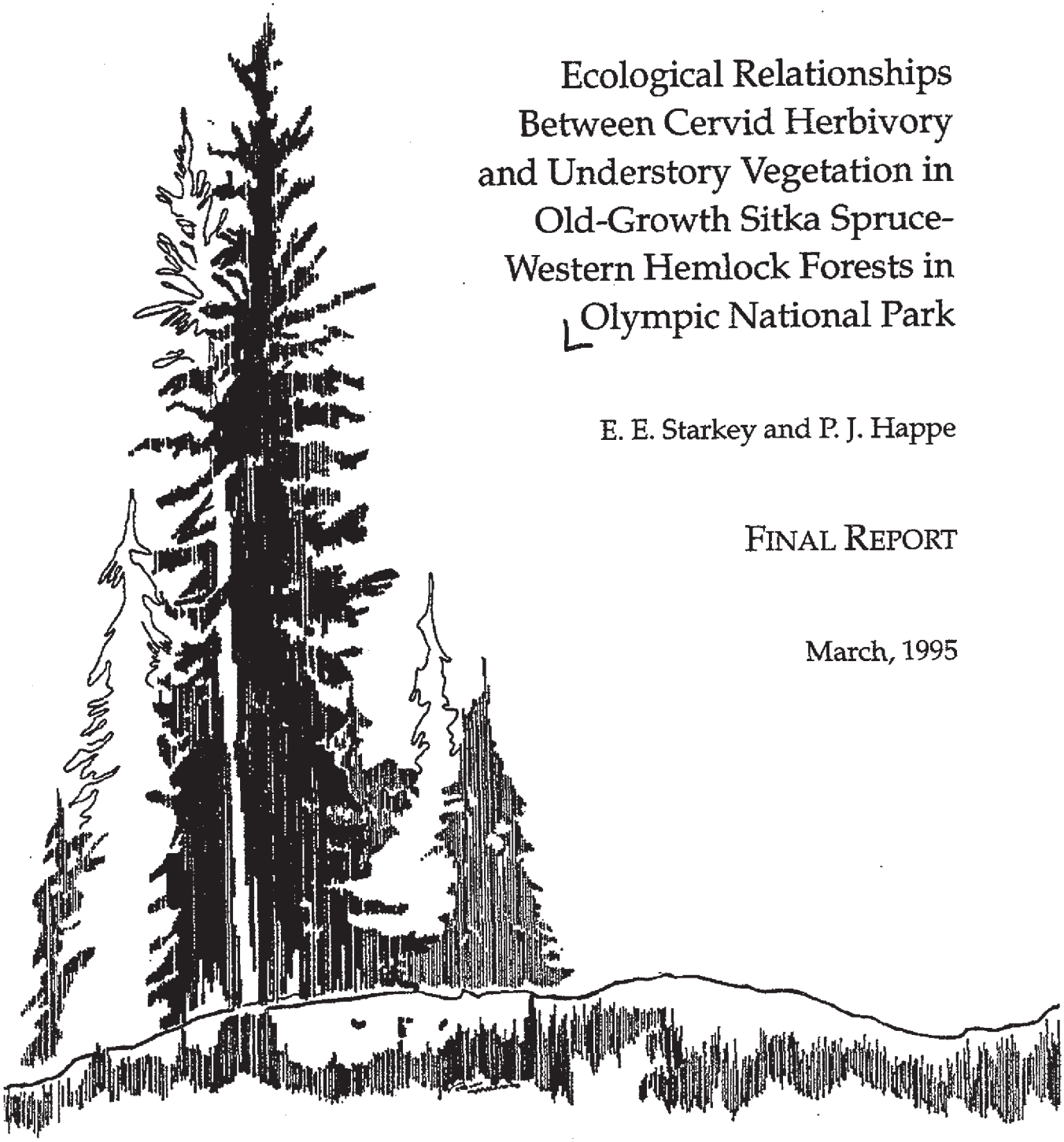
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Ecological Relationships Between Cervid Herbivory and Understory Vegetation in Old-Growth Sitka Spruce-Western Hemlock Forests in Olympic National Park

E. E. Starkey and P. J. Happe

FINAL REPORT

March, 1995

United States Department of Interior - National Park Service - Pacific Northwest Region

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The relationships between black-tailed deer (*Odocoileus hemionus columbianus*) and Roosevelt elk (*Cervus elaphus roosevelti*) herbivory and understory vegetation in unharvested forests in Olympic National Park were studied from 1985 - 1989. This study is completely described in Appendix A (doctoral dissertation of P.J. Happe). References cited in the following summary may be found in the literature cited section (pp. 130-137) of Appendix A.

Results and Discussion

We studied cervid herbivory in the understory of old-growth forests along the South Fork of the Hoh River and the effects of that herbivory on herb, fern, and shrub biomass, production, and nutrient content. The amount, timing, and impacts of cervid herbivory varied among understory plant communities, plant species, and years. Forage biomass, production, herbivory, and the influence of herbivory, were greatest in areas with grass-dominated understories. In those sites, production was either stimulated or not affected by herbivory, and herbivory altered plant structure and nutrient content such that foraging efficiency was improved during both summer and late winter. In sites with a forb-moss herb layer, biomass, production, and herbivory were less. Although herbivory either stimulated or had

no effect on production in forb sites, it had no effect on forage nutrient content or structure, and thus did not impact foraging efficiency.

With long-term exclusion of ungulates in the study area, grass-dominated understories disappeared. Thus, cervid herbivory was found to influence understories in old-growth forest on several spatial and temporal scales. In the short-term, cervid herbivory improved forage structure and nutrient concentration in grass dominated understories. In the long term, cervid herbivory maintained grass-dominated patches within the system. On both temporal and spatial scales, the net result of cervid herbivory was the creation of a more favorable foraging environment for both deer and elk.

Long-term protection from cervid herbivory had little effect on nutritional attributes of individual plants, such as fiber content, digestibility, crude protein levels, tannin content, or tannin astringency. However, herbivory reduced leaf area, leaf weight, and plant standing crop biomass.

Cervid herbivory is a natural phenomenon along the South Fork of the Hoh River, shaping old-growth spruce-hemlock communities over several spatial and temporal scales. For the most part, cervid herbivory created more favorable foraging environments, including the creation and maintenance of a "grazing lawn" (McNaughton 1986a, 1986b). In the short term, and on a small scale, herbivory increased biomass and nutrient concentration of herbaceous and salmonberry biomass within grass-

dominated patches. Additionally, except for salmonberry stems, cervid herbivory did not lead to increased tannin astringency and the generally associated decrease in digestible protein. The effects of herbivory were most prevalent during summer, when the ungulates faced their greatest nutrient and energy demands (i.e., growth, lactation, fat deposition), but some effects carried over into the winter months.

Concerns over reductions in preferred shrub species, such as elderberry and salmonberry, caused many earlier researchers to conclude that cervids were overutilizing the forage. The cervid-induced reduction in salmonberry and height and volume did preclude it from dominating grass-dominated understories, and appeared to totally inhibit sexual reproduction. However, because it was rhizomatous, salmonberry was poised to take advantage of release from herbivory. Such release occurred naturally in the study area, in refugia created by windthrow of large trees. In several long term exclosure experiments in Olympic National Park, salmonberry rapidly increased in stature and cover, and dominated a site in as little as 3 years (Schwartz and Mitchell 1945, Newman 1958, Harmon 1987).

Although ladyfern comprised a small percent of elk or deer diets, and was a small percent of grazed plot biomass, the heavy utilization that it received was highly significant ecologically. Upon release from herbivory, ladyfern overtopped, shaded out, and outcompeted almost all other herbaceous forage in sites where salmonberry is not present (Schwartz 1943, Newman 1958, Harmon

1987). In conjunction with the increase in salmonberry and ladyfern dominance, a total disappearance of grasses and decrease in some forbs was recorded in grass-dominated patches in exclosures (Schwartz 1943, Newman 1958, Harmon 1987, Schreiner et al. in prep, Woodward et al. 1993).

