during lactation, although only 5 forages were sampled. Additionally, grasses comprised a relatively small percentage of the average summer diet of both cervids (see Fig. 3), and a mix of other forages, adequate in Mg, could minimize problems associated with grass tetany.

Excessive levels of Ca (Chicco et al. 1973), K (Fontenot et al. 1973, Kubota et al. 1980) and N (Mayland et al. 1974) in forages can reduce availability of dietary Mg. Kubota et al. (1980) noted that ratios of $K/(Ca + Mg)$ in excess of 2.2 reduce Mg availability but that incidences of regional problems were most closely associated with grasses that had < 0.20 percent Mg. The ratio exceeded 2.2 in only a few cases (e.g., huckleberry and ladyfern in spring).

Sodium (Na) and Potassium (K)

K concentrations in forages (Table 7) exceeded requirements for domestic animals in all physiological conditions and during all seasons. Although excessive amounts of K can cause hypertrophy of the adrenal cortex (Church and Pond 1974) and suppress Mg absorption (Fontenot et al. 1973), the amounts that were observed in this study were not excessive. However, levels of Na were inadequate in many

forages, based on requirements of domestic livestock (Tables 6, 7). Most forages that had adequate Na would satisfy the needs of domestic sheep better than domestic cattle. Some forages did have adequate levels in some seasons for large ruminants (e.g., salmonberry, deer fern and coolwort), but they were not major components of elk diets (see Table 4), probably due to availability. Thus, elk may be more likely to be deficient in Na than deer.

Demands for Na increase during lactation, while requirements of K remain stable (Table 6). Na is generally limited in foliage in forest ecosystems (Seastedt and Crowsley 1981), and some cervid populations may be limited by availability of Na (Belovsky 1981, Belovsky and Jordan 1981, Weeks and Kirkpatrick 1976). Widespread Na deficiencies also occur in tropical areas (Stobbs and Minson 1980). K, on the other hand, is usually abundant in forages, particularly in the West (Allaway 1975).

Some ungulates may obtain Na from natural licks (Dalke et al. 1965, Dean 1980, Weeks and Kirkpatrick 1976), but such behavior was not observed in this study. Elk may possess means of conserving Na, as Belovsky and Jordan (1981) proposed for moose and as Denton (1956) demonstrated for domestic sheep. Aquatic vegetation can be high in Na; Belovsky and Jordan (1981) reported an average of 0.295 percent. Elk frequently foraged in swamps and areas of impeded drainages, that supported dense mats of water parsley, Oenanthe sarmentosa Presl. Perhaps that was related to the acquisition of Na.

Copper (Cu)

Levels of Cu in this study were more than adequate (Table 7) based on requirements of domestic animals (Table 6). Concentrations increased during growing periods and tended to decrease with maturity. Three shrubs and 1 grass had levels in spring that were considered toxic to domestic livestock (Table 7); however, despite the relatively high occurrence of salmonberry and huckleberry in deer and elk diets, respectively, a mix of other species probably minimized any effects of excessive Cu in those forages (Church and Pond 1974).

Cu deficiency can impair reproduction; levels < 6 ppm have been implicated as a causative factor in low reproductive rates of moose on the Kenai Peninsula, Alaska (Flynn et al. 1977). However, requirements of Cu are relatively constant throughout the year (Table 6). Geographically, copper deficiencies are infrequent (Kubota and Allaway 1972), but high levels of Mo can induce Cu deficiencies (Kubota et al. 1961, 1967; Kubota 1975), as well as antagonize Zn, Fe and Ca (Church and Pond 1974, Underwood 1971). Mo induced Cu deficiencies are more common from forages that grow in areas of poor drainage (Kubota et al. 1961). The absolute requirements for Cu are low in domestic livestock (~ 1.0 ppm), but because of the synergistic reactions with other elements that reduce its availability, standard requirements are considered to be higher (Underwood 1971; Table 6).

Selenium (Se)

Concentrations of Se were low in this study and displayed inconsistent variability among forage classes (Table 7). If 0.10 ppm

can be accepted as the minimum requirement, cervids would not be able to acquire a diet that was sufficient in Se.

Areas of Se deficiency and toxicity occur in irregular patterns throughout the United States and appear to be related to volcanism and resulting distribution and deposition of ash (Carter et. al. 1978, Kubota and Allaway 1972, Muth and Allaway 1963). In the Pacific Northwest, Se levels generally are low, and white muscle disease, the principle sign of deficiency, is common in young domestic animals (Muth and Allaway 1963). Se is required in small amounts (> 0.10 ppm) and functions as a component of glutathione peroxidase, which maintains cellular membranes by minimizing lipid peroxidation damage (Church and Pond 1974).

Not all of the metabolic functions of Se are clear (Church and Pond 1974, Muth et al. 1967, Underwood 1971), but alphanatocopherol (Vitamin E) and other biological antioxidants may mitigate problems of Se deficiency in both domestic and wild animals (Brady et al. 1978, Combs and Scott 1977, Scott 1971, Tappel 1970, Whanger et al. 1977, Underwood 1971). Brady et al. (1978) concluded that Se requirements of white-tailed deer were low (< 0.04 ppm) and that Vitamin E (> 5.5 ppm) was a more important dietary constituent with regard to the glutathione peroxidase system.

Levels of vitamin E in plants vary greatly (Bunnell et al. 1968, Dicks 1965), and unlike most other elements, can reach maximum levels in autumn and winter (Booth and Hobson-Frohock 1961). Additionally, conifer or evergreen species can be higher in Vitamin E than grasses or forbs (Booth and Hobson-Frohock 1961). Although values of Vitamin

E in forages in the Hoh Valley were not determined, the possibility exists that Vitamin E minimizes problems that could be associated with Se deficiencies. It was therefore difficult to predict the effects of marginal Se levels (Table 7) on these cervids.

Summary

Although conclusions are tentative, the preliminary survey of various elements in forages in the Hoh Valley indicated that P, Ca, Mg and K occurred in sufficient quantities to meet nutritional requirements. Cu was excessive in some plants, but a mix of forages in a ruminant's diet probably minimized adverse effects (Church and Pond 1974). Most plants contained adequate levels of Cu. On the other hand, Na and Se were limited in most forages and may influence the nutritional condition of cervids.

Dietary Quality

Relatively few attempts have been made to determine proportions of specific nutrients in diets of wild elk or deer (Thomas and Toweill 1982, Wallmo 1981a). However, the literature is replete with observations of nutritional attributes of various plants; data generally are used to descriptively assess the value of a forage, given that it is consumed by a herbivore. No attempts have been made to calculate seasonal changes in diet quality of Roosevelt elk, and only recently has Rochelle (1980) attempted to do so for diets of black-tailed deer on Vancouver Island. Rochelle (1980:104) only included the 3 most common dietary components based on a weighted

importance value (IV) in rumen samples. Direct comparisons are therefore difficult. Dietary quality of closely related subspecies has been reported (Rocky Mountain elk, Hobbs et al. 1979, 1981; desert mule deer, O. h. crooki, Boeker et al. 1972, Short 1977, Urness et al. 1971, Urness 1981), but again comparisons are difficult because of differences in the forage base and phenology.

Crude Protein (CP)

Mean dietary CP in deer diets ranged from 7.9 percent in Winter 1981 to 21.1 percent in Spring 1981 (Table 8). CP in elk diets ranged from 8.3 percent in Winter 1981 to 18.9 percent in Spring 1981. Seasonal trends and the magnitude of seasonal change for both cervids was very similar. Seasonal changes in dietary CP (Fig. 12A) reflected protein levels in forage species. Rochelle (1980) reported dietary levels of CP for deer of 4.8 percent in fall-winter, 21.6 percent in spring, and 13.6 percent in summer, but indicated that the fall-winter value was underestimated. Most values in this study were notably higher (Table 8) and indicated that protein in the diet was adequate, assuming adequate intake, digestibility, and a minimum maintenance requirement of 7 percent. Only during winter did dietary CP decline to that level.

Dry Matter Digestibility (DMD)

Mean dietary DMD of deer diets ranged from 26.1 percent in Winter 1981 to 38.6 percent in Spring 1981; in elk diets, it ranged from 25.5 percent in Winter 1981 to 41.2 percent in Summer 1980 (Table 8). Seasonal trends were similar, except during summer and fall when elk

Table 8. Mean dietary levels (\pm S.E.) of crude protein (CP), dry matter digestibility (DMD), and phosphorus (P) for elk and deer in the Hoh Valley, 1979-81.

Seasons	ELK			DEER		
	CP (%)	DMD (%)	P (%)	CP (%)	DMD (%)	P (%)
Fall 1979	13.0 (0.56)	37.3 (0.90)	0.23 (0.012)	14.2 (0.11)	34.8 (0.67)	0.21 (0.017)
Winter 1980	9.2 (1.03)	29.3 (3.13)	0.19 (0.014)	8.0 (0.66)	26.5 (0.89)	0.19 (0.006)
Spring 1980 ^a	18.7 -	38.6 -	0.42 -	20.2 -	37.2 -	0.43 -
Summer 1980	15.9 (0.33)	41.2 (1.38)	0.32 (0.013)	16.7 (0.28)	36.8 (1.26)	0.27 (0.004)
Fall 1980	13.8 (0.56)	40.4 (1.39)	0.26 (0.010)	13.9 (0.33)	35.4 (0.40)	0.23 (0.006)
Winter 1981	8.3 (0.36)	25.5 (0.67)	0.19 (0.005)	7.9 (0.53)	26.1 (1.14)	0.20 (0.006)
Spring 1981	18.9 (0.26)	37.3 (1.23)	0.41 (0.006)	21.1 (0.15)	38.6 (0.92)	0.45 (0.006)

^aInsufficient sample size to compute S.E.; see Table 4 for sample sizes.

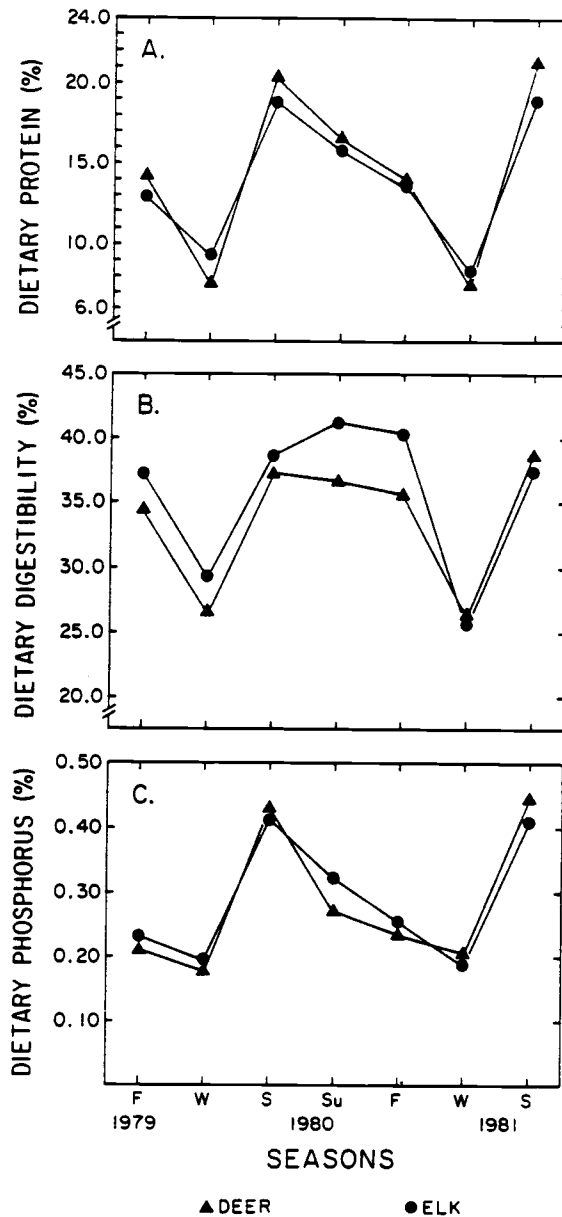


Figure 12. Seasonal mean dietary levels of crude protein (A), dry matter digestibility (B), and phosphorus (C) for elk and deer in the Hoh Valley, 1979-1981. (See Table 11 for sample sizes.)

tended to maintain a diet higher in digestibility than did deer (Fig. 12B). Seasonal changes in dietary DMD paralleled trends displayed by some individual forages (see Fig. 6).

Values in the present study were noticeably lower than those reported for other cervids. For example, Hobbs et al. (1979) reported levels for Rocky Mountain elk of about 52 percent in July, 50 percent in November, and 40 percent in March. A number of factors could be responsible for this discrepancy. Plant species that occur in old-growth forests may invest considerable energy in antiherbivore strategies (Cates and Orians 1975). Secondary compounds, such as phenolics, monoterpenes and tannins, and structural elements, such as lignin and silica, can repel herbivores (e.g., Laycock 1978, McLeod 1974, Rhoades 1979, Swain 1977, 1979); the former can reduce microbial activity in vitro (Prins and Geelen 1968, Radwan 1972) as well as protein digestibility in some herbivores (Sinclair et al. 1982).

Schwartz et al. (1980a) found that juniper (Juniperus spp.) oil inhibited starch, cellulose and dry matter digestion in vitro, while Welch and Pederson (1981) found no correlation between total monoterpenoid content and in vitro digestibility. Person et al. (1980) observed wide differences in results from in vivo and in vitro methods for determining digestibility; those species that were suspected to be high in phenolics, particularly shrubs, had consistently low in vitro levels. They speculated that the closed system of the in vitro method allowed stronger antibacterial effects of phenolics and negated normal in vivo pathways that may be capable of reducing the effects of such compounds. That hypothesis was

supported in part by Cluff et al. (1982), who reported that the percentage of monoterpenes in rumen ingesta of mule deer was 82 percent less than was expected based on known levels in ingested forages. Ruminants may have evolved means of minimizing levels of, and therefore effects of, naturally occurring antibacterial compounds (Cluff et al. 1982) to some unknown degree.