Thus, in the long term cervid herbivory increased species diversity on a small spatial scale, within grass-dominated patches. On an even longer temporal scale, the distinction between grass- and forb-dominated patches diminishes with long term exclusion (Schreiner et al. in prep). Thus cervid herbivory also leads to diversity of plant associations within the old-growth forest matrix. The loss of grass-dominated patches with long-term cervid exclusion would result in the loss of the most productive understory sites, decrease in the cervid forage base, and ultimately cervid carrying capacity, particularly for elk. Although grass-dominated areas comprised only 25% of old-growth terraces, production and utilization were 6.5 and 5.7 times greater, respectively, than in forb-dominated areas, and grass-dominated areas provided 69 and 66% of herbaceous production and utilization, respectively, in old-growth stands. The loss in herbaceous production would be partially offset by increased shrub availability, but herbs provide better quality forage throughout longer periods of the year than shrubs.

McNaughton (1986a) postulated that the grazing lawn theory is most applicable to co-evolved systems. Many of the herbaceous species in grass-dominated areas were exotic, which is

problematical when discussing how "natural" the grazing system is, or determining if the herbivore-vegetation system is co-evolved. Because the exotics were so ubiquitous, it was impossible to determine how the system functioned prior to the introduction of these species. However, with the current species mix, the grazing lawn hypothesis appears to be valid.

Cervid-induced habitat alteration seemed to benefit both deer and elk. The maintenance of grass-dominated areas clearly benefitted elk, because which they are well adapted to grass consumption. Furthermore, grass-dominated areas contained large patches containing abundant concentrated biomass, which are more suitable to foraging by large herds (Hanley 1980). However, herbivory also increased forage quality and maintained shrubs at low stature, which should benefit deer which are more limited by forage quality and are smaller than elk (Hanley 1982).

Old-growth sitka spruce-western hemlock stands do not supply all elk and deer forage needs, but they supply a relatively stable, year-round forage base, and are an important component of the system for cervids along the South Fork of the Hoh River. In periodic severe winters the canopy provides crucial snow interception, and forage in the form of browse and windthrow.

Management Implications

Prior concerns about excessive use and overpopulation (Riley 1918, Sumner 1938, Schwartz 1943) have given way to the view that elk populations in western drainages in Olympic National Park are stable, and at ecological carrying capacity (Newman 1958, Jenkins

1981). This more recent hypothesis is supported by the observations that the elk population has stable social groups, a high proportion of old-age individuals, and low recruitment (Jenkins 1980, Jenkins and Starkey 1982, Leslie and Jenkins unpublished data). Our study suggests that the existing level of herbivory, although greatly influencing the structure and composition of the forest understory, may actually produce greater and more stable forage for herbivores. Along the South Fork of the Hoh River, as in other areas where herbivores are a natural component, the removal of herbivory would cause noticeable changes to the system. Any significant reduction in populations of deer and elk would result in a much less open understory, dominated by shrubs.

APPENDIX A

ECOLOGICAL RELATIONSHIPS BETWEEN CERVID HERBIVORY AND UNDERSTORY VEGETATION IN OLD-GROWTH SITKA SPRUCE-WESTERN HEMLOCK FORESTS IN WESTERN WASHINGTON

by

Patricia J. Happe

A THESIS

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Dean of Graduate School

Date thesis is presented 16 September 1993

Typed by researcher for Patricia J. Happe

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ECOLOGICAL RELATIONSHIPS BETWEEN CERVID HERBIVORY AND UNDERSTORY VEGETATION IN OLD-GROWTH SITKA SPRUCE-WESTERN HEMLOCK FORESTS IN WESTERN WASHINGTON

INTRODUCTION

Ungulate herbivory influences many facets of plants and plant communities, including nutrient content, plant defense mechanisms such as secondary compounds and spines, biomass, structure, production, species composition and diversity, and ecosystem stability (Crawley 1983, Caughley et al. 1987, Roundy and Ruyle 1989, Mopper et al. 1991). In addition, ungulate herbivory operates on several spatial and temporal scales (Brown and Allen 1989). However the direction and magnitude of the effects of herbivory varies widely over plant communities, herbivore species, and grazing systems.

Herbivory has a variable influence on plant chemistry. Forage nutrient content has been observed to either increase, not change, or decrease with herbivory (McNaughton 1976, Moss et al. 1981, Hanley 1987, Ruess et al. 1989, Bryant et al. 1991). Tannins, a group of secondary plant compounds that may deter ungulate herbivory (Cooper and Owen-Smith 1985, Provenza et al 1990), also have been observed to increase, not change, or decrease following herbivory (Bryant et al. 1991). In addition, the response of herbivores to tannins, the effect of tannins on herbivores, and the response of tannin content to herbivory varies with the type of tannin (Schultz and Baldwin 1982, Zucker 1983, Cooper and Owen-Smith 1985).

Considerable discussion has centered around the response of plant production to herbivory (Westoby 1985, Belsky 1986, McNaughton 1986a, 1986b, Westoby 1986, Hobbs and Swift 1988, Westoby 1989). To obtain uniformity in nomenclature and clarity, Belsky (1986) proposed using the terms overcompensation, exact compensation, and undercompensation to correspond to greater production in grazed than ungrazed plants, equal production in grazed and ungrazed plants, and lesser production in grazed than ungrazed plants, respectively. Herbivory has been observed to result in overcompensation (Paige and Whitham 1987, Hik and Jefferies 1990, Paige 1992), exact compensation (Roundy and Ruyle 1989), and undercompensation (Maschinski and Whitham 1989), on both annual and long-term time frames.

Ungulate herbivory has also been shown to have variable influences on plant populations and communities. On an individual species level, herbivory can either increase or decrease plant abundance (Smart et al. 1985, Stewart and Burrows 1989, Veblen et al. 1989). On a community level, herbivory can either increase or

decrease species diversity and evenness (Crawley 1983). Shifts in species diversity and abundance, coupled with herbivore effects on production, can either increase or decrease ecosystem stability (Smart et al. 1985, Frank and McNaughton 1992).

In his research on the ungulate grazing system in the Serengeti, McNaughton (1979, 1984, 1985) observed that herbivory resulted in increased production, greater forage nutrient content, modification of forage structure into more compact growth forms, extension of production during the growing season, and maintenance of productive, grazing adapted species. From these observations he hypothesized that in addition to protection from predation, aggregation by herbivores may be an adaptation to increase foraging efficiency, because the end result of their actions was the creation and maintenance of a more favorable foraging environment, or a "grazing lawn". In addition, he hypothesized that plants which have coevolved with herbivores have evolved mechanisms to cope with herbivory, and that fitness of some plant species may increase as a direct or indirect result of grazing pressure. McNaughton (1986a) later asserted that grazing lawns are most likely to arise in natural situations, where native herbivores have coevolved with their forage base, and that in some systems, removal of herbivory was 'unnatural' and would alter plant communities (McNaughton 1986a).

Most research on the effects of herbivory has been conducted in graminoid-dominated ecosystems with migratory herbivores (McNaughton 1979, Hik and Jefferies 1990, Frank and McNaughton 1992). There is much less information on the role of ungulate herbivory in forest systems. The relative importance of the influence of herbivory on vegetation can be expected to change with the stability of ecosystem driving factors (eg, climate, disturbances such as fire, flood, drought) (Caughley et al. 1987) and the relative selective pressure of herbivory as compared to other factors influencing plant growth and evolution, such as competition for nutrients and light (Maschinski and Whitham 1989). The majority of information on ungulates in forests indicates that herbivory is destabilizing, however most of this research was conducted in areas where animal numbers were artificially high (Anderson and Loucks 1979), or herbivores were exotic (Stewart and Burrows 1989, Veblen et al. 1989). Several investigations of native cervid exclosures in the U.S. have revealed that cover or biomass of herbaceous species in forested systems decreased with cervid exclusion (Tiedeman and Berndt 1972, Peek et al. 1978, Hanley and Taber 1980, McInnes et al. 1992). Shrub cover either increased

(Tiedeman and Berndt 1972, Hanley and Taber 1980) or decreased with exclusion (Peek et al. 1978, Hanley 1987, McInnes et al. 1992). However, only Hanley (1987) worked in climax communities, and only McInnes et al. (1992) researched a naturally regulated population.

I studied the effects of Roosevelt elk (*Cervus elaphus Roosevelti*) and Columbian black-tailed deer (*Odocoileus hemionus columbianus*) herbivory on browse and herbaceous species in climax and seral forests in western Washington, in Olympic National Park (ONP). ONP presented a unique research opportunity within the continental U.S. in containing a naturally regulated, seemingly stable, system of large herbivores and forested plant communities. The ungulates in my study area were largely year-round residents of the park and were thought to be at ecological carrying capacity and regulated by the forage base (Newman 1958, Jenkins 1980).

The specific areas of research covered in this study were:
1) An examination of the effects of several years of cervid exclusion on browse nutrient and tannin content, morphology, and maximum standing crop biomass of selected species. The specific hypotheses that I tested were:

a) Ho: cervid herbivory had no effect on browse nutrient content,

b) Ho: cervid herbivory had no effect on tannin content, composition, or astringency,

c) Ho: cervid herbivory had no influence on browse biomass and structure.

2) An investigation of the amount of cervid herbivory in old-growth forest stands, to determine if herbivory resulted in the formation of a grazing lawn. If a grazing lawn was formed, I expected to find a greater concentration of palatable forage and nutrients in grazed than ungrazed areas. The specific hypotheses that I tested were:

a) Ho: cervid herbivory had no effect on forage standing crop biomass,

b) Ho: cervid herbivory had no effect on forage structure,

c) Ho: cervid herbivory had no effect on forage concentration,

d) Ho: cervid herbivory had no effect on forage nutritional quality,

e) Ho: cervid herbivory had no effect on forage production.

My research was conducted in conjunction with research by ONP staff, who 1) revisited 8 to 55 year old cervid exclosures and tested the effects of cervid exclusion on shifts in species composition (Woodward et al. 1993), and 2) quantified the distribution and extent

of vegetation patches and shrub refugia in seral and old-growth communities (Schreiner et al. in prep).

A better understanding of cervid-forage relationships will benefit elk and deer management within ONP, and in the Pacific Northwest region. Throughout the history of ONP, there have been questions about the amount and ecological consequences of the observed level of herbivory. Some earlier researchers viewed the situation as overgrazing or excessive use (Riley 1918, Sumner 1938, Schwartz 1943), however others have thought that this was the natural condition of the range (Newman 1958, Jenkins 1980).

STUDY AREA DESCRIPTIONS AND HISTORICAL BACKGROUND

Location

This research was conducted in the South Fork of the Hoh (SFH) and Elwha valleys on the Olympic Peninsula, within ONP, Washington (Fig. 1). The SFH study area was located in Jefferson County (47°40'N, 123°56'W), 3-5 km east of the ONP boundary. The Elwha study area was located in Clallam County, (48°01'N, 123°35'W), near the junction of Hughes Creek and the Elwha River, approximately 3 km south of the ONP boundary.

These 2 study areas were chosen because they both are representative of unmanaged forests on the Olympic Peninsula, supported populations of deer and elk, and have been the sites of long-term research on the influence of cervid effects on vegetation. The SFH study area consisted of approximately 4 km^2 around 2 0.5 ha cervid exclosures that were constructed in 1980. The study area in the Elwha valley was associated with a 23x15 m cervid exclosure constructed in 1956.

Climate

Climate in ONP was maritime, characterized by cool, relatively dry summers and mild, wet, winters. Mean January minimum and July maximum temperatures during 1987 and 1988 averaged -1° and 18°C respectively. Mean annual precipitation in western ONP was 324 cm, of which 250 cm fell from October through March (Natl. Oceanic and Atmos Adm. 1980). Precipitation decreased along a gradient from the west to the northeast. Typically, snowfall was uncommon on valley bottoms, and did not persist when it occurred. However, severe winters characterized by persistent deep snow occurred sporadically in the study areas, usually at least once a decade (Moreland et al. 1953). Temperatures and precipitation recorded in the Main Fork of the Hoh Valley (MFH) during this study were "normal", however, 1988 was slightly colder and wetter than 1987 (Fig. 2).

Physiography and Vegetation

The SFH and Elwha River valleys consisted of U-shaped troughs scoured by glaciers and flat valley floors shaped by fluvial

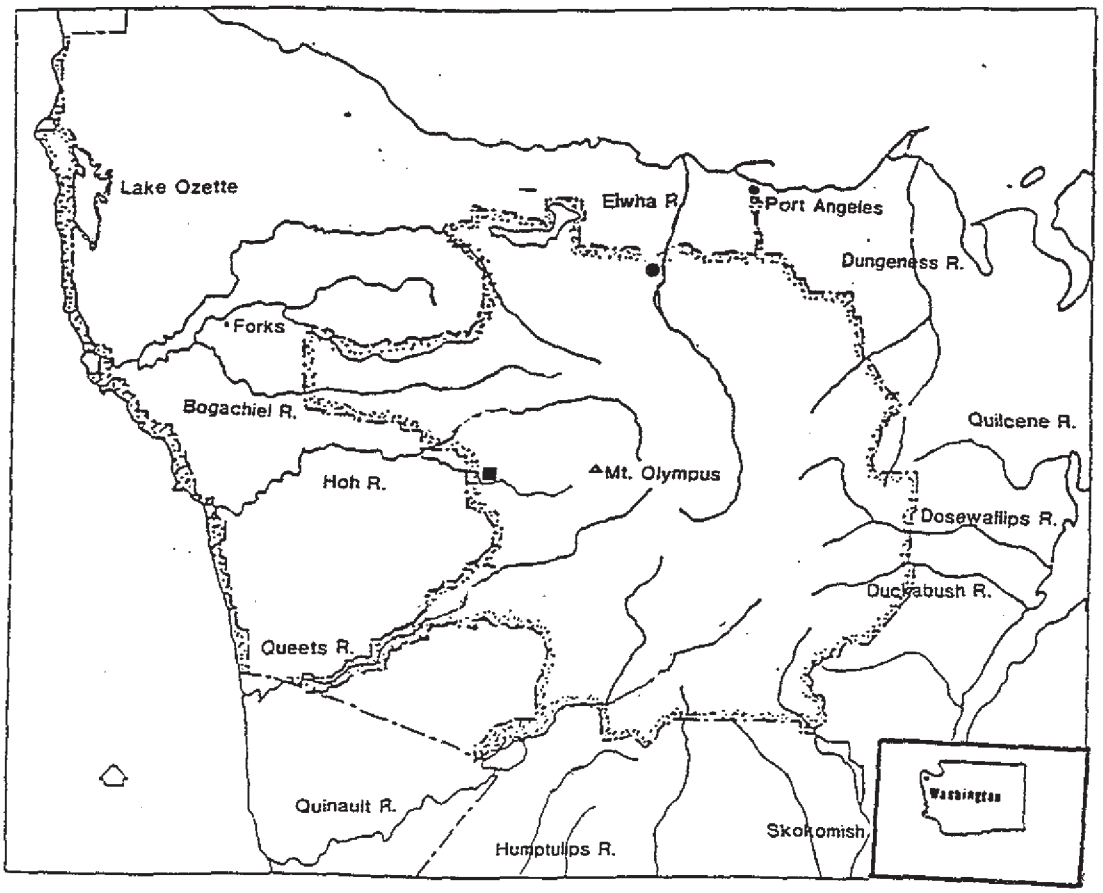


Figure 1. Location of Olympic National Park and the South Fork Hoh (■) and Elwha (●) study areas.