Thus, in vitro dry matter digestibilities of forages (see Fig. 6) that were high in phenolics and other compounds may have underestimated seasonal dietary DMD (Fig. 12B). Important forages in all seasonal diets, such as swordfern, alder, salmonberry and trailing blackberry, possess strong antibacterial phenolics, such as caffeic, ferulic and vanillic acids (Li 1974, C.Y. Li, pers. comm.). The extent to which a ruminant and its microbes can digest a diet with a complex mix and relatively high levels of secondary compounds has not been explored in great detail (Oh et al. 1967, cited by Person et al. 1980), but evidence that some herbivores avoid plants high in these compounds (Bryant and Kuropat 1980) may reflect an adverse effect on nutrient intake. Heavily browsed shrubs are low in digestibility (Laycock and Price 1972), and frequently produce adventitious shoots that can be significantly higher in secondary compounds than other parts of the plant (Bryant 1981). Heavy browsing of shrub species in the Hoh Valley stimulates growth of adventitious shoots, particularly in willow and salmonberry, and may further increase phenolic levels and decrease digestibility. Both cervids used alder leaves heavily at abscission; use of this species then may be least detrimental to

digestion, as translocation of phenolics may occur before the leaf is dropped (J.P. Bryant, pers. comm.).

Cervids in the old-growth forests may have little choice but to consume forages of secondary quality, based on the relative availability of more preferred species, and high levels and complex ratios of various compounds may decrease dietary digestibility in a significant manner. Future research will be required to clarify the complex role of secondary compounds in ruminant nutrition.

Phosphorus (P)

Mean dietary P in deer diets ranged from 0.19 percent in Winter 1980 to 0.45 percent in Spring 1981; in elk diets, it ranged from 0.19 in Winter 1981 to 0.42 in Spring 1980 (Table 8). Trends were similar for both cervids and paralleled dietary CP (Fig. 12C), reflecting phenology of the forage base. Dietary P in spring and summer was notably higher than levels reported for desert mule deer (Urness 1981). It exceeded the minimum requirements for sheep and cattle during all seasons (see Table 6). Growth of white-tailed deer is optimum when dietary P is 0.26 percent and dietary Ca is about 0.45 percent (Short 1981). During spring and summer, dietary P exceeded that level. Therefore, it was not considered a limiting factor to cervids, and its relationship to Ca levels was not considered a problem (see Table 7).

Dietary Interrelationships

Dietary CP and P were significantly ($P < 0.001$) and curvilinearly related in both elk ($F_{1,29} = 358.35$) and deer ($F_{2,22} = 256.74$) diets,

but the functional relationships were different (Fig. 13). The difference seemed to reflect a greater selection of forages by elk that displayed the relationship of increasing CP and increasing P (compare Tables 4 and 5). Seasonal levels increased from winter to spring. Similarly, dietary CP and DMD were significantly correlated for both elk ($F_{1,29} = 53.92$; $P < 0.001$) and deer ($F_{1,23} = 120.09$; $P < 0.001$), and the relationships were significantly different ($F_{2,54} = 4.45$; $P < 0.05$) (Fig. 14). Elk diets were more digestible than deer diets at levels of CP exceeding about 8 percent. Overall, both cervids selected diets whose nutritional properties followed similar trends.

Index To Dietary Quality and Interspecific Differences

Fecal nitrogen (N) has been shown to be correlated positively with intake (Arnold and Dudzinski 1963, Fels et al. 1979, Gallup and Briggs 1948, Langlands et al. 1963, Milford 1957, Stallcup et al. 1975), digestibility (Greenhalgh et al. 1960, Holloway et al. 1981, Lancaster 1949, Marten et al. 1963, O'Donovan et al. 1967), and crude protein (Erasmus et al. 1978, Fels et al. 1959, Greenhalgh and Corbett 1960, Holloway et al. 1981, Hebert 1973, Mould and Robbins 1981, Raymond 1948, Stallcup et al. 1975) in diets from a variety of ruminants. Most diets consisted of grasses and forbs (principally legumes), but in several cases, diets of greater variety were involved (Erasmus et al. 1978, Hebert 1973). Difficulties with using fecal N as an index of dietary quality usually have involved seasonal trends in growth and development of forages, particularly as they relate to

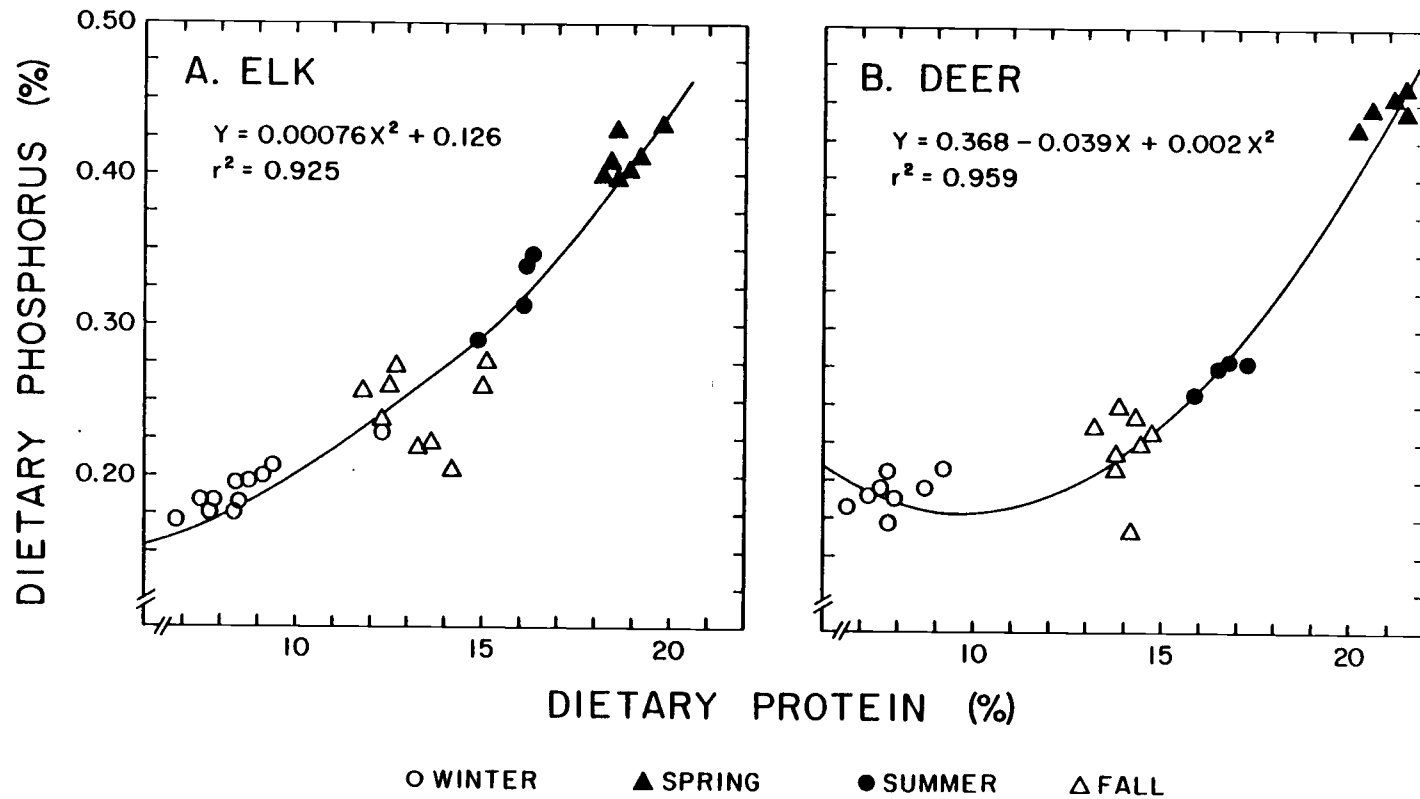


Figure 13. Relationship of dietary protein to dietary phosphorus for elk (A) and deer (B) in the Hoh Valley, 1979-1981.

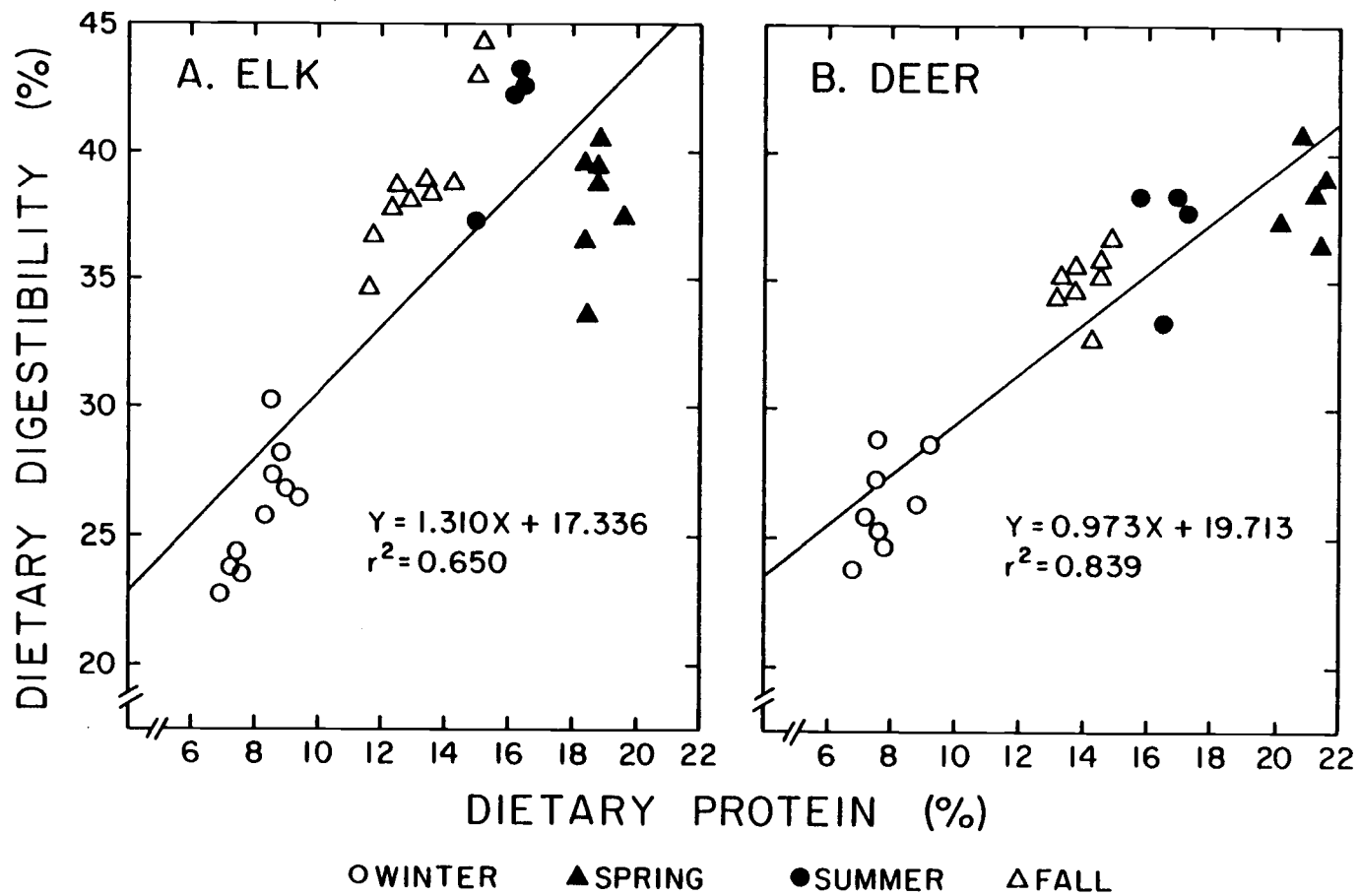


Figure 14. Relationship of dietary protein to dietary dry matter digestibility for elk (A) and deer (B) in the Hoh Valley, 1979-1981.

digestibility (Greenhalgh et al. 1960, Milford 1957, Minson and Kemp 1961).

Fecal N has received limited attention and thus application in wildlife management. Arman et al. (1975) contended that fecal N could be a valuable index if the relationship of dietary CP and fecal N could be established for a particular species in a given locality. Widespread use is limited because of the great variability in species, forages, and seasons (Arman et al. 1975). Mould and Robbins (1981) concluded that it may have limited utility as an indicator of dietary quality of wild ruminants, because of protein-complexing properties of some secondary compounds (McLeod 1974, cited by Mould and Robbins 1981) that are common in forages and that elevate N levels in the feces. In feeding trials with captive Rocky Mountain elk, Mould and Robbins (1981) found that rations of 100 percent fireweed, Epilobium angustifolium L., or maple, Acer spp., (both high in phenolics) elevated fecal N levels, which departed significantly from the regression of dietary CP and fecal N in grass and alfalfa rations. However, the same departure was not indicated when rations contained 33 percent fireweed or maple (Mould and Robbins 1981:328, Fig. 2). Apparently, the binding effect of phenolics was mitigated in the mixed rations.

Regardless of the complex ways in which phenolics affect protein availability, seasonal changes in fecal N of a given species will reflect dietary CP (Crampton and Rutherford 1954), dry matter intake (Moen 1973), fiber content (Crampton and Harris 1969), metabolic fecal nitrogen (MFN) from endogenous sources, and phenolic content. MFN

varies positively as a function of dry matter intake (Church and Pond 1974, Moen 1973) and is important in the overall nitrogen balance of ruminants. Although dry matter intake may be expected to decrease (Moen 1973, Nordan et al. 1970, Westra and Hudson 1979) and MFN increase as forage decreases in value toward winter, the effects on total fecal N as an index to dietary CP may be insignificant from a practical standpoint. However, if phenolic content of the diet varies widely between seasons, a complex regression, or none at all, between fecal N and dietary CP might exist. If levels of phenolics remain relatively constant between seasons, or if their effects are minimized in heterogeneous diets, which seemed to be the case in mixed rations used by Mould and Robbins (1981, 1982), or by some ability of rumen microbes (Oh et al. 1967), a simple regression function might exist.