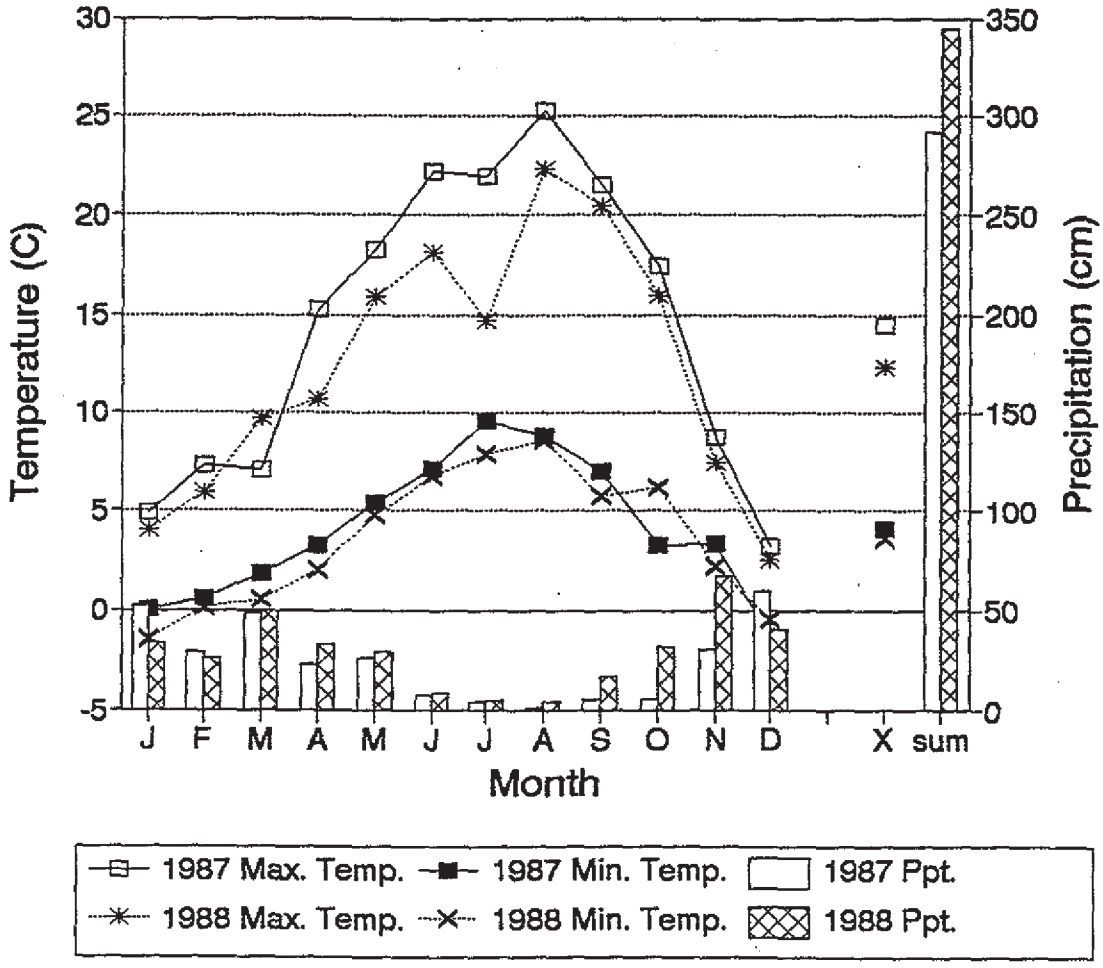


Figure 2. Mean maximum and minimum monthly temperatures (°C) and total monthly precipitation recorded in the Main Fork Hoh Ranger Station, Olympic National Park, during 1987 and 1988.

processes. The study sites were located on alluvial terraces at 215 and 100 m elevation in the SFH and Elwha, respectively.

The valley floor of the SFH within the study area contained 6 successively older and higher river terraces (Swanson and Lienkaemper 1982). The 3 youngest, and lowest, terraces supported early seral vegetation communities, predominantly willow-red alder (*Salix /Alnus rubra)* shrub, and mature alder on third terraces which were greater than 100 years old. The next 3 terraces (4-6) supported climax Sitka spruce-western hemlock (*Picea sitchensis - Tsuga heterophyla*) forests. The seral and climax communities comprised 15 and 85% of the valley floor, respectively (Schreiner et al. in prep). Most of the vegetation within the park has not been altered by logging or human settlement, however exotic herbaceous species are present in all communities. It is thought that these species were introduced by cattle grazing in the early 1900's.

Environmental stress and disturbance factors such as snow, drought, ice and fire are uncommon on the valley floor (Franklin 1982, Smith and Henderson 1986). Flooding is a frequent and significant phenomenon in the early seral communities adjacent to the river, whereas windstorms and associated blowdowns occur in localized areas every few decades in climax communities (Franklin 1982). Additionally, small tree-fall gaps are a constant and important disturbance in the climax communities. Our research in the SFH was conducted within old-growth spruce-hemlock forests, however deer and elk had access to, and used, all vegetation communities in the valley.

Vegetation has been previously described in the SFH (McKee et al. 1982) and in the adjacent MFH (Fonda 1974, Smith and Henderson 1986). Climax spruce-hemlock stands were composed of multilayered canopies consisting of an overstory of large spruce and hemlock, a midlayer of regenerating conifers, and variable shrub and herbaceous understories (Fonda 1974, McKee et al. 1982, Smith and Henderson 1986). Mean overstory and understory cover were 70% (range 30-95%) and 90% (range 8-99%) respectively, and vascular species richness was estimated at 130 (Smith and Henderson 1986). Dead logs covered 6-11% of the valley floor (Graham 1982). Schreiner et al. (in prep) identified 2 dominant understory strata, 1) areas where the herbaceous layer was dominated by graminoids (i.e, grass strata, GS), and 2) areas dominated by forbs and moss (i.e., forb strata, FS). GS and FS comprised 25 and 73% of the spruce-hemlock terraces respectively. GS patches were distributed throughout a FS matrix; on transects running perpendicular to the river, the number of GS and FS patches in old-

growth spruce-hemlock did not differ (number of patches per transect: GS=11.5, FS=12.9 P=0.4768), but mean patch intercept length was greater for FS than GS (GS=19.3 m vs. FS=55.4 m P=0.0001) (Schreiner et al., pers comm).

Mean maximum conifer age in the SFH ranged from 205-220 years, and did not vary significantly between surfaces 4-6 (McKee et al. 1982). However some stand characteristics varied; forests on surface 4 tended to be more open, and contain more grass and exotic forb species than the higher surfaces (McKee et al. 1982).

In 1980 Franklin et al. and ONP staff installed 2 0.5 ha exclosures in old-growth spruce-hemlock stands in the SFH. Exclosure 1 (ex1) was on a 6th terrace, about 4 km the from park boundary. Understory vegetation in and out of ex1 was predominantly FS, however small patches of GS were present. Exclosure 2 (ex2) was located on a fourth terrace, about 0.8 km upriver from ex1. The forest matrix at ex2 was characterized by larger and more sparsely distributed spruce than in ex1, and the understory by more frequent and larger patches of GS.

Geomorphology and vegetation were less well described in the Elwha than in the Hoh valley. The Elwha valley was narrower and had less prominent terraces than in the Hoh. The Elwha study site was located in a mid-seral alluvial terrace. The overstory was dominated by red alder and big-leaf maple (*Acer macrophyllum*). The understory cover was dense, and dominated by grasses and forbs, the most notable of which were nettle (*Urtica diocia*) and youth-on-age (*Tolmia menziesii*). Swordfern (*Polystichum munitum*) and salmonberry (*Rubus spectabilis*) were also ubiquitous in the understory. Vegetation at the Elwha site was similar to an alder site described by Smith and Henderson (1986: p166-167) in the Dosewalips drainage, on the northeast side of ONP; in the Dosewalips drainage mean canopy cover and understory cover was 85 and 99% respectively, and stand age was 80 yr.

Cervid Populations

Deer and elk are sympatric throughout the Olympic Peninsula, including the Hoh and Elwha drainages. Elk density was recently estimated at 8.7 /km^2 valley floor in the SFH during late winter (Houston et al. 1987). Comparable estimates are not available for the Elwha, but elk are thought to be less numerous there. Deer densities are unknown in either drainage. It is thought that elk are more

numerous than deer, particularly in western drainages. Leslie (1982) estimated that the elk:deer numerical ratio was 3:1 and biomass ratio 100:7, however no survey testing this estimate has been done. In the northern drainages, the proportion of deer increased; deer were thought to be the most numerous ungulate in the Elwha drainage (Newman 1954).