Fecal N of elk and deer followed a distinct and similar trend (Fig. 15) that was comparable to general changes in CP and DMD of the forage base (see Figs. 5, 6) and to dietary CP and DMD (see Fig. 12). Values for both cervids were slightly lower than those reported by Hanley (1980) for elk and deer and by Janz (1980) for elk. A significant difference between cervids ($F_{1,36} = 90.53; P < 0.001$) and seasons ($F_{5,36} = 109.30; P < 0.001$) was noted, but the interaction was not significant ($P > 0.05$). Fecal nitrogen was significantly correlated with dietary CP (Fig. 16) in elk ($F_{1,29} = 98.00; P < 0.001$) and in deer ($F_{1,23} = 405.31; P < 0.001$), and the relationships themselves were significantly different ($F_{2,54} = 19.50; P < 0.001$). Additionally, fecal N and dietary DMD were significantly correlated

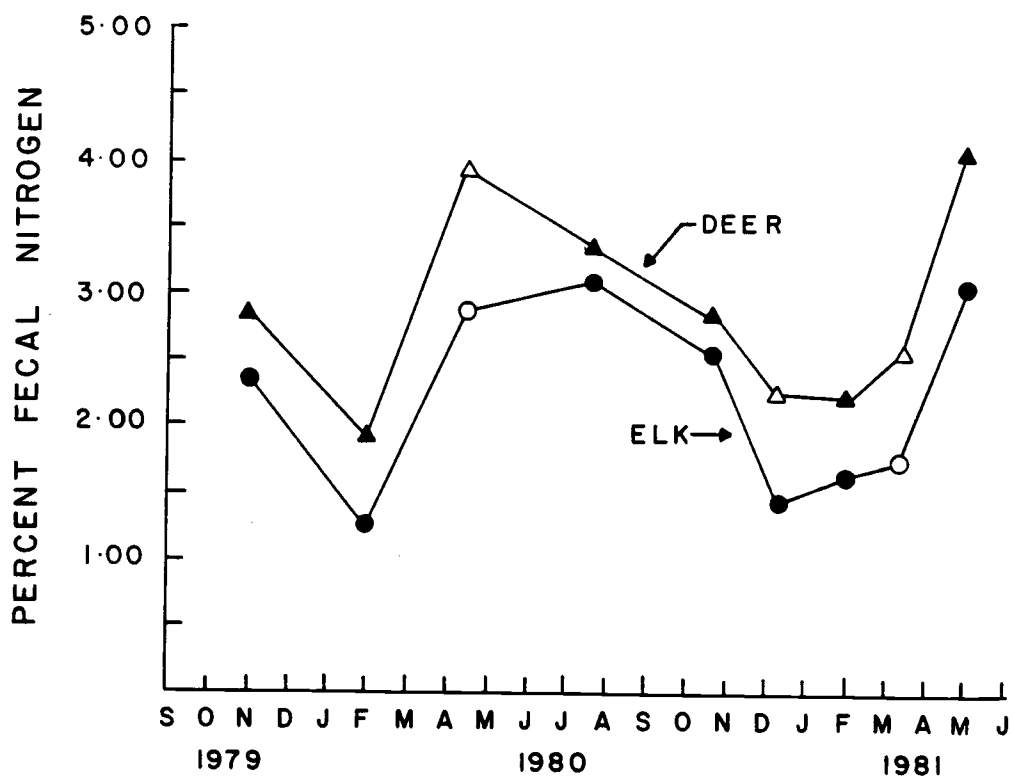


Figure 15. Seasonal mean levels of fecal nitrogen of elk and deer in the Hoh Valley, 1979-1981. Open symbols indicate that only limited numbers of composite fecal samples (3 or less) were available; they were not included in statistical analyses.

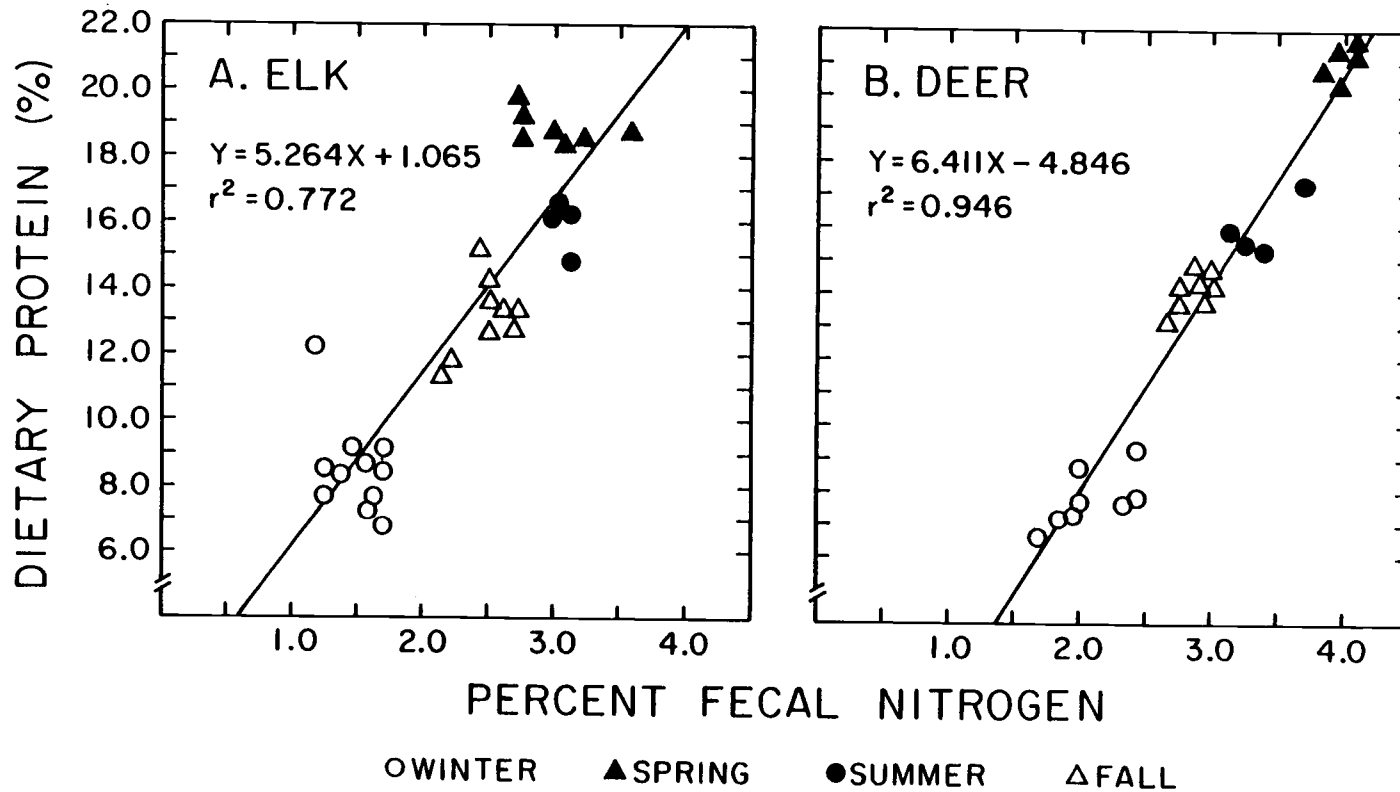


Figure 16. Relationship of fecal nitrogen to dietary crude protein for elk (A) and deer (B) in the Hoh Valley, 1979-1981.

for both cervids (elk, $F_{1,29} = 39.81$, $P < 0.001$; deer, $F_{1,23} = 69.29$, $P < 0.001$), which was expected since dietary CP and DMD were related.

All seasonal diets probably contained forages that were high in phenolics (C.Y. Li, pers. comm.), and the linearity of the regression relationships in Fig. 16 may support that evaluation. Equations predicted greater levels of fecal N than dietary N (dietary CP/6.25), which suggested that apparent protein digestibility of all seasonal diets was low. Thus, protein-complexing substances may occur at comparable and relatively high levels at all seasons, assuming that estimates of dietary CP are not seriously underestimated. Except for diets low in protein (winter; Fig. 12), fecal N was higher at lower levels of dietary CP than reported by Mould and Robbins (1981) for elk on grass-alfalfa rations, which probably reflected high levels of browse in most seasonal diets (Arman et. al. 1975) in this study. Interestingly, rations that contained fireweed and maple or 100 percent fireweed (Mould and Robbins 1981:328, Fig. 2) corresponded well to the relationship in Fig. 16A.

It was hypothesized that deer would select a diet of greater nutritional value than elk. Results in previous sections did not support that hypothesis statistically, yet mean protein levels of deer diets were consistently higher than those in elk diets in all seasons except winter. Physical characteristics of commonly used forages in most seasons (see Table 4) did not seem to allow selection of highly nutritious plant parts by either cervid, yet fecal N was significantly greater in deer feces than in elk feces (Fig. 15). Assuming that both cervids selected diets that contained comparable levels of phenolics

and other characteristics that could increase fecal N (largely substantiated by the high degree of dietary similarity; see Fig. 4), and that overall, metabolic fecal losses (MFN) were comparable (Mould and Robbins 1982), it could be concluded that deer did select a diet higher in CP than elk. On the other hand, small ruminants may have higher total fecal N than large ruminants (even on the same diet), due to higher fermentation rates, greater bacterial N produced, and larger surface to volume ratio in alimentary tract (Arman et al. 1975). Such relationships remain unresolved.

Forage Production and Use

The amount of forage that can be considered "available" to free-ranging species is difficult to quantify (Nudds 1980), but a measure is necessary to assess relative preference (Krueger 1972) and to draw inferences on the potential for interspecific competition. Normal movements, traditions, habitat heterogeneity and/or alterations, climate and physiological constraints, to name a very few, affect the manner in which an individual selects a home range, and within it, food items. The manner in which a resource is measured is an important consideration (Johnson 1980).

Plants bear evidence of past and current use by large herbivores, and the presence of use may provide the best indication of physical availability of a food item. Virtually all species in the diet that were in reach of cervids had noticeable use and thus were measured as available. As discussed above, cervid populations in the Park are believed to exist at ecological carrying capacity, a limit that may be

determined by food supply (Caughley 1976). The extent of use of a food item that is important to 2 or more species, relative to its availability, may suggest possible interspecific competition (e.g., Anthony and Smith 1977, Zaret and Rand 1971).

Herbaceous Vegetation

A total of 1,650 plots was measured in 7 major habitat units (Appendix 2). Seasonal changes of herbaceous biomass followed predictable patterns of increasing yield that peaked in August in big leaf maple, mature alder, and cottonwood terrace habitat units (Fig. 17). Herbaceous biomass production in the mature forest was variable, but no pronounced effect of season was apparent. Willow clearings were the only areas that lacked a dense overstory, and growth, maturity, and curing occurred early because of increased insolation. Bigleaf maple and mature alder stands produced more herbaceous biomass in 1980 than 1981 ($F_{1,179} = 23.844$; $P < 0.001$). They also were more productive during peak yield than other habitat units ($F_{1,960} = 38.805$; $P < 0.001$). Grasses comprised the greatest proportion of the green biomass in all habitat units, except the mature forest (Fig. 18).

On an annual basis, mosses comprised about 60 percent of the herbaceous material in the mature forest stand (compare Fig. 17 to Fig. 18; biomass unaccounted for by grasses and forbs represents mosses); its importance was no doubt related to the closed canopy that resulted in adequate shade and rain drip (Tamm 1964, Johnson 1981). Many forbs (coolwort, Tiarella trifoliata L., and oxalis) and sedges

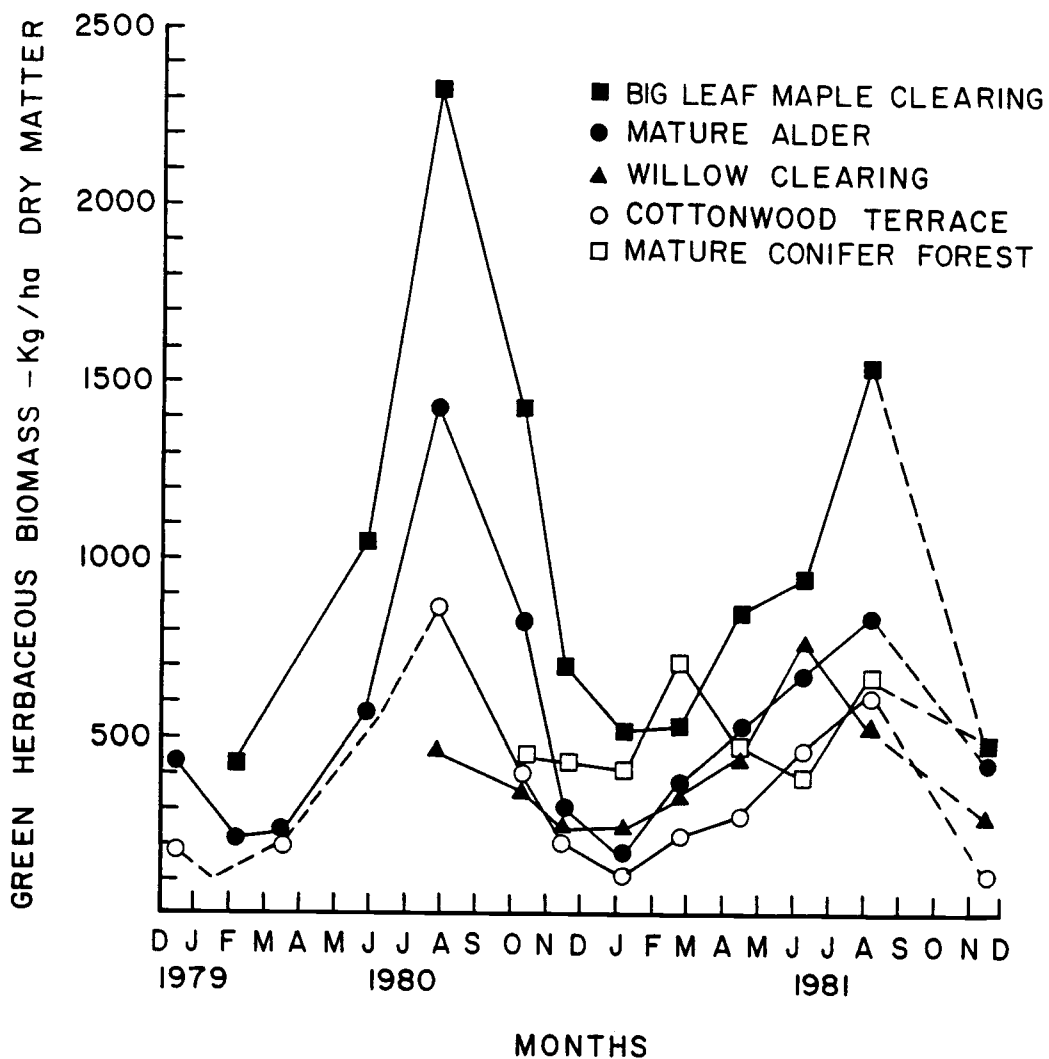


Figure 17. Yields of green herbaceous biomass (kg/ha dry matter) in 5 selected habitat units in the Hoh Valley, 1979-1981.