Herbivore-vegetation dynamics have been of interest on the Olympic Peninsula since before the establishment of ONP in 1938. Elk and deer have been present in North America since the Pleistocene epoch (Bryant and Maser 1982), and have been on the Peninsula for at least 3000 yr BP (Croes and Hackenberger 1988, cited by Houston et al. 1990), however the western valleys were last glaciated 18,000 yr BP (Heusser 1974, cited by Smith and Henderson 1986). In recent years, elk were thought to be plentiful in parts of the Olympics (Morganroth 1909, cited by Moreland et al. 1953) prior to settlement in the 1890's. In approximately 10 years following settlement of the region, elk numbers were reported to be decimated due to pressures from market and subsistence hunting. Morganroth (an early resident of the Peninsula and forester for the U.S. Forest Service) estimated that the elk population on the entire Peninsula was reduced to a low of 2000 in 1904. In the MFH homesteaders reported having to go further upstream than normal to hunt elk. Due to the public outcry associated with the perceived low elk numbers, bounties were established to control cougar in 1904 (wolves were extirpated by 1930), Washington State initiated a 10 year ban on elk hunting in 1905 (the ban lasted until 1933), and Mount Olympus National Monument was established in 1909, principally for the protection of elk, and ONP was created in 1938.

The response of elk populations to protection from hunting and predation pressures is unknown, because no censuses were conducted. However, we do have observations and educated guesses from long time residents, foresters and range conservation officers for the Forest Service, and researchers from the Biological Survey. Protection from hunting and predation appeared to have some effect, because signs of perceived "overpopulation", in the form of "range deterioration", were reported as early as 1915 (Riley 1918). During the winters of 1915-16 and 1917-18 there reportedly were large winter kills of elk. The die-offs and concerns of range deterioration led to further attention, and in 1918 Vernon Bailey of the US Biological Survey made a trip to ONP to survey the situation. At that time he reported a population of 7,000 to 8,000 elk on the Peninsula (Bailey 1918). The population estimate were unchanged through 1934 when O.J. Murie did a preliminary

survey of the park. Following his visit, Murie (1935) expressed a concern about range conditions. These concerns lead to the research conducted by J.E. Schwartz, assistant range examiner for the USFS, from 1933-1937. Schwartz made note of the extent and species composition of forage utilization, determined allowable use on key species, and installed several exclosures to measure the effect of herbivory on forage. Two of the 3 winters that Schwartz worked were severe, and led to large winter kills.

Concerns of overpopulation resulted in resumption of elk hunting on the peninsula, including within the Monument, in 1933. All hunts ceased within the Monument in 1938 with formation of the Park. It is interesting to note that when Schwartz did his work, even though there were concerns of overpopulation, his population estimates did not vary from Morganroth and Muries' estimates of 7-8000 for the peninsula (Moreland et al. 1953).

Little attention was paid to elk and elk-range relationships until 1952, when C.C. Newman, a biologist for ONP, returned attention to elk-vegetation relationships within the Park. His efforts were preceded by a severe winter and associated heavy winter kill of elk in 1949. Like Schwartz, he noted particularly heavy use of some forage species, installed exclosures to measure the effects of elk herbivory on forage, and had a severe winter leading to winter kill during his study. However, he believed that the level of herbivory was not detrimental to the range, and that perhaps it was the natural situation (Newman 1958). Throughout Newmans work, the elk population estimate for the peninsula averaged around 8000.

Thus, it appears that elk were abundant in ONP before the arrival of European settlers. Following settlement, elk numbers were depleted, at least in areas close to settlement, but after only 10 years of protection the numbers increased. Whether elk erupted to numbers greater than pristine densities, or returned to their original numbers, is unknown, but from at least the early 1950's elk populations in the Park seem to have been relatively stable, characterized by periodic die-offs during occasional severe winters, and heavy herbivory on some forage and browse species. Because the SFH is relatively inaccessible, it is seems likely that hunting pressure there was not severe. It is possible that the elk population in the study site has been primarily influenced and regulated by natural forces since before the park was formed.

Currently, cougar and black bear are abundant within ONP. The impact of predation on elk and deer populations is unknown, however

cougar in the Elwha preyed principally on deer (Newman 1954a). Wolves remain extirpated on the Olympic peninsula.

In the MFH, 8 km distant and at elevations similar to the SFH study site, Jenkins and Starkey (1984) found that elk selected valley floor habitats year-round. Although habitat selection patterns varied seasonally, elk selected alder flat and old-growth sitka-spruce habitats during both summer and winter. In the MFH, mean elk home range size was 1064 ha, which was larger than observed values for elk in prairie or managed forest habitats (Jenkins and Starkey 1984). Elk social groups, primarily consisting of cow-calf aggregations, were larger and more stable than those of elk groups in managed forests (Jenkins and Starkey 1982). It was hypothesized that the relatively large home range size was due to the more diffuse distribution of the forage base in undisturbed forests, whereas large group size and social group stability was a consequence of the stability and predictability of the foraging environment (Jenkins and Starkey 1982). Elk natality and recruitment were low, typical of a population at ecological carrying capacity. Similar information on deer habitat selection and social group structure is not available.

In the MFH there was a high degree of dietary overlap, at the plant species level, between elk and deer diets, although elk used more grasses than deer, and deer consumed more browse and forbs than elk (Leslie et al. 1984). There also was no difference between elk and deer diet quality. Both diets appeared to be adequate in crude protein (CP) and phosphorus, but deficient in digestible energy. Leslie et al. (1984) hypothesized that both ungulates were at ecological carrying capacity, and that they were limited by seasonal undernourishment, principally in winter.

STUDY I: EFFECTS OF CERVID HERBIVORY ON BROWSE NUTRITIONAL QUALITY AND TANNINS IN FORESTED SYSTEMS, OLYMPIC NATIONAL PARK, WA.

Methods

From July 1985 through July 1986, I compared nutrient content, tannin concentration, morphology, and biomass of cervid forages in and out of 3 long-term cervid exclosures. Exclosures 1 and 2 (ex1 and ex2) were the exclosures constructed in 1980 in spruce-hemlock stands in the SFH. Exclosure 3 (ex3) was the exclosure constructed by Newman in 1956 in an alder-flat in the Elwha valley.

In July 1985, October 1985, January 1986, and April 1986 I collected entire shoots of current annual growth of vine maple (*Acer circinatum*), salmonberry, red huckleberry (*Vaccinium parvifolium*), swordfern, deerfern (*Blechnum spicant*), wood sorrel (*Oxalis oregana*), and youth-on-age. In addition, samples of western hemlock were collected in January 1986. All forage species have been observed in elk and deer diets in the region (Leslie et al. 1984, Study 2, this paper). Plants were collected both inside and outside of the ungulate exclosures, however not all species were available in all exclosures (Table 1).

With one exception, I collected 3 sub-samples of vine maple, salmonberry, red huckleberry, and swordfern from inside and outside of each exclosure where the species occurred. I collected only 2 samples of swordfern at ex3 due to low plant availability. For the remaining species, including deerfern, wood sorrel, youth-on age, and hemlock, I collected 1 sample in and out of the exclosures. Forage samples were composited from 1 to 50 randomly selected plants from mutually exclusive sample plots inside and outside of the exclosures. Samples were obtained by harvesting 50% of the current annual growth of each shrub sampled: I collected every other twig along each branch for the shrubs, and every other frond for the ferns. Plant material was gathered until an estimated 10 g of dry material was obtained. Each shrub and swordfern sampled was tagged so that the plant was not resampled in subsequent seasons. Forbs, hemlock, and deerfern were collected incidentally to harvesting shrubs, and no attempt was made not to resample those plants in later seasons.

During summer and fall sample periods, leaves and stems of vine maple, salmonberry, and red huckleberry were separated prior to analysis. Winter samples consisted of stems only, spring samples were

Table 1. Forage species sampled in cervid exclosures in the South Fork Hoh and Elwha Valleys, 1985-1986. X indicates that the species was collected at a site.

	EXCLOSURE		
SPECIES	1	2	3
Vine Maple		x	
Salmonberry	x	x	x
Red Huckleberry	x	x	
Swordfern	x		x
Deerfern		x	
Wood sorrel		x	
Youth-on-age			x
Hemlock	x	x	

succulent shoots of both leaves and stems. Fern samples were entire current years fronds. Forb samples were leaves and petioles.