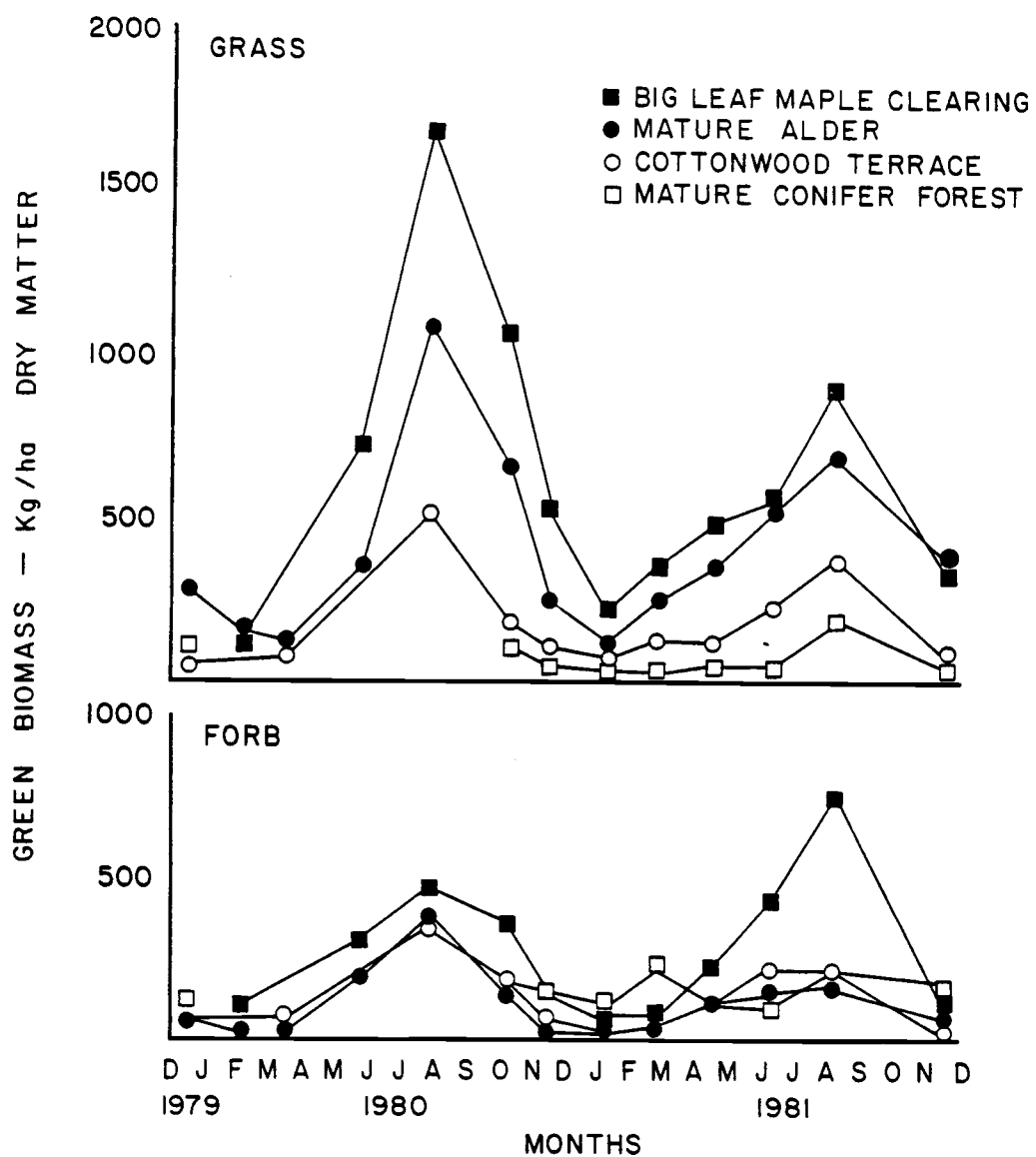


Figure 18. Yields of green grass and forb biomass (kg/ha dry matter) in 5 selected habitat units in the Hoh Valley, 1979-1981.

were closely associated with mosses. The occurrence of fern moss in both cervid diets (see Table 4) may have been incidental to use of those species, as mosses are generally thought to be of low palatability and nutritional quality (Dearden et al. 1975, Person et al. 1980). Values of CP and DMD in fern moss substantiated that (see Fig. 11 and Appendix 1).

Green biomass was least available in mid-winter in all areas (Fig. 17 and 18), and similarity between areas suggested a homogenous forage base with no stand producing more forage than another. Species composition, however, was notably different, as well as the spatial availability of habitat units (see Table 9).

Limited data were collected on the degree of use of the herb layer by cervids. A 30-day trial using paired caged plots in the bigleaf maple stand was conducted in July-August 1980; herbivores removed only 15 percent of the available biomass. Similar trials were conducted in the mature alder stand from March to July 1980 (the rise in production; Fig. 17) and only a small amount of the total biomass was consumed.

Unfortunately, no trials were conducted in winter, when limited green-up occurred. However, the low occurrence of herbaceous species in cervid diets in winter suggested that availability was restricted, which was supported by biomass estimates (assuming that such species were preferred).

Shrubs

Distributions and abundances of shrubs in conifer and hardwood forests in the Pacific Northwest are variable (Fonda 1974, Franklin

and Hemstrom 1981, Henderson 1978, Long and Turner 1975, Newton et al. 1968). In the Hoh Valley, swordfern and huckleberry reached maximum abundance in conifer forests; salmonberry was ubiquitous in occurrence, but not abundant; and willow was restricted to a narrow band along the river. Bud and leaf (or frond) formation began early in all species (ca. late March), but salmonberry and willow were the earliest. Bud burst of willow in 1981 occurred in late January. That may be an adaptation to avoid interspecific competition for light with deciduous overstory species, such as red alder, that leaf out later (Barber 1969). Twig development and elongation continued into summer, but that relationship was not quantified.

Annual production of those 4 species in 1980 was determined after growth had ceased in fall. Considerable use of salmonberry leaves was noted prior to that. Available biomass then decreased through winter to its lowest point before bud burst. Each species produced its maximum biomass in different habitat units (Table 9). Within the composite home range, swordfern was the most abundant (111.5 kg/ha), followed by huckleberry (18.0 kg/ha), willow (8.2 kg/ha), and salmonberry (5.9 kg/ha).

Current year's growth (CYG) of shrubs was consumed by cervids in winters 1980 and 1981, but swordfern occurred in diets to a much greater extent in both years than other shrubs (see Table 4), which generally, paralleled availability. Use of 4,000 shrubs was recorded at 200 forest sites at the end of Winter 1981 (Table 10), and provided an index of relative shrub use in all parts of the composite home range. Hormay's (1943) method provided an efficient appraisal of the

Table 9 . Shrub production (calculated after Wetzel et al. 1975) in predominant habitat units the Hoh Valley at the end of the growing period in 1980.

Cover Types	No. Plots	Percent of Composite Home Range	PLANT SPECIES							
			Sa ^a		Rusp ^b		Va ^c		Pomu ^d	
			Stems/4m ² (± S.E.)	kg/ha Dry matter	Stems/4m ² (± S.E.)	kg/ha Dry matter	Plants/4m ² (± S.E.)	kg/ha Dry matter	Stems/4m ² (± S.E.)	kg/ha Dry matter
Gravel Bar	130	11.6	0.64 (0.26)	47.0	0.0	0.0	0.0	0.0	0.02 (0.02)	3.0
Alder	120	9.6	0.39 (0.19)	28.6	0.12 (0.05)	1.3	0.0	0.0	0.32 (0.14)	47.6
Cottonwood Terrace	100	3.8	0.0	0.0	0.26 (0.17)	2.7	0.01 (0.01)	0.1	1.68 (0.30)	249.8
Bigleaf maple	180	7.7	0.0	0.0	1.85 (0.37)	19.4	0.02 (0.02)	0.2	1.05 (0.16)	156.2
Mature forest	480	67.3	0.0	0.0	0.59 (0.16)	6.2	3.45 (0.49)	26.7	0.85 (0.11)	126.4
TOTALS ^e	1000	100.0	-	8.2	-	5.9	-	18.0	-	111.5

^a 28.8 (± 2.27) twigs/stem; 1.02 grams dry wt/twig.

^b 9.11 (± 0.76) twigs/stem; 0.46 grams dry wt/twig.

^c 20.6 (± 1.66) twigs/stem; 0.15 grams dry wt/twig.

^d 23.7 (± 1.55) fronds/plant; 2.51 grams dry wt/frond.

^e Weighted biomass estimates in composite home range using spatial contribution of each habitat unit.

Table 10. Average shrub use and form class for 4 browse species in the Hoh Valley.

Species	Number of Forest Sites ^a	Average % Use ^b (± S.E.)	Average Form Class ^c (± S.E.)
Pomu (swordfern)	138	-	4.7 (1.96)
Va (huckleberry)	75	22.1 (1.85)	3.8 (0.11)
Rusp (salmonberry)	75	22.9 (1.61)	3.8 (0.12)
Sa (willow)	50	39.4 (3.00)	4.5 (0.21)

^aTwenty shrubs measured at each site.

^bAfter Hormay (1943).

^cModified from Cole (1956).

relative use of shrubs between forest sites, but may have underestimated use in general, particularly in light of previous observations and exclosure studies that suggested heavier use (> 50%) of shrubs (Schwartz 1939, Schwartz and Mitchell 1945, Newman 1958, Jenkins 1981). In most cases, the degree of use that was indicated from the average form class (a measure of both current and past use) exceeded the average percent use (Table 10). Also, a random selection of 100 willow twigs that were tagged in winter 1981 indicated an average use of 65 percent. Use of shrubs was heavy, despite their low occurrence in winter diets, which suggested that those species were limited in availability.

The impact of herbivory on the shrub layer has been noted by numerous Park biologists (Schwartz 1939, Schwartz and Mitchell 1945, Newman 1958, Jenkins 1981). Browsing maintains an open understory in many habitat units, as exemplified (yet, sparsely quantified) by exclosures throughout the Park. For example, an exclosure was constructed in an alder stand with a grass understory in the Elwha Valley in the 1950s and was dominated by salmonberry (and still is) several years later (B. Moorhead, pers. comm.). During the caged-plot trial in the mature alder stand (discussed above), notably more seedlings and/or stolons of Rubus spp. were noted inside cages than outside. Additionally, several preferred shrubs only grow out of reach of cervids or in areas of restricted access: on root wads or atop snags, in steep ravines, or in areas of intense human activities, such as campgrounds. Those species include elderberry, Sambucus

racemosa L., currant, Ribes spp. L., thimbleberry, Rubus parviflorus Nutt., and Devil's club, Oplopanax horridum (Smith) Miq.

Trees

Red alder and western hemlock were very important dietary components in fall and winter, respectively (see Table 4). Unfortunately, specific data were not collected on available biomass of conifers and deciduous trees. Previous studies, however, allowed a reasonable assessment of available biomass relative to rankings of other forages.

As a class, trees dominated, and their contribution to overall biomass of the forest was significant. Sitka spruce and western hemlock were co-dominants (Franklin and Dyrness 1973) and contributed over 95 percent to the total foliar biomass of the overstory (McKee et al. 1980). About 10,000 Kg/ha of overstory foliage can be sustained (McKee et. al. 1980), yet the majority of it was unavailable to cervids. Other trees, such as bigleaf maple, western red cedar and Douglas-fir, were either very localized in their distribution (i.e., bigleaf maple was restricted to colluvial areas [Fonda 1974]), or widely scattered as single individuals. Vine maple was nearly ubiquitous (Fonda 1974, Smith and Henderson, in prep.).

Spruce and hemlock regenerated with success, but only on nurse logs (Franklin and Dyrness 1973, Franklin et al. 1980, McKee et al. 1980), whereas other species did not. Age structures of western redcedar and Douglas-fir comprised only old, somewhat decadent individuals; seedlings of either were observed rarely. Spruce and

hemlock seedlings were abundant on nurse logs (McKee et. al. 1980), and many were in reach of elk. Black cottonwood and bigleaf maple seedlings were observed regularly (the latter particularly in March-April as seedlings emerged), so reproduction occurred successfully. However, the only individuals of either species that were aged between about 3 years and full maturity were observed in areas completely protected from cervids. It was not possible to quantify effects of cervid herbivory beyond those generalities, but it was apparent that it played a decisive role in the distribution and in some cases, demography of certain plants in the Hoh Valley, as well as other westside drainages in the park (Schwartz 1939, Jenkins 1981).

The lowest branches of mature hemlock had a pronounced browse line at the uppermost reach of elk; they appeared to produce little current year's growth, or if they did, it was readily consumed. Therefore, those branches generally were not available to deer, except in cases where they could achieve access by walking on a downed log. That was observed in a few cases. Elk were not observed walking and foraging for any distance on downed logs, so some regeneration of hemlock was not available to them. Heavy use of hemlock seedlings was apparent in many areas; many probably were consumed entirely, leaving no evidence of use. That was not the case for spruce which received little use and displayed a more representative age structure than hemlock.

Vine maple also had a pronounced browse line and displayed only isolated regeneration. Most regrowth was in the form of copicing (Anderson 1969, Russel 1974), yet even that was limited. Vine maple production was most pronounced above the reach of elk. Growth

occurred on heavily hedged parts of a plant, but twig length was only about 25 mm and leaves were very small. Little vine maple was found in seasonal diets, which may have indicated limited availability and/or decreased palatability of regrowth. Spring estimates of vine maple in the diet were probably underestimated somewhat, because a spring correction factor was not available. Yet, the overall contribution was still judged to be low (see Table 4). K.J. Jenkins (pers. comm.) observed considerable use of vine maple leaves by elk in spring; that may have occurred after fecal samples were collected in late April-early May.

Autumn use of red alder was limited to abscission. Although some leaves persisted on the ground into winter, very little use was observed after about mid-December. Abscission is controlled by many factors, such as temperature, frost, rainfall, and age of the tree (Carns 1966) and may last for more than 2 months (Campbell and Franklin 1979). Biomass of abscissing alder leaves depends on stand age, but can be as high as 5,000+ Kg/ha (Zavitkovski and Stevens 1972). Luken (1979) reported that mature alder stands in the Hoh Valley produced about 2,500 Kg/ha of leaves. Alder leaves from mature trees were therefore an abundant, but transient, source of forage. Young alder were common along the river and were used by deer in summer, but not to a large extent by elk (see Table 4). Luken (1979) reported that young trees provided about 1,500 Kg/ha of leaves.

Douglas-fir, western redcedar, black cottonwood, and bigleaf maple were eagerly consumed by both cervids when they were available, but overall, they represented very ephemeral sources of food. Because

virtually all individuals of those species were old and had little or no biomass in reach of cervids due to growth form, foliage and twigs were available only when limbs and twigs broke off or when entire trees fell.

In December 1979, heavy rains (63.5 cm in 4 days) fell in the study area and many trees of several species fell as soil slid under shallow roots. At the peak of the storm, trees could be heard falling every several minutes. A wind storm produced the same effect in February 1979. Such storms increased the availability of those tree species; similar storms did not occur in winter 1981.

Boughs of those species frequently were browsed to a point of over 1.5 cm in diameter. In December 1980, a large Douglas-fir fell across the Hoh River and landed on a large gravel bar on the opposite side. Elk discovered it the day it fell and visited it frequently for a 2-week period, until all foliage was consumed. Conspicuous lichens, primarily Lobaria oregana (Tuck.) Müll. that are common on old-growth trees (Franklin et al. 1981) and are important to deer on Vancouver Island during periods of deep snow (Harestad et al. 1982), were not eaten. A special collection of fecal material of elk was collected near the tree. It contained 17.4 percent Douglas-fir, which was the only significant finding of that forage in either cervid's diet (see Table 4).

Summary

Overall, forages were most limited in winter, due to reduced biomass of herbaceous plants, abscission of shrubs and deciduous

trees, and cervid use with little or no regrowth. Table 11 summarizes biomass contributions of various forage bases at maximum production. Over 65 percent of the composite home range was late seral and climax conifer forests; therefore a significant part of the forage base was old-growth flora (swordfern, huckleberries, and mosses). Some data in Table 11 must be considered tentative since they are from other studies and/or localities, but they do allow a preliminary and relative assessment of forage availability.

An important feature of the overall forage base appeared to be winter litterfall from conifers and deciduous trees, and the variability of that process, as it depends on winter weather conditions, was not quantified in the present study. However, it was an important determinant of forage selection, based on cervid behavior in that season, and ultimately may influence the nutritional condition of cervids as well as the extent of competitive interactions.

Synthesis

Cervid Preferences

Relative preference is a measure of the degree of selectivity (or avoidance) between 2 or more items (Heady 1964) and can be difficult to quantify (Cock 1978, Emlen 1966, Johnson 1980, Lechowicz 1982). Forage preference depends on temporal forage availability (Krueger 1972, Nudds 1980) and animal choice. Yet, relative preference is a useful index for comparing populations of a species across its range and for comparing sympatric populations. In this study, cervid

Table 11. Summary of probable biomass contributions (kg/ha dry matter) of various forage bases in the Hoh Valley at maximum production. See text for discussion of the applicability of these estimates.

Forage Type	Maximum Biomass (kg/ha) in specific stands	Overall Biomass in Composite Home Range ^a	Source
Conifer			
Total Foliage	10,000 ^d	6730	McKee et al. (1980)
Seedlings (Cyg)	32.0	21.5	Rochelle (1980)
Tshe	31.9	21.4	" "
Litterfall ^b	8.4	5.7	" "
Tshe	4.0	2.7	" "
Psme	3.8	2.6	" "
Thpl	0.6	0.4	" "
Alder			
Mature stand	2,500		Luken (1979)
Young Stand	1,500	360	" "
Lichen-Litterfall ^b	37.2	25	Rochelle (1980)
Shrub			
Total	1,222.9		
Acci	880.0 ^d	-	Campbell & Franklin (1979)
Rusp	19.4	5.9	This study
Sa	47.0	8.2	" "
Va	26.7	18.0	" "
Pomu ^c	249.8	111.5	" "
Herbaceous			
Total	-	927	" "
Green	-	835	" "
Grass	-	279	" "
Forb	-	276	" "
Moss	-	280	" "

^aWeighted estimates in composite home range using spatial contribution of each habitat unit; see Table 9.

^bLitterfall strongly dependent on wind; Rochelle (1980) did not report any major storms during period of measurement.

^cDue to growth form, evaluated as a shrub.

^dIncludes all current production, much of which would be unavailable to cervids under normal conditions.

preferences were evaluated with 2 interdependent features of forage and habitat: 1) forage availability relative to diet selection and 2) the sere in which food was acquired.

Food Items

Data on production of the overall forage base were incomplete, but a reasonable ranking of important dietary items (> 5% of a given diet) was feasible, when information from the literature was incorporated. Generally, seasonal ranks (Table 12) followed maximum biomass availability at the end of the growing season (Table 11). It was assumed that the rank availability was the same for both cervids, as well as individuals in the 4 study blocks where fecal material was collected, and that it was the same in both years. Diets from the same season, but from different years, were pooled to maximize intraseasonal sample size. That approach greatly simplified the assessment of preference due to annual differences in herbaceous production and litterfall and probable differences in absolute availability of forages in the 4 blocks. Yet, ranks tended to minimize effects of relatively small quantitative changes and provided a simple index of preference, not a measure of selection or avoidance (Johnson 1980). The latter can be difficult to assess accurately due to great variability in diet and availability. Hobbs and Bowden (1982) demonstrated that confidence intervals around preference indices frequently included 1.0 (i.e., the point above or below which avoidance or selection is indicated). Therefore, conclusions

Table 12. Seasonal rank-order of availability of important dietary items (> 5% of cervid diets) in the Hoh Valley. Acronyms are identified in Table 1.

Rank	Spring	Summer	Fall	Winter
1	Pomu	Pomu	Tshe	Tshe
2	Va	Tshe	Alru	Pomu
3	Oxor	Alru	Oxor	Va
4	Rusp	Oxor	Aggi	Tome/Titr
5	Poa	Aggi	Tome/Titr	Thpl ^a
6	Cade	Ruur	Poa	
7		Ptaq	Sa	
8			Ruur	
9			Blsp	

^aAvailability dependent on wind-fall.

regarding selection or avoidance were erroneous. The rank-order, however, remained the same.

Vegetation sampling was conducted in different habitat-units within known home ranges of elk (Jenkins 1979). It was assumed that deer used the same areas and thus, had access to the same forages (at least the herb and shrub layer), which was supported with random observations. The following important similarities between cervids were noted: 1) both were resident and confined most activity to the valley bottom (only 1 sighting and no sign of deer were noted on side slopes in the lower Hoh Valley; elk used the side slopes infrequently [Jenkins 1979]), 2) both foraged extensively in all habitat units at all times of the year, 3) general habitat preferences appeared very similar, although temporal differences probably occurred, and 4) total sympatry was indicated by their distributions in the study area. Although deer probably occupied smaller home ranges (Hanley 1980, Harestad 1979) than elk (Jenkins 1979, Hanley 1980, Witmer 1981) and thus, encountered less absolute forage, relative availabilities of herbs and shrubs to cervid populations was judged to be quite similar.

Hemlock, swordfern, and oxalis were among the most abundant species in the study area, and they tended to make up a substantial part of the diets of both cervids (see Table 4). However, they were not the most preferred species (Table 13). Elk preferred grasses and sedges in spring and summer, whereas deer tended to prefer browse throughout the year (Table 13). In spring and summer, species that were most preferred by deer and also most heavily consumed

Table 13. Seasonal rank-order of important dietary items from most preferred to least preferred relative to mean crude protein and dry matter digestibility.

Season Rank	ELK				DEER			
	Forage Species ^a	Forage Class ^b	\bar{x} CP	\bar{x} DMD	Forage Species ^a	Forage Class ^b	\bar{x} CP	\bar{x} DMD
Spring								
1	Cade	G	17.9	65.9	Rusp	S	24.3	34.4
2	Poa	G	26.0	76.8	Oxor	F	24.1	57.5
3	Oxor	F	24.1	57.5	Pomu	FN-B	18.0	18.1
4	Pomu	FN-B	18.0	18.1	Va	S	27.3	48.7
5	Va	S	27.3	48.7	-	-	-	-
Summer								
1	Aggi	G	15.0	57.7	Ruur	F ^c	21.0	24.7
2	Oxor	F	20.5	58.9	Alru	T	15.0	36.8
3	Ptaq	FN	-	-	Oxor	F	20.5	58.9
4	Pomu	FN-B	11.3	-	Tome/Titr	F	13.7	35.7
5	Tshe	T	7.4	26.8	-	-	-	-
Fall								
1	Blsp	FN	9.7	30.2	Ruur	F ^c	15.3	32.2
2	Alru	T	13.8	33.2	Alru	T	13.8	33.2
3	Sa	S	6.3	21.6	Oxor	F	14.8	48.6
4	Poa	G	22.0	69.9	Tome/Titr	F	14.9	26.8
5	Aggi	G	-	-	-	-	-	-
6	Oxor	F	14.8	48.6	-	-	-	-
7	Tshe	T	6.2	21.2	-	-	-	-
Winter								
1	Thpl	T	6.2	31.9	Thpl	T	6.2	31.9
2	Pomu	FN-B	9.9	20.4	Tome/Titr	F	13.4	34.9
3	Va	S	5.8	28.8	Tshe	T	7.3	23.9
4	Tshe	T	7.3	23.9	Va	S	5.8	28.8
5	-	-	-	-	Pomu	FN-B	9.9	20.4

^a Acronyms identified in Table 1.

^b T = tree, S = shrub, F = forb, FN = fern, G = graminoid, B = considered browse.

^c Taxonomically a shrub; growth form relative to cervid use resembled a forb.

(salmonberry in spring and trailing blackberry in summer) did not contribute more than 5 percent to elk diets.

Redcedar was preferred by both cervids in winter (Table 13), as reflected by heavy use in 1980 (see Table 4). Both species readily used redcedar, Douglas-fir, black cottonwood, and bigleaf maple when available from winter wind-throw, but otherwise those trees afforded little available biomass due to demography of their respective populations. Deer have been observed to prefer Douglas-fir and redcedar over other conifers (Cowan 1945, Hines 1973), and elk have been observed to prefer deciduous trees, such as black cottonwood (Janz 1980). The response of cervids to the transient availability of those browse species indicated that they were preferred over regular winter staples of hemlock and swordfern. Those latter species comprised 70.3 and 69.4 percent of elk and deer diets, respectively, in Winter 1981, in contrast to 41.8 and 64.0 percent in Winter 1980 when availability of redcedar appeared to be high.

Recently, Hanley (1980, 1982) synthesized existing information on ungulate foraging strategies into a word model that explained overt diet selection of forage classes relative to morphological and anatomical constraints. The model considered 1) mouth size, 2) rumino-reticular volume, 3) body size, and 4) type of digestive system and basically was an extension of the Jarman-Bell principle (Geist 1974). It predicted that large ungulates should be less selective and acquire a high cellulose diet (i.e., high in graminooids); small ungulates should be more selective and acquire a diet high in cell solubles and/or lignin (i.e., high in browse).

Local availabilities of forages obviously will influence the degree to which those proclivities manifest themselves. In the Hoh Valley, preferences for forages were consistent with those generalizations and with Hanley's model. Yet, low availability of graminoid-forb forages minimized the degree to which elk could rely on those resources and maintain adequate intake. Similarly, heavy past use of shrubs restricted availability and minimized the degree to which deer could rely on those resources. Therefore, coniferous browse was a very important part of both cervid diets.

Bryant and Kuropat (1980) concluded that food selection by subarctic herbivores was determined by levels of secondary compounds rather than proximal nutrient content. Others have noted that general trends in preference are positively correlated with levels of protein and soluble carbohydrates, but negatively with fiber (Bland and Dent 1964, Hines 1973) and volatile oil content (Schwartz et al. 1980b). In this study, there were no significant relationships between preference and protein or digestibility. The role that secondary compounds played could not be addressed. Arnold and Hill (1972) argued that preference is a multidimensional process, and correlation (or lack of it) with any single nutrient does not prove that it determines preference. Aside from nutrient content, a wide range of factors affect palatability and preference (Arnold 1966a, 1966b; Crawford and Church 1971, Longhurst et al. 1968, McNamara 1979, Silen and Dimock 1978).

The Sere

Classically, elk and deer are considered successional species (Leopold 1966); both do well in early seral stages that generally provide abundant and nutritious forage (Bunnell and Eastman 1976, Wallmo and Schoen 1979), given that other requirements for their well-being are satisfied. Physiological constraints related to size and relative metabolic requirements suggest that a small ruminant will seek a diet higher in nutritional value than will a large ruminant (Bell 1970, 1971; Geist 1974, Schwartz and Nagy 1976, Schwartz et al. 1977). Some evidence suggests that early seral communities provide more palatable forage (Cates and Orians 1975) and abundant macronutrients (Turner et al. 1978) to generalized herbivores than climax communities. Therefore, it could be hypothesized that deer, to maximize nutrient intake, select a diet that contains young seral forages to a greater extent than elk. However, Hanley (1980) proposed that deer favor older stages of a sere, whereas elk prefer younger stages. Hanley (1980) reasoned that deer were better equipped to exploit the typical shrubby understory (i.e., high cell solubles/lignin) of late successional communities, by virtue of their selective feeding abilities (i.e., small mouth size) and short turnover time in the rumen (i.e., small rumino-reticular to body weight ratio). Inversely, elk are better equipped to exploit the typical herbaceous understory (i.e., high cellulose) of some early successional communities. Therefore, an alternate hypothesis could be that elk select a diet that reflects younger seral forages to a greater extent

than deer. Such relationships would depend on the physiognomy of a given sere (i.e., plant composition and availability).

The first axis of the ordination of forage species provided an "idealized sere" that was very similar to Fonda's (1974) interpretation of forest development in the Hoh Valley (Smith and Henderson, in prep.) It reduced the complexity and variability of the forage base and allowed delineation of 3 major forest-types in which cervids acquired forage: 1) early seral forests (i.e., pioneer alder-willow, willow clearings, and alder flats), 2) mixed forests (i.e., spruce-cottonwood terrace, bigleaf maple, and vine maple), and 3) climax forests (i.e., spruce-hemlock). This "idealized sere" represented distributional affinities of each forage, relative to each other, but it had no relationship in itself to relative availabilities or geographic localities of those 3 forest-types. It merely mimicked relative distributions of forage species as they occurred when measured (i.e., it is time-specific), but did not have to invoke a rigid ecological explanation of succession in the Hoh Valley.