Each plant sample collected in the field was divided into 2 sub-samples. One sub-sample was weighed, dried at 30-40°C to a constant weight, ground through a 20 - mesh (1 mm) screen, and used in subsequent analysis of dry-matter, fiber, protein, and digestibility. Forage fiber was determined using sequential detergent analysis (Goering and Van Soest 1970) with modifications of Waldern (1971) and Van Soest and Robertson (1980). Crude protein (CP) was measured using the micro-Kjeldahl technique (Horwitz 1980:858). Two-stage *in vitro* digestibility (IVD) was determined (Tilley and Terry 1963) with inoculum from a fistulated heifer on a diet of ryegrass hay supplemented with 4.54 kg of grain per day.

The second subsample was frozen within 8 hours of collection, and was used for analysis of tannin and leaf area. Frozen samples were lyophilized at -20 to -10 C. Leaf area of lyophilized leaves was measured with a LI-3100 (Li-Corr Inc., Lincoln, Nebr.) leaf area meter. Lyophilized plant material was ground through a 40-mesh (0.5 mm) screen and was stored frozen under desiccation until it was analyzed. Tannins were extracted using a modification of Hagerman and Robbins' (1987) method (Happe et al. 1990). Presence of protein precipitating tannins were assayed with the protein precipitating phenolic assay (Hagerman and Butler 1978). Tannin astringency was measured using modifications (Hagerman and Robbins 1987) of the dye-labeled protein method (Asquith and Butler 1985). Both assays were run at the equivalence point of optimal protein and tannin concentration (Hagerman and Robbins 1987). I determined the equivalence point for 1 sample of each species, season and plant part combination, and the remaining similar samples were assayed at that equivalence point. Finally, I measured the amount of both condensed and hydrolyzable tannins. Condensed tannins (CT) were measured using the vanillin method (Price et al. 1978), and hydrolyzable tannins (HT) were measured using techniques developed by Schultz (Schultz and Baldwin 1982, Schultz and Hollis pers. comm), with the modification of reading the samples 15 sec after the addition of KIO^3.

Mean biomass of individual salmonberry, red huckleberry, and swordfern plants was measured in and out of the exclosures during July 1986. Salmonberry and red huckleberry plants were defined as rooted stems, whereas swordfern plants were defined as individually recognizable clumps. Plants were sampled using the same methods used to gather samples for forage quality analysis, but in addition I

recorded basal stem diameter (BSD), height, length, and width of each salmonberry and red huckleberry sampled, and number of fronds of each swordfern plant. Biomass per plant was estimated by doubling the weight of the composited sample (to account for harvesting only 50% of CAG) and dividing by the number of plants per sample.

I tested the hypotheses that browse nutrient and tannin levels and morphological characteristics did not vary among seasons or between grazed and enclosed plants using analysis of variance (ANOVA). The ANOVA model for salmonberry, red huckleberry and swordfern was a split plot in time with exclosure as block, treatment (grazed or enclosed) as main plot, and season as split plot, using exclosure and treatment subsample means in the ANOVA. Because it only occurred in 1 exclosure, data for vine maple were analyzed in a 2-way split plot ANOVA with treatment as main plot, season as split plot, and subsamples as replicates. Also, since vine maple was found in only 1 site, it is pseudoreplicated (Hurlbert 1984). Because the number of replications in all ANOVAs were small, I used a P value of < 0.10 in determining significance to increase power and guard against unacceptable risk of type II error. Even with the higher alpha level, significance tests for treatment effects still had low power, because the degrees of freedom for the error term was 1 for swordfern and red huckleberry, and 2 for salmonberry. The remaining species were not replicated, and thus were not subjected to statistical analysis. Plant biomass data were analyzed in a 2-way factorial ANOVA, with exclosure as block, and species and treatment as factors. There were 6 degrees of freedom for error in this analysis.

Results

Forage quality differed between species, plant parts, and seasons, but there were few significant differences between grazed and ungrazed plants of the same species. The few treatment effects that were significant were more frequent in the summer than in other seasons, and occurred more often in salmonberry than in the other species (Table 2).

Shrub and swordfern percent dry matter varied significantly among seasons ($P < 0.10$) (Table 2a); dry matter for all species was least in the spring and greatest in the winter. The effect of herbivory on shrubs differed between leaf and stem components. Shrub leaf percent dry matter did not differ between grazing treatments ($P >$

Table 2. Seasonal nutrient content (% dry matter), astringency (mg bovine serum albumin precipitated/mg plant tissue), and condensed (catechin equivalent) and hydrolyzable tannin (tannic acid equivalent) concentration (mg tannin/mg plant dry matter) in selected browse and herbaceous species inside and outside of exclosures in Olympic National Park, Washington, 1985-1986.

Nutrient plant species, and plant part	SUMMER				FALL				WINTER				SPRING			
	Grazed		Enclosed		Grazed		Enclosed		Grazed		Enclosed		Grazed		Enclosed	
	X	(SE)	X	(SE)	X	(SE)	X	(SE)	X	(SE)	X	(SE)	X	(SE)	X	(SE)
a) Percent Dry Matter																
Vine maple[a]																
Leaf[S]	32.10	(1.11)	33.90	(1.08)	23.90		24.60	(0.85)					16.60	(2.96)	19.07	(2.24)
Twig[SI]	41.10	(0.35)	42.80	(1.68)*	46.40	(0.58)	48.10	(0.52)	46.90	(0.35)	45.00	(1.10)				
Salmonberry[b]																
Leaf[S]	24.90	(0.99)	28.10	(0.97)	18.73	(0.64)	19.96	(1.79)					18.34	(1.68)	19.69	(1.54)
Twig[TS]	27.04	(0.91)	35.01	(1.12)	34.44	(1.26)	41.06	(2.05)	30.41	(0.27)	35.58	(3.32)				
Red huckleberry[c]																
Leaf[S]	29.72	(0.45)	32.13	(1.37)	23.43	(0.30)	21.78	(0.32)					18.40	(0.27)	19.28	(1.48)
Twig[SI]	37.62	(0.33)	39.42	(2.25)*	39.42	(0.15)	37.92	(0.12)	40.53	(0.40)	39.95	(0.18)				
Swordfern[dS]	29.82	(1.22)	29.30	(2.50)	27.13	(0.58)	24.51	(0.66)	27.12	(1.15)	23.03	(0.78)	15.82	(0.68)	17.41	(1.54)
Deerfern[e]	20.2		21.20		21.60		21.50		17.30		17.50		10.80		9.10	
Wood sorrel[e]	9.3		8.60		6.30		7.20						19.40		17.90	
Youth-on-age[f]	15.8		13.90		13.10		10.50		14.30		12.50		13.90		15.10	
Western hemlock[g]									33.60	(1.30)	32.60	(0.50)				
b) Cell wall constituents																
Vine maple																
Leaf[SI]	30.00	(0.89)	31.20	(1.23)	39.60		33.80	(1.31)*					16.20	(0.68)	17.40	(1.62)
Twig[S]	69.50	(0.56)	71.80	(1.27)	65.80	(0.73)	65.50	(3.85)	65.30	(0.94)	70.40	(1.98)				
Salmonberry																
Leaf[S]	38.05	(1.83)	38.27	(0.23)	40.62	(2.12)	38.63	(2.02)					31.18	(0.61)	31.54	(0.80)
Twig[TS]	75.12	(1.53)	79.31	(1.93)	69.72	(0.80)	73.47	(0.24)	72.82	(1.14)	75.86	(1.00)				
Red huckleberry																
Leaf[S]	35.33	(0.04)	35.86	(0.42)	33.37	(0.66)	34.36	(0.51)					31.00	(1.13)	31.30	(1.67)
Twig[TSSI]	71.58	(1.64)	71.71	(0.53)	71.91	(1.72)	68.21	(1.51)*	67.78	(0.53)	67.91	(1.74)				
Swordfern [S]	68.11	(0.82)	67.59	(0.69)	65.55	(0.39)	65.45	(0.24)	63.13	(2.58)	65.17	(2.88)	46.32	(0.77)	44.70	(3.24)
Deerfern	49.70		51.98		46.55		49.22		44.54		46.24		36.81		31.70	
Wood sorrel	30.58		31.38		29.38		30.39						24.07		24.84	
Youth-on-age	31.05		33.70		32.75		34.43		36.03		33.78		25.45		23.78	
Western hemlock									53.74	(1.70)	52.50	(1.49)				
c) Lignin																
Vine maple																
Leaf[SI]	6.62	(0.24)	6.10	(0.05)	10.56		8.79	(0.89)*					1.61	(0.21)	2.11	(0.33)
Twig[TS]	14.14	(0.13)	14.40	(0.14)	16.90	(0.44)	17.00	(1.01)	14.20	(1.03)	16.60	(0.69)				

Table 2. Continued.

Nutrient plant species, and plant part	SUMMER Grazed X	SUMMER Grazed (SE)	SUMMER Enclosed X	SUMMER Enclosed (SE)	FALL Grazed X	FALL Grazed (SE)	FALL Enclosed X	FALL Enclosed (SE)	WINTER Grazed X	WINTER Grazed (SE)	WINTER Enclosed X	WINTER Enclosed (SE)	SPRING Grazed X	SPRING Grazed (SE)	SPRING Enclosed X	SPRING Enclosed (SE)
c) Lignin (continued)																
Salmonberry																
Leaf[S]	4.97	(0.47)	5.32	(0.08)	7.41	(0.92)	6.87	(0.71)					2.65	(0.49)	2.70	(0.55)
Twig	17.12	(0.83)	18.27	(0.82)	18.56	(0.60)	19.46	(0.82)	17.98	(1.08)	17.29	(1.16)				
Red huckleberry																
Leaf	7.90	(0.53)	8.58	(0.29)	7.37	(0.18)	8.52	(0.48)					7.50	(0.97)	8.56	(0.69)
Twig[S]	17.60	(0.18)	15.80	(0.54)	20.10	(0.10)	19.70	(0.81)	15.90	(0.68)	15.80	(0.02)				
Swordfern [S]	13.75	(0.86)	14.43	(0.62)	16.80	(1.32)	17.42	(0.41)	12.23	(0.15)	12.10	(1.63)	13.34	(0.16)	12.54	(2.22)
Deerfern	9.11		8.97		6.37		8.18		7.10		8.21		7.93		8.86	
Wood sorrel	2.82		3.87		3.89		3.69						2.20		2.03	
Youth-on-age	6.44		7.75		8.91		6.53		6.86		6.10		3.00		3.81	
Western hemlock									14.12	(0.91)	14.28	(1.74)				
d) Crude Protein																
Vine maple																
Leaf[SI]	12.60	(0.30)	12.60	(0.63)	4.40	(0.37)	4.20	(0.26)					22.40	(0.78)	25.20	(1.03)*
Twig[ST]	4.60	(0.31)	3.70	(0.24)	6.20	(0.25)	5.40	(0.44)	5.00	(0.12)	4.30	(0.68)				
Salmonberry																
Leaf[IBS]	16.86	(0.90)	15.26	(0.79)	13.59	(0.83)	12.94	(0.68)					21.92	(0.63)	21.84	(0.23)
Twig[I]	5.39	(0.54)	4.43	(0.86)*	5.18	(0.22)	5.69	(0.64)*	4.80	(0.10)	4.82	(0.35)				
Red huckleberry																
Leaf[S]	15.10	(0.51)	13.60	(0.21)	10.40	(0.37)	9.04	(0.02)					25.00	(1.33)	23.80	(2.25)
Twig[SI]	5.48	(0.11)	5.12	(0.09)	5.46	(0.59)	6.85	(0.32)*	5.40	(0.08)	5.56	(0.12)				
Swordfern [S]	10.92	(1.92)	10.93	(1.82)	10.00	(0.33)	9.59	(2.11)	9.11	(0.15)	9.00	(1.14)	15.16	(0.04)	18.07	(0.84)
Deerfern	10.45		10.34		9.15		9.51		9.79		8.11		22.02		18.09	
Wood sorrel	15.47		16.03		12.37		11.07						21.62		19.91	
Youth-on-age	21.66		20.18		20.10		23.85		15.81		17.25		21.20		22.82	
Western hemlock									5.78	(0.08)	5.81	(0.35)				
e) In vitro dry-matter digestibility																
Vine maple																
Leaf[S]	50.10	(2.34)	47.00	(3.24)	34.80		37.80	(0.06)					56.90	(2.00)	58.60	(1.94)
Twig	35.50	(0.92)	34.90	(1.54)	34.70	(2.03)	33.10	(1.68)	48.80	(9.13)	36.30	(2.53)				
Salmonberry																
Leaf[S]	35.85	(1.82)	37.50	(2.42)	36.25	(1.89)	36.20	(1.06)					37.92	(0.72)	39.88	(1.85)
Twig[S]	21.96	(1.27)	18.08	(1.76)	25.16	(0.64)	24.22	(0.77)	25.24	(1.12)	23.93	(1.77)				
Red huckleberry																
Leaf[S]	49.43	(3.06)	49.65	(0.71)	52.15	(0.43)	50.26	(2.97)					59.53	(0.66)	61.95	(0.24)
Twig[S]	30.45	(0.43)	29.53	(0.08)	24.14	(1.21)	25.72	(1.46)	29.57	(1.81)	30.12	(3.47)				

Table 2. Continued.

Nutrient plant species, and plant part	SUMMER Grazed X	(SE)	SUMMER Enclosed X	(SE)	FALL Grazed X	(SE)	FALL Enclosed X	(SE)	WINTER Grazed X	(SE)	WINTER Enclosed X	(SE)	SPRING Grazed X	(SE)	SPRING Enclosed X	(SE)
e) In vitro dry-matter digestibility (continued)																
Swordfern [SI]	16.74	(1.53)	19.86	(2.60)*	17.13	(1.23)	19.24	(2.25)*	22.56	(1.90)	23.58	(2.78)	19.60	(1.10)	20.13	(1.80)
Deerfern	25.94		24.27		21.80		24.09		39.78		21.13		26.39		34.36	
Wood sorrel	72.71		70.83		68.90		73.79						74.31		73.86	
Youth-on-age	35.7		40.46		32.85		39.76		40.77		47.15		42.32		46.94	
Western hemlock									28.44	(2.23)	26.78	(1.71)				
f) Astringency																
Vine maple																
Leaf	0.625	(0.045)	0.775	(0.015)	0.490	(0.070)	1.415	(0.645)					1.093	(0.152)	0.724	(0.095)
Twig	0.000		0.000		0.000		0.000		0.000		0.000					
Salmonberry																
Leaf[BS]	0.791	(0.138)	0.666	(0.175)	0.457	(0.233)	0.653	(0.322)					1.364	(0.079)	1.326	(0.064)
Twig[T]	0.140	(0.075)	0.042	(0.010)	0.136	(0.009)	0.088	(0.024)	0.110	(0.019)	0.042	(0.014)				
Red huckleberry																
Leaf	0.015	(0.003)	0.029	(0.012)	0.038	(0.005)	0.042	(0.006)					0.038	(0.001)	0.032	(0.002)
Twig	0.000	(0.0)	0.000	(0.0)	0.000	(0.0)	0.000	(0.0)	0.000	(0.0)	0.000	(0.0)				
Swordfern [S]	0.367	(0.005)	0.236	(0.130)	0.340	(0.005)	0.203	(0.144)	0.284	(0.063)	0.160	(0.088)	1.443	(0.086)	1.538	(0.050)
Deerfern	0.430		0.220		0.410		0.410		0.280		0.250		0.840		0.730	
Wood sorrel	0.000		0.000		0.000		0.000						0.000		0.000	
Youth-on-age	0.803		0.767		0.555		0.358		0.582		0.550		0.693		0.662	
Western hemlock									0.530	(0.030)	0.540	(0.030)				
g) Hydrolyzable tannin																
Vine maple																
Leaf	0.245	(0.015)	0.270	(0.010)	0.305	(0.035)	0.485	(0.195)					0.331	(0.016)	0.277	(0.024)
Twig	0.000		0.000		0.000		0.000		0.000		0.000					
Salmonberry																
Leaf[BS]	0.167	(0.024)	0.163	(0.030)	0.088	(0.017)	0.094	(0.017)					0.167	(0.013)	0.154	(0.014)
Twig[S]	0.044	(0.008)	0.032	(0.001)	0.037	(0.003)	0.030	(0.002)	0.029	(0.002)	0.019	(0.002)				
Red huckleberry																
Leaf[S]	0.010	(0.001)	0.010	(0.002)	0.006	(0.001)	0.006	(0.001)					0.000	(0.0)	0.000	(0.0)
Twig[S]	0.002	(0.001)	0.001	(0.001)	0.000	(0.0)	0.000	(0.0)	0.000	(0.0)	0.000	(0.0)				
Swordfern [BS]	0.000	(0.0)	0.000	(0.0)	0.005	(0.002)	0.004	(0.003)	0.007	(0.001)	0.006	(0.002)	0.006	(0.001)	0.009	(0.001)
Deerfern	0.01		0.01		0.01		0.01		0.01		0.01		0.00		0.00	
Wood sorrel	0.00		0.00		0.00		0.00						0.00		0.00	
Youth-on-age	0.013		0.018		0.018		0.011		0.01		0.014		0.02		0.017	
Western hemlock									0.00	(0.0)	0.005	(0.005)				

Table 2. Continued.