Forages in young seral communities may be more nutritious than those in older stands. Mean levels of crude protein of forages that occurred in the 3 forest-types and were consumed by cervids supported that hypothesis (Fig. 19), but a significant difference between forest types could not be demonstrated. However, those results were consistent with Turner et al. (1978) who suggested that macronutrients were more abundant in young stands than micronutrients. Data in Fig. 19 were not weighted by availability or proportion of occurrence in a

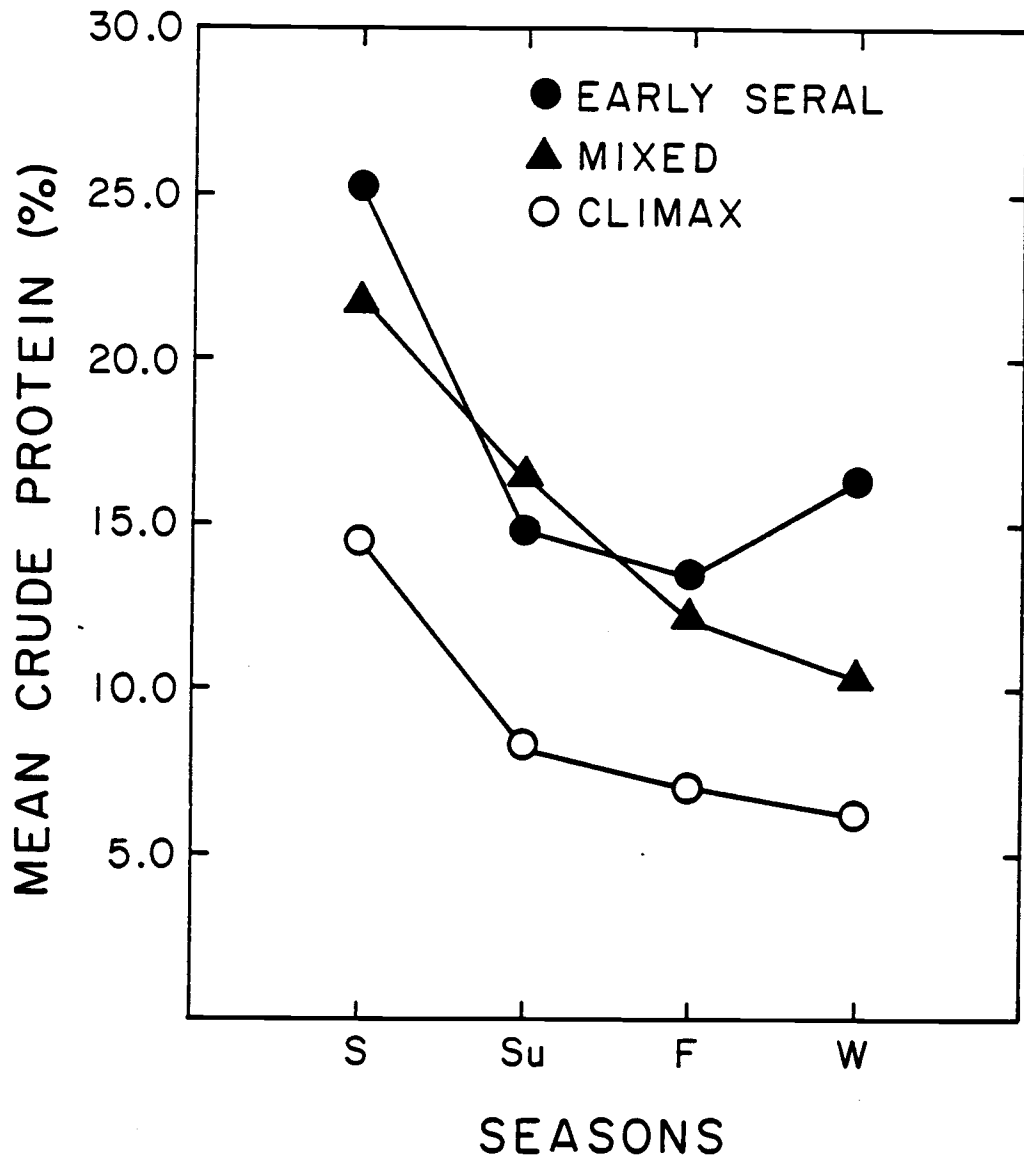


Figure 19. Mean protein levels of forages used by cervids from 3 predominant forest-types. See text for discussion.

cervid diet and therefore, only demonstrated that the "average forage item" in a given forest-type contained a given amount of protein. Yet, if forages were weighted either way, the value of the climax forest-type would have been depressed even further because abundant species (e.g., hemlock and table moss) were low in CP (see Fig. 5), as well as DMD (see Fig. 6) and P. The same generalization was not the case for abundant species in the other 2 forest-types.

Weighted dietary scores for both cervids indicated a similar seasonal trend of forage acquisition along the sere (Fig. 20). Dietary affinities for seral stands were greatest in fall and lowest in winter. That corresponded to heavy use of alder in fall and hemlock in winter (see Table 4) and general availability of dietary components in the 3 forest-types. Consistent with 1 hypothesis, deer tended to acquire a diet of stronger affinity to young seral forest-types in spring, summer, and fall than elk (Fig. 20); the corollary of those seasonal diets being more nutritious was only weakly supported above (see Fig. 12). Nevertheless, the greatest dissimilarity among cervid diets occurred in summer (Fig. 20), which was the period of greatest forage availability.

Differences in dietary affinities were not great; both cervids acquired diets of very similar proportions from the 3 forest-types (Fig. 21). A seasonal sequence of use of the 3 forest-types tended to follow availability between types. Forages from mixed stands were used most heavily in spring, followed by a decreasing trend through winter (Fig. 21). Concomitantly, use of forages from early seral stands increased after spring and peaked in fall; use of forages from

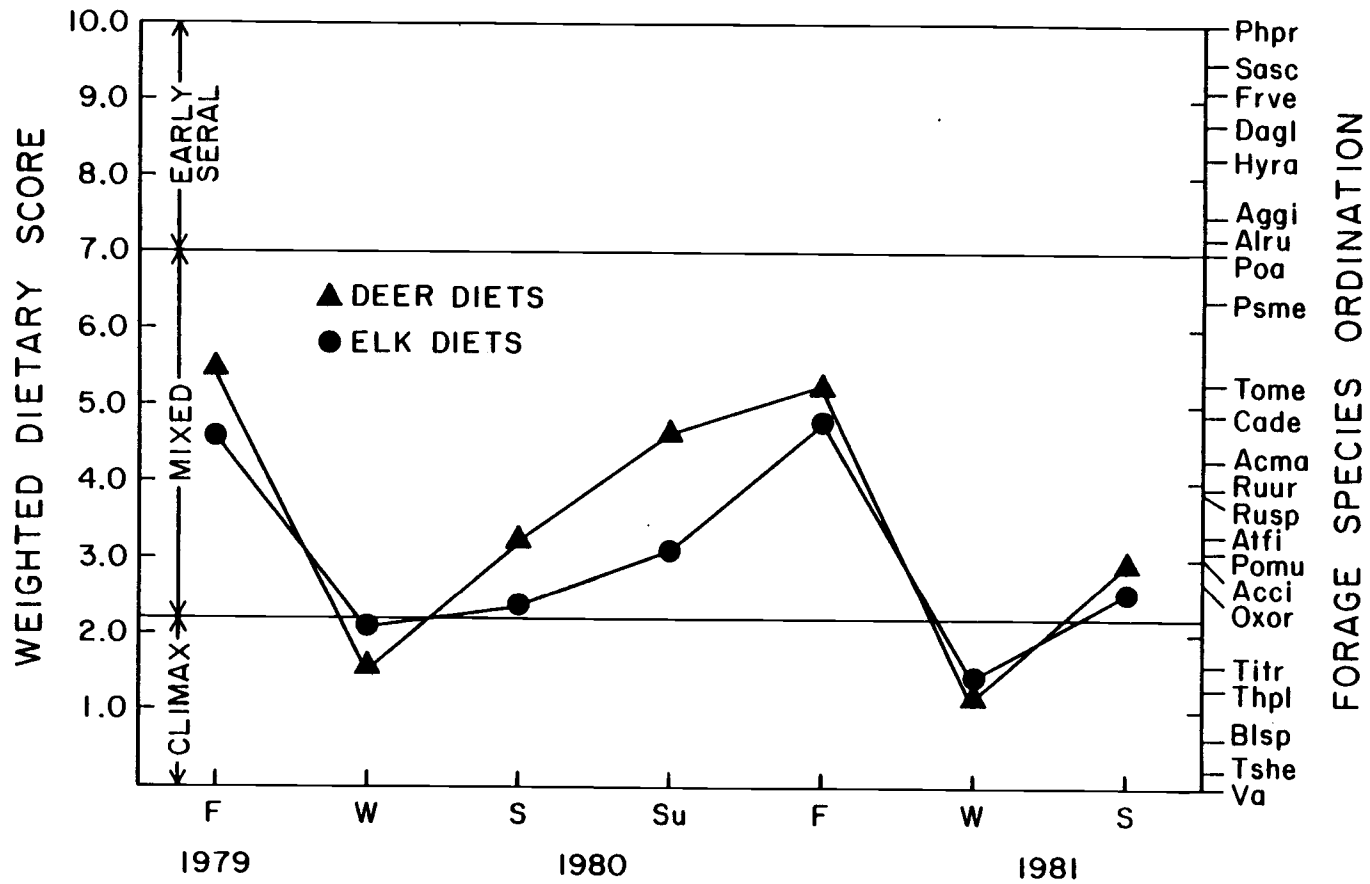


Figure 20. An ordination of seasonal diets of cervids relative to an "idealized sere" in the Hoh Valley. Three forest-types were subjectively delineated based on knowledge of physical appearance of plant communities in the study area and the ordination of species distributions on the right side of the figure. See text for discussion.

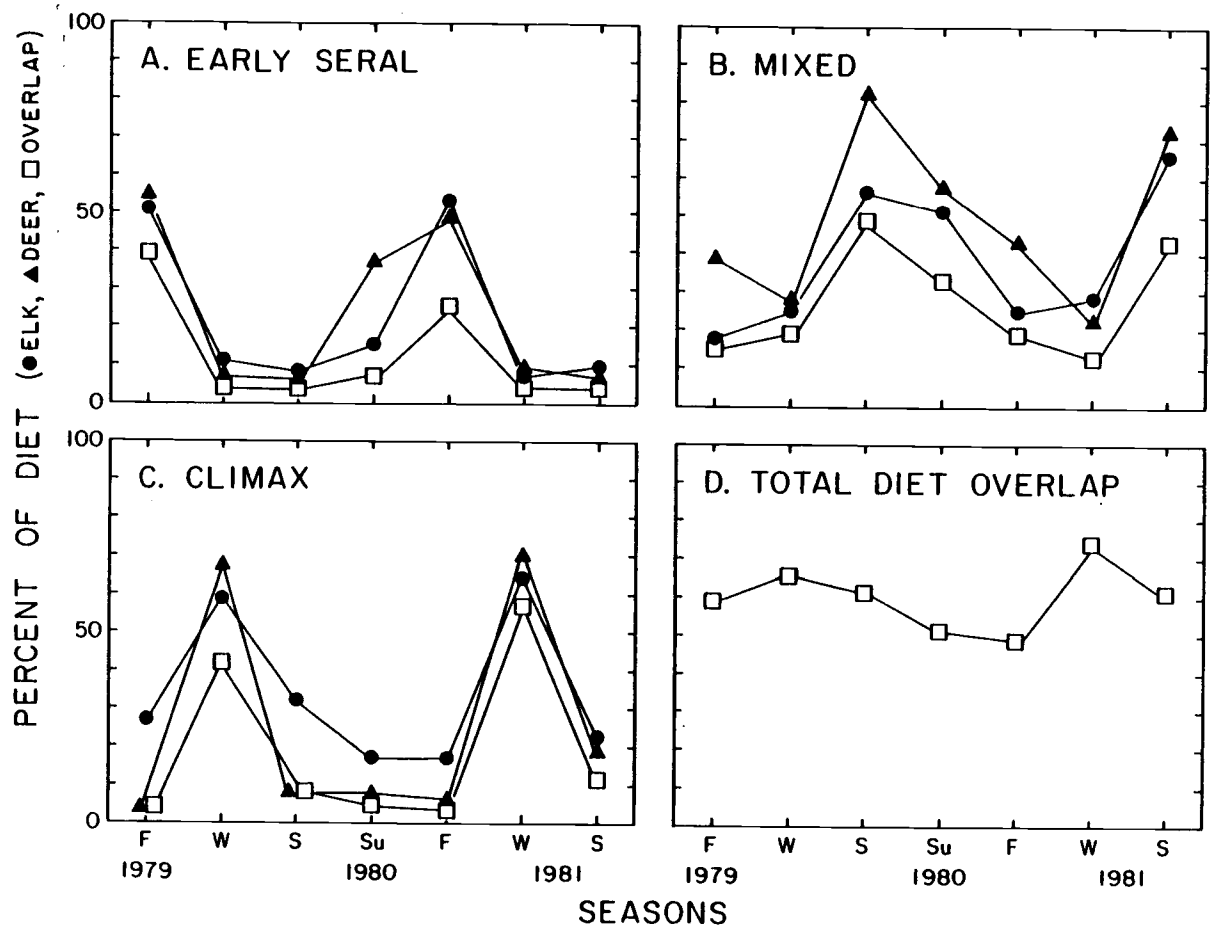


Figure 21. Percent of seasonal diets acquired by elk and deer in 3 predominant forest-types and dietary overlap of forage species in those areas.

climax stands increased after fall and was highest in winter (Fig. 21). Deer tended to use climax species less in spring, summer and fall than elk (Fig. 21). Overall, acquisition of a diet by both cervids in the various forest-types was judged to be very similar, and did not strongly support either hypothesis.

Sympatry

By historical accounts, elk and deer have coexisted in the Hoh Valley for over 100 years, although elk have been noted to be most abundant. In the present study, sympatry was typified by 1) a high degree of dietary overlap (see Fig. 4) that peaked in winter when food resources were least available, 2) diets that seemed to afford little opportunity for partitioning plant parts, particularly in fall and winter (see Table 4), 3) a similar pattern of seasonal food acquisition in 3 predominant forest-types (see Fig. 21), and 4) heavy use of the forage base to the point of restricting distributions of preferred forages and influencing general physiognomy of the shrub layer in some forest communities. Those observations suggest that Roosevelt elk and black-tailed deer either have evolved very similar dietary niches or have little opportunity for dietary divergence in the Hoh Valley, perhaps due to limited availability and diversity of forage. The latter postulate is favored, yet both imply significant competitive interactions between cervids.

Wilson (1975:581) defined competition as "the active demand by 2 or more organisms (or 2 or more species) for a common resource"; the degree or intensity of competition will depend on the abundance of the

common resource. Competition can take 2 forms: interference or exploitation (Miller 1967). The former involves behavioral interactions that directly or indirectly exclude a species from using a resource. No direct behavioral interactions between elk and deer were observed during this study, so that form of competition could not be addressed. It may have less importance among ungulates (Anthony and Smith 1977, Krämer 1973) than exploitative competition, which involves the joint use of a common resource.

Resources frequently are partitioned among coexisting species (e.g., Schoener 1974). Each species is typified by unique modes of behavior, function, and form (e.g., Pianka 1976) that are presumed to be evolutionary consequences of interspecific constraints. Large herbivores usually are generalists, and many species display plasticity in their choice of food and space. However, various modes of ecological separation have been observed among ungulate assemblages in Africa (Bell 1970, 1971; Crawford et al. 1968, Field 1968, Gwynne and Bell 1968, Hofman 1968, Jarman and Sinclair 1979, Lamprey 1963) and in North America (Anthony and Smith 1977, Hanley and Hanley 1982, Hansen and Clark 1977, Hudson 1976, Hudson et al. 1976, Mackie 1970, Nelson 1982, Peden et al. 1974, Schwartz and Nagy 1976, Stevens 1974). Habitat and/or food frequently are partitioned among species, but given sympatry, characteristics of the food supply generally are considered to be the most important determinants of competitive interactions among ungulates (Nelson 1982:417).

The theory of competitive exclusion (Cole 1960, Hardin 1960), predicts that 2 or more species cannot occupy the same niche, or if

they do, one will eventually exclude the others. Zaret and Rand (1971:341) observed that diets of tropical fishes diverged most when food was least abundant and concluded that "those consequences were predicted by the principle of competitive exclusion." Conflicting observations have been documented for ungulates. Hansen and Clark (1977) and Hansen and Reid (1974) found that diets of 5 ungulates (including 2 domestics) were least similar in winter, which supported Zaret and Rand (1971). Similarly, Mackie (1970) found that elk and mule deer diets were least similar in winter. On the other hand, some evidence suggest that periods of highest dietary similarity among North American ungulates occurs during periods of lowest forage abundance (Anthony and Smith 1977, Schwartz and Ellis 1981, Singer 1977). In the present study, the latter trend was very apparent and therefore, did not support the principle of competitive exclusion, as interpreted by Zaret and Rand (1971).

Anthony and Smith (1977:275) noted that the theory of competitive exclusion failed to consider interspecific competition "as a temporary or transient phenomenon in response to changing environment or catastrophic disturbance" (e.g., fire or fire suppression, livestock grazing or successional changes) which decrease the abundance of the food supply. However, habitat stability in the Hoh Valley is high relative to such changes; it is unlikely that forest composition will be altered quickly enough for dietary similarity to be considered "transient."

Competing species can coexist if population densities are depressed and resources are not in short supply (Pianka 1978). Krämer

(1973) suggested that minimal competition for food among white-tailed deer and mule deer in southern Alberta may have been an artifact of low population densities that increased the relative amount of forage available to both species. In the Hoh Valley, the density of ungulates was high, and the forage base was used heavily. Therefore, coexistence was not likely a result of abundant food resources due to low population levels. Competing species also can coexist if enough variation occurs in the resource base to allow specialization by 1 species (MacArthur and Connell 1966). In the Hoh Valley, dietary complexity and similarity implied that neither species specialized on any particular resource. Rather, both depended on a limited number of forage items that were largely similar (i.e., oxalis, hemlock, swordfern and alder), particularly during seasons of limited forage availability.

Competition is related inversely to forage availability, and if resource availability is reduced by common utilization, the level of competition increases (Nelson 1982:417). Clearly, intensive use of forage resources in the Hoh Valley (Schwartz 1939, Newman 1958, Jenkins 1981) and high dietary overlap, particularly in critical seasons, suggested that competition could occur between elk and deer. Elk are generally considered to be better competitors than deer under conditions of sympatry and similar forage availabilities, due to their larger size and greater reach, group size and mobility (Cliff 1939, Cowan 1947, Mackie 1970, 1976; Nelson 1982). If this is the case, elk should competitively exclude deer from the Hoh Valley.

General observations suggested that elk were ecologically dominant over deer. K.J. Jenkins (pers. comm.) estimated that a minimum of 100 elk inhabited 2 home range areas that extended from about 2 km east of the Hoh Ranger Station down river about 5 km. That estimate was based on repeated total herd counts in 1979-80. Observations of deer between September 1980 and June 1981 indicated that groups were stable associations of mother and offspring; group size averaged 2.3 deer (Fig. 22). Males were observed primarily during breeding in late fall. Repeated observations of the same numerical groupings in the same general areas suggested that a minimum of 18 deer inhabited the north half of the 2 elk home ranges (i.e., the north side of the Hoh River). Assuming an equal number of deer on the south side of the river, 36 deer to 100 elk (0.36/1) was indicated. Given that elk are approximately 5 times as large as deer, the secondary biomass ratio was 0.07/1. Those observations reinforced the idea that elk were capable of excluding deer in old-growth forests in the Hoh Valley.

General feeding observations and foraging behavior suggested that 2 factors enhanced sympatry and minimized interspecific competition between cervids. Spatial heterogeneity has been positively correlated with species richness, particularly for avian species (MacArthur and MacArthur 1961, Recher 1969). Habitats that are structurally diverse afford a greater variety of microhabitats than simple habitats (Pianka 1978). Dead and down logs are dominant features of old-growth forests (Franklin et al. 1981), and in the Hoh Valley, their pattern of occurrence appeared to be a significant determinant of cervid mobility, forage availability, and forage use.

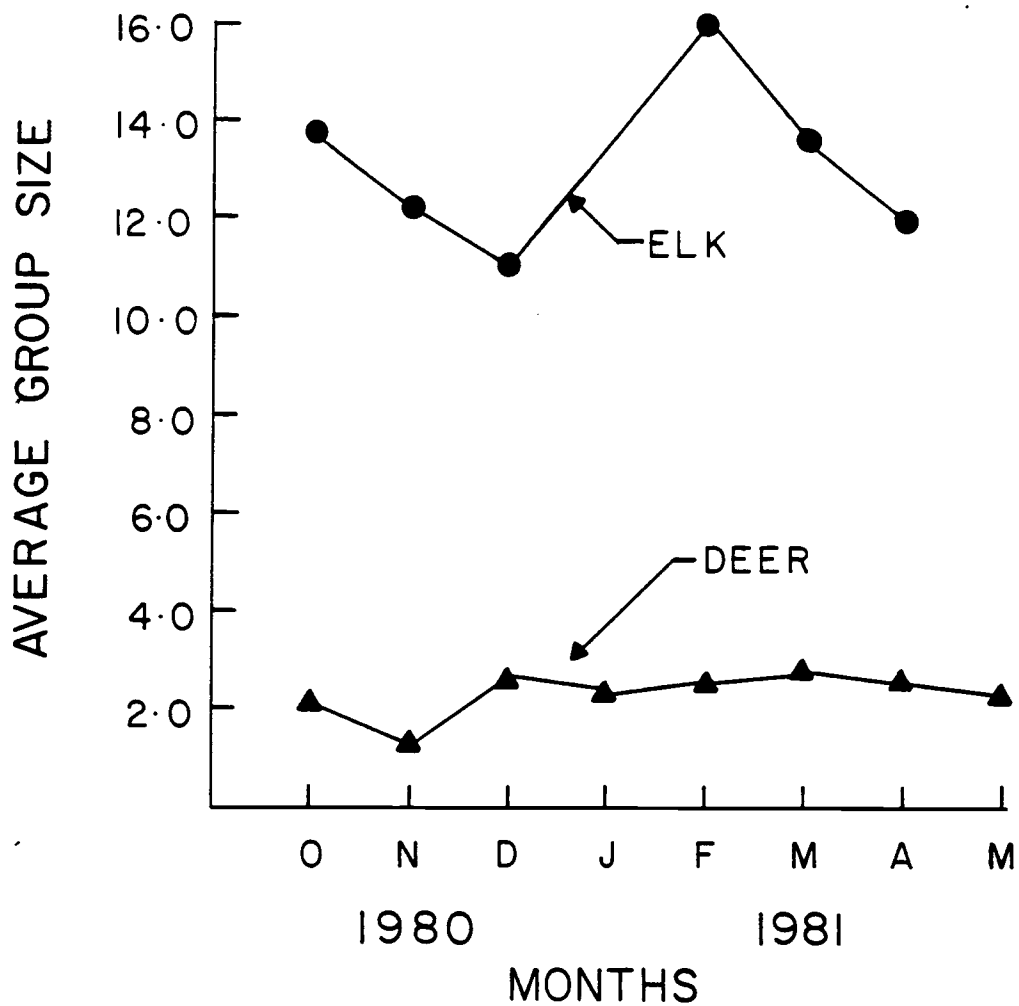


Figure 22. Average monthly group size of elk and deer from October 1980 to May 1981 from 650 random observations of elk and from 553 random observations of deer.

Forage that grew in a maze of wind-thrown trees, even though access seemed possible, invariably was used less than forage in completely accessible areas. Forage use appeared to follow a continuum from light to heavy that was inversely related to the degree of protection that was afforded by downed logs. Elk trails frequently by-passed such areas, and elk themselves rarely were observed in them. Strategies of predator avoidance may inhibit elk from entering areas of restricted mobility. Vertical characteristics and size of logs influenced accessibility to elk. Deer, on the other hand, were observed more frequently in such areas. They achieved greater access and mobility because of their small size (i.e., greater freedom to go under logs) and ability to jump. Cover requirements, both security and thermal, may be higher for deer than elk (Thomas et al. 1979), and therefore, such areas may be preferred by deer. Nevertheless, some areas of downed trees created habitat that was only accessible to and used by deer. Without those enclaves, it is speculated that elk would competitively exclude deer from the Hoh Valley.

The other factor that may minimize the competitive advantage of elk in winter, and thus allow sympatry, is the transient occurrence of windthrown boughs of conifers. The availability and quantity of such forage depends on weather-related factors, and the use of that forage depends on cervid preference, which in turn may influence the degree of dietary overlap and thus potential competition in a given winter (see Fig. 4).

Elk appear to significantly outnumber deer in the Hoh Valley and also to reduce the biomass of important browse species that is

available to deer by their greater reach. Both characteristics suggest that elk have a competitive advantage over deer in old-growth forests of the Hoh Valley. The effects of that competitive advantage are accentuated at maximum density of the collective cervid population, which is unmanaged and theoretically at ecological carrying capacity. The principle of competitive exclusion would be verified if deer have to select microhabitats that are inaccessible to elk (i.e., areas of downed trees) in order to exist in the Hoh Valley, or if deer would otherwise be excluded by elk without those enclaves. That relationship and the transient availability of some forages with differential preference in winter are no doubt complex and variable, and at present, they can be viewed only as hypotheses for future investigations.

CONCLUSION

Herbivores usually do not eat all vegetation that is available to them (Slobodkin et al. 1967); even at ecological carrying capacity, large herbivores do not completely consume all available biomass (Caughley 1976). Empirical observations strongly suggest that the quantity of usable forage is determined by some characteristic(s) or quality that decreases palatability and thus herbivore use.

It may be more useful to think of the "capacity" (Warren et al. 1979:301) of the forage base to sustain herbivores relative to population density. At ecological carrying capacity, herbivores are assumed to be limited by food and therefore, the greatest "capacity" of the forage base to sustain herbivores is realized. In other words, the quantity of forage (i.e., intake) is limited only at that density. Likewise, forage quality is likely to reach its lowest point at that density (Klein 1965, 1981). Thus, the limitation at ecological carrying capacity is actually the quantity of quality forage - forage capable of sustaining life of a given herbivore at maximum population density.

Ecological carrying capacity can be set by a wide range of factors that act singularly or synergistically. Some evidence suggests that single elements limit large herbivores in some areas (Cu, Flynn et al. 1977; Na, Belovsky 1981, Belovsky and Jordan 1981). More frequently, nutritional limitations are believed to be general; energy and protein are often discussed (Hobbs et al. 1982).

Forage capacity can be assessed by empirical observations that address the following questions: 1) is it possible for an individual to meet its nutritional requirements for maintenance and production (Crampton and Harris 1969, Moen 1973), given a certain density of herbivores but assuming adequate intake, and 2) is it possible for the population to satisfy the sum of the individual nutritional requirements at an observed density.

In the Hoh Valley, the protein requirement of an individual appeared to be satisfied assuming a minimum maintenance requirement of 7 percent CP and assuming little effect of phenolics on overall protein availabilities. Dietary phosphorus also was adequate during all seasons. On the other hand, levels of dietary DMD suggested that digestible energy (DE) was low, which may significantly influence the nutritional condition of an individual. Hobbs et al. (1981) felt that dietary DMD of about 35 percent was submaintenance for Rocky Mountain elk. In this study, the maximum level for both cervids was about 35-40 percent. However, the complicated role that phenolics play in vitro and in vivo for wild species needs further research. At present, it is not possible to make definitive conclusions.

Most other elements occurred in sufficient amounts in forages to satisfy requirements of similarly-sized domestic species with the exception of selenium and sodium. However, it is not believed that either of those elements singularly limit cervids in the Hoh Valley, but probably contribute to general undernutrition when forage is least available.

Ecological carrying capacity in the Hoh Valley is likely set by the quantity of quality forage that is available, rather than by a deficiency of a single nutrient. An individual may be able to obtain adequate intake but in winter when forage is least available, the impasse between intake of maintenance and submaintenance diets is likely to be reached by some individuals. The welfare of an individual at this point probably depends on its physical condition upon entering the winter period (Mautz 1978), as well as its age and sex.

Sinclair (1977:267) proposed a "nutrition hypothesis" as a limiting mechanism for African buffalo, Syncerus caffer. Two factors must act in sequence. First, individuals experience a primary lack of food (quality or quantity) that leads to undernutrition and impaired immunity to disease. Second, disease becomes pathogenic resulting in death. Cervids in the Hoh Valley probably are limited in a similar manner; survival of offspring may be lower at maximum population density, as noted for red deer, C. e. elaphus (Guinness et al. 1978). However, on the average, the percentage of the population that succumbs to the consequences of undernutrition probably is replaced by annual recruitment. Low reproductive rates are expected at maximum population density (Fowler 1981), but undernutrition at any density also may influence fecundity of individual females in a significant manner (Thorne et al. 1976, Trainer 1971).

Elk and deer populations in lowland valleys of Olympic National Park appear stable (i.e., no pronounced changes in numbers over the past 50 years from general observations and consistent calf/cow ratios

of about 20-30/100) and healthy (i.e., no indication of chronic disease and good physical appearance). These characteristics probably will be perpetuated indefinitely if the National Park Service policy remains unchanged (Cole 1971, Leopold et al. 1963, Houston 1971). The essential factors are an unaltered habitat and no manipulation of animal numbers. Also, non-migratory populations of elk and deer in lowland forests are not influenced to a significant degree by activities outside the park, due to their sedentary habits (Jenkins 1979).

Elk and deer should be able to coexist indefinitely if old-growth trees remain a dominant feature of the forests. However, subtle changes to the habitat from increases or decreases of wind-thrown trees will alter the size of the area that is exclusively available to deer and may in turn alter the relative proportions of deer and elk.

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APPENDICES

Appendix 1. Specific values ($\bar{x} \pm S.E.$; $n = 4$) for crude protein (CP), phosphorus (P), in vitro dry matter digestibility (DMD), and moisture (1-moisture = dry matter) illustrated in Figs. 5, 6, and 7 and used for determining dietary levels.

A. Fall 1979

Species		Percent (dry matter basis)			
		CP	P	DMD	Moisture
Shrub:	Rusp	8.56 (0.125)	0.17 (0.017)	24.7 (0.49)	77.1 (1.71)
	Sa	6.28 (0.093)	0.10 (0.011)	21.6 (0.60)	62.9 (2.34)
	Va	7.11 (0.364)	0.12 (0.008)	26.3 (1.07)	68.4 (1.86)
	Acci	6.00 (0.153)	0.19 (0.008)	32.5 (0.60)	63.0 (2.89)
Tree:	Psme	7.28 (0.226)	0.18 (0.013)	27.0 (0.41)	60.9 (1.21)
	Alru	14.17 (0.637)	0.13 (0.003)	31.7 (0.28)	67.2 (1.53)
Forb:	Ruur ^b	16.67 (0.652)	0.21 (0.009)	30.5 (1.43)	74.7 (0.91)
	Titr	11.39 (0.250)	0.36 (0.016)	22.1 (0.24)	83.2 (0.43)
	Tome	19.74 (0.635)	0.25 (0.009)	31.3 (0.46)	86.6 (0.26)
Fern:	Blsp	9.97 (0.140)	0.29 (0.013)	30.7 (0.54)	80.0 (0.65)

B. Winter 1980

Shrub:	Rusp	6.57 (0.243)	0.14 (0.005)	20.1 (0.68)	56.1 (4.77)
	Sa	5.49 (0.230)	0.12 (0.006)	25.3 (0.75)	57.1 (1.64)
	Va	5.84 (0.344)	0.14 (0.003)	28.8 (0.60)	56.5 (1.31)
	Acci	7.30 (0.453)	0.19 (0.011)	34.4 (0.39)	52.1 (0.68)
Tree:	Psme	7.06 (0.000)	0.18 (0.005)	31.4 (0.67)	55.7 (1.13)
	Tshe	6.41 (0.180)	0.16 (0.011)	26.0 (0.08)	60.9 (2.72)
	Thpl	6.50 (0.242)	0.15 (0.008)	32.5 (0.40)	57.3 (1.80)
Fern:	Blsp	8.49 (0.516)	0.21 (0.018)	36.2 (0.38)	73.9 (2.51)
	Pomu	10.27 (0.524)	0.19 (0.005)	22.6 (0.39)	61.3 (2.88)

^aSpecies scientific names given in Table 1.

^bDue to growth form, here considered a forb; taxonomically a shrub.

Appendix 1. Continued.

C. Spring 1980^c

Species		Percent (dry matter basis)			
		CP	P	DMD	Moisture
Acronyms ^a					
Shrub:	Rusp	26.10	0.53	33.6	80.7
	Sa	23.94	0.65	29.0	77.8
	Va	29.94	0.61	49.0	83.1
	Acci	26.63	0.73	56.3	78.9
Grass:	Aggi	28.06	0.44	77.8	82.8

D. Summer 1980

Shrub:	Rusp	15.03 (0.905)	0.21 (0.030)	25.4 (2.20)	76.9 (0.92)
	Sa	13.66 (0.494)	0.26 (0.015)	20.4 (1.00)	70.7 (0.55)
	Va	11.27 (0.570)	0.15 (0.003)	33.3 (0.79)	70.6 (0.60)
	Acci	13.57 (0.325)	0.25 (0.026)	44.7 (1.61)	65.1 (0.86)
Tree:	Tshe	7.44 (0.440)	0.20 (0.008)	26.8 (0.87)	65.1 (1.15)
	Alru	15.00 (0.781)	-	36.8 (0.81)	67.9 (2.26)
Forb:	Ruur ^b	20.98 (0.865)	0.29 (0.003)	24.7 (0.38)	77.2 (0.54)
	Oxor	20.47 (0.109)	-	58.9 ^c	91.5 ^c
	Titr	10.83 (0.549)	-	43.3 (2.41)	80.9 (0.22)
	Tome	16.59 (0.235)	-	28.2 (1.18)	82.4 (0.80)
Fern:	Blsp	10.07 (0.132)	0.28 (0.022)	27.5 (0.76)	82.3 (0.49)
	Ponu	11.31 ^{2c}	-	-	68.1 ^c
	Arfi	18.09 (1.621)	0.46 (0.031)	31.9 (3.42)	86.0 (0.92)
Grass:	Poa	15.49 (0.955)	0.22 (0.009)	55.9 (0.67)	73.7 (1.02)
	Aggi	15.00 (0.460)	-	57.7 (1.59)	77.1 (1.05)
Moss:	Hysp	4.58 (0.208)	0.14 (0.003)	12.3 (0.34)	25.6 (2.39)

^aSpecies scientific names given in Table 1.

^bDue to growth form, here considered a forb; taxonomically a shrub.

^c_n = 2 for all samples.

Appendix 1. Continued

E. Fall 1980

Species		Percent (dry matter basis)			
		CP	P	DMD	Moisture
Tree:	Psme ^a	7.83 (0.631)	0.20 (0.010)	28.0 (0.28)	62.9 (1.91)
	Tshe	6.17 (0.258)	0.22 (0.031)	21.2 (1.00)	74.3 (2.66)
	Alru	13.49 (0.456)	0.13 (0.011)	34.7 (0.47)	65.0 (4.16)
Forb:	Ruur ^b	15.33 (0.723)	0.22 (0.009)	32.2 (1.57)	72.2 (2.54)
	Titr	11.69 (0.600)	0.40 (0.026)	22.7 (0.29)	83.6 (0.58)
	Tome	16.61 (0.334)	0.23 (0.010)	31.0 (0.19)	84.4 (0.65)
	Oxor	14.77 (0.516)	0.48 (0.035)	48.6 (0.73)	91.2 (0.36)
Fern:	Blsp	9.50 (0.312)	0.27 (0.024)	29.7 (0.59)	81.0 (1.03)
Grass:	Poa	22.09 (0.958)	0.38 (0.022)	69.9 (0.71)	80.2 (1.92)
	Cade	14.56 (0.750)	0.22 (0.028)	36.4 (0.60)	75.5 (2.46)
Moss:	Hysp	4.64 (0.160)	0.14 (0.003)	8.6 (0.64)	83.7 (2.99)

F. Winter 1980

Shrub:	Sa	5.00 (0.254)	0.12 (0.007)	22.7 (0.43)	58.9 (0.79)
Tree:	Psme	7.50 (0.133)	0.20 (0.007)	29.0 (0.78)	60.7 (0.75)
	Tshe	5.30 (0.223)	0.18 (0.015)	21.8 (0.45)	66.6 (1.45)
	Thpl	5.83 (0.970)	0.13 (0.025)	31.3 (0.16)	62.5 (1.61)
Forb:	Titr	11.14 (0.124)	0.41 (0.007)	38.0 (0.69)	83.5 (0.15)
	Tome	15.61 (0.418)	0.25 (0.007)	31.7 (1.13)	84.4 (0.40)
Fern:	Blsp	9.34 (0.355)	0.26 (0.020)	36.3 (0.93)	81.0 (0.97)
	Ponu	9.52 (0.230)	0.22 (0.005)	18.2 (0.84)	69.3 (1.41)
Grass:	Poa	26.98 (1.045)	0.50 (0.035)	71.3 (1.11)	86.1 (0.85)
	Cade	13.38 (0.206)	0.20 (0.005)	35.7 (0.99)	76.3 (0.36)
Moss:	Hysp	4.70 (0.074)	0.14 (0.005)	8.7 (0.54)	83.5 (1.18)

^aSpecies scientific names given in Table 1.

^bDue to growth form, here considered a Forb; taxonomically a shrub.

Appendix 1. Continued.

G. Spring 1981

Species		Percent (dry matter basis)			
		CP	P	DMD	Moisture
Acronyms ^a					
Shrub:	Rusp	22.55 (0.759)	0.45 (0.020)	35.1 (0.63)	84.5 (1.48)
	Sa	19.77 (0.592)	0.56 (0.011)	20.8 (0.44)	82.6 (0.21)
	Va	24.59 (0.351)	0.56 (0.010)	48.4 (0.61)	86.1 (0.48)
	Acci	22.78 (0.955)	0.61 (0.022)	48.3 (0.46)	81.2 (1.76)
Tree:	Tshe	5.31 (0.340)	0.19 (0.019)	26.9 (0.55)	56.7 (3.84)
	Thpl ^c	6.13	0.14	37.4	50.5
Forb:	Titr	17.41 (1.174)	0.43 (0.025)	45.8 (2.56)	87.7 (0.91)
	Tome	18.44 (1.418)	0.32 (0.027)	36.1 (0.57)	82.2 (1.61)
	Oxor	24.05 (0.659)	0.48 (0.022)	57.3 (0.86)	91.7 (0.58)
Fern:	Pomu ^c	18.00	0.42	18.1	86.7
	Ptaq ^c	29.66	0.73	59.7	90.9
Grass:	Poa	25.95 (0.680)	0.53 (0.021)	76.8 (0.58)	89.1 (0.35)
	Cade	17.97 (0.358)	0.30 (0.015)	65.9 (0.16)	85.3 (0.73)
Moss:	Hysp	4.50 (0.153)	0.14 (0.003)	9.6 (0.31)	82.3 (2.11)

^a Species scientific names given in Table 1.

^b Due to growth form, here considered a Forb; taxonomically a shrub.

^c n = 2

Appendix 2. Total and green herbaceous biomass (kg/ha dry matter \pm S.E.; n = 25) in 7 habitat units in the Inn Valley, 1979-81.

Cover Types ^b	APPROXIMATE SAMPLING DATES ^a												
	12/15/79	2/6/80	3/14/80	5/29/80	7/31/80	10/6/80	11/19/80	1/4/81	2/28/81	4/15/81	6/9/81	8/3/81	11/13/81
Mature Alder													
Total	1485 (90)	1285 (106)	1305 (57)	610 (23)	1525 (120)	1850 (331)	1495 (376)	830 (81)	700 (102)	603 (80)	664 (45)	938 (70)	908 (99)
Green	431 (26)	252 (21)	238 (10)	581 (22)	1429 (112)	1025 (184)	478 (120)	181 (18)	444 (65)	515 (69)	664 (45)	846 (63)	443 (43)
Young Alder^d													
Total	-	-	-	-	840 (80)	337 (77)	182 (45)	195 (44)	322 (50)	-	170 (22) ^c	-	-
Green	-	-	-	-	748 (71)	258 (59)	103 (25)	136 (31)	294 (45)	-	169 (22)	-	-
Willow clearing^d													
Total	745 (106)	-	-	-	1130 (189)	851 (221)	675 (146)	855 (144)	814 (124)	651 (107)	869 (128)	1011 (159)	646 (132)
Green	419 (60)	-	-	-	371 (62)	451 (117)	296 (64)	414 (70)	481 (73)	505 (83)	844 (124)	494 (77)	274 (39)
Cottonwood Terrace													
Total	460 (74)	-	618 (120)	-	890 (79)	480 (53)	417 (55)	207 (34)	260 (57)	304 (38)	419 (31)	644 (93)	154 (30)
Green	222 (36)	-	209 (41)	-	870 (78)	416 (46)	281 (37)	120 (20)	233 (51)	282 (36)	419 (31)	632 (90)	104 (18)
Big-leaf Maple													
Total	-	1320 (145)	-	1148 (86)	2588 (191)	2185 (217)	1705 (146)	1260 (160)	1133 (132)	1204 (95)	1023 (78)	1698 (144)	1109 (119)
Green	-	448 (49)	-	1040 (78)	2329 (172)	1503 (149)	814 (70)	514 (65)	672 (79)	920 (72)	951 (73)	1579 (134)	449 (39)
Forest Clearing													
Total	-	-	-	-	2335 (101)	2167 (132)	1839 (83)	1990 (163)	1454 (139)	-	962 (79) ^c	-	-
Green	-	-	-	-	2111 (92)	1543 (94)	577 (26)	553 (45)	477 (46)	-	685 (57)	-	-
Mature Forest													
Total	632 (54)	-	-	-	-	522 (103)	562 (73)	567 (62)	818 (109)	502 (71)	393 (51)	658 (151)	553 (86)
Green	540 (46)	-	-	-	-	491 (97)	471 (61)	455 (49)	728 (97)	476 (67)	393 (51)	655 (150)	491 (69)

^a Sampling generally took 3-5 days to complete; date given is midpoint.

^b See 'Study Area' for discussion of these delineations of habitat unit.

^c Samples actually taken on 5/19/81.

^d Stands sampled subject to winter flooding.