Nutrient plant species, and plant part	SUMMER Grazed X	(SE)	SUMMER Enclosed X	(SE)	FALL Grazed X	(SE)	FALL Enclosed X	(SE)	WINTER Grazed X	(SE)	WINTER Enclosed X	(SE)	SPRING Grazed X	(SE)	SPRING Enclosed X	(SE)
h) Condensed tannin																
Vine maple																
Leaf[TS]	0.020	(0.010)	0.025	(0.005)	0.000		0.000						0.008	(0.006)	0.000	(0.018)
Twig	0.000		0.000		0.000		0.000		0.000		0.000					
Salmonberry																
Leaf	0.013	(0.004)	0.011	(0.002)	0.014	(0.004)	0.026	(0.004)					0.013	(0.003)	0.010	(0.003)
Twig	0.046	(0.005)	0.047	(0.010)	0.041	(0.003)	0.040	(0.013)	0.044	(0.002)	0.041	(0.009)				
Red huckleberry																
Leaf	0.012	(0.001)	0.010	(0.003)	0.020	(0.002)	0.003	(0.018)					0.022	(0.003)	0.027	(0.013)
Twig[S]	0.065	(0.001)	0.067	(0.015)	0.000	(0.000)	0.000	(0.000)	0.000	(0.0)	0.000	(0.0)				
Swordfern [ST]	0.269	(0.028)	0.223	(0.078)	0.333	(0.007)	0.247	(0.099)*	0.312	(0.048)	0.215	(0.097)*	1.200	(0.024)	1.334	(0.097)*
Deerfern	0.31		0.11		0.25		0.24		0.24		0.16		0.60		0.65	
Wood sorrel	0.00		0.00		0.00		0.00						0.00		0.00	
Youth-on-age	0.226		0.281		0.321		0.258		0.23		0.22		0.342		0.348	
Western hemlock									0.565	(0.015)	0.48	(0.04)				

[a] Site 1 only; ANOVA treatment season with 3 subsamples per treatment/season
[b] Site 1,2,3; ANOVA Treatment main plot, Season subplot, site as replication.
[c] Site 1,2; ANOVA same as with b.
[d] Site 1,3; ANOVA same as with b.
[e] Site 2, no subsamples.
[f] Site 3, no subsamples.
[g] site 1,2, no samples.

[T] Treatment effect significant at $p < 0.10$.
[S] Site effect significant at $p < 0.10$.
[S] Season effect significant at $p < 0.10$.
[I] Treatment*Season interaction significant at $p < 0.10$.
* Grazed significantly different than Enclosed $P < 0.10$ (LSD test, conducted if interaction was significant)

0.10), but salmonberry twigs were more succulent in grazed than ungrazed plants in all seasons, whereas grazed vine maple and red huckleberry twigs were more succulent than enclosed twigs during summer only (Table 2a).

Percent cell wall constituents (CWC) and lignin varied among seasons ($P < 0.10$) (Table 2b,c); fiber content was least during spring and increased with plant maturation from summer through winter. The effect of herbivory on plant fiber varied with plant part. Herbivory had no effect on fern or shrub leaf fiber, however salmonberry stem CWC and vine maple twig lignin were greater in enclosed than grazed plants ($P < 0.10$). Conversely, red huckleberry twig CWC was greater in grazed than enclosed plants during fall (Table 2c). Herbivory had no effect on swordfern fiber ($P > 0.10$).

Crude protein and IVD also varied among seasons and plant parts ($P < 0.10$); CP and IVD were least in winter and greatest in spring. Crude protein content differed more between grazed and enclosed treatments than any other forage quality parameter measured. Crude protein content of several species, notably vine maple stems and salmonberry leaves, was greater in the grazed than ungrazed plants ($P < 0.10$). However, that difference was greatest in the summer (Table 2d); salmonberry and red huckleberry twig CP content was greater in grazed than ungrazed plants during summer, but less in grazed than ungrazed during fall ($P < 0.10$). There was no consistent effect of herbivory on digestibility in the shrubs, although swordfern digestibility was less in grazed than ungrazed plants during summer and fall (Table 2e).

Although forb samples were not replicated and statistical differences could not be analyzed, nutrient and fiber content of forbs followed similar seasonal patterns as shrub leaves. Forb CP and IVD appeared greatest and fiber content lowest during spring, however, forb forage quality remained relatively high throughout the year. Wood sorrel was always the highest quality forage; wood sorrel was highly digestible and had high CP content. Forage quality of youth-on-age was relatively poor (low IVD, high lignin), however, youth-on-age was high in CP, especially during winter. During winter, hemlock forage quality was generally low (high fiber, low IVD, low CP), and appeared only slightly better than shrub stems.

Tannin astringency varied among seasons, species, and plant parts (Table 2f). Astringency in shrubs was greatest in spring and summer and least in winter, greatest in salmonberry and least in red huckleberry, and greater in shrub leaves than twigs. Swordfern

astringency did not vary among seasons ($P > 0.10$), and levels were similar to salmonberry. Astringency of deerfern was similar to that of swordfern. Among the forbs, wood sorrel had no astringency whereas youth-on-age was astringent year-round. Astringency levels of youth-on-age and hemlock appeared to be greater than all other species during winter (Table 2f).

The type of tannin varied with plant species and part. The ratio of HT/CT was greater in the shrub leaves, with almost all of vine maple tannin being HT. The proportion of CT and HT was about equal in salmonberry stems, and there was more CT than HT in the ferns, hemlock and youth-on-age. Hydrolyzable tannin concentration was greatest in salmonberry and vine maple, but was also present in red huckleberry and youth-on-age. Hydrolyzable tannin was either not present, or present in low amounts in swordfern, deerfern, and vine maple and red huckleberry stems (Table 2g). Hydrolyzable tannin content varied among seasons for salmonberry, huckleberry, and swordfern, but not vine maple (Table 2g). Condensed tannin was present in all astringent species, thus CT was the only tannin detected in the ferns. Seasonal variation of CT differed among plant species. In the ferns and youth-on-age, which were wintergreen, CT was greatest in the spring, and decreased to lower, relatively constant levels from summer through winter. Condensed tannin in salmonberry leaves and twigs and red huckleberry leaves did not vary among seasons ($P > 0.10$), however CT in vine maple leaves and red huckleberry twigs was greatest during summer.

Herbivory had little effect on tannin amounts or astringency (Table 2f,g,h). Among the species sampled, cervid herbivory only affected salmonberry twig astringency; astringency was greater in grazed than ungrazed twigs ($P < 0.10$) (Table 2f). Herbivory had no effect on HT ($P > 0.10$) (Table 2g). Condensed tannin tended to be greater in grazed plants, but this was only significant for vine maple in the spring, and swordfern in the fall and winter ($P < 0.10$) (Table 2h). However, level of swordfern CT was greater in protected than in grazed plants during spring ($P < 0.10$).

Some forage qualities differed among exclosure sites. Exclosure 3, which was in a late seral deciduous community, was the most dissimilar site. Crude protein and IVD content of salmonberry was greater in ex3 than in the other sites, but astringency and HT were less. Forage quality of swordfern did not differ between sites, but swordfern HT was also less in ex3. Cell wall constituents of red huckleberry stems were greater in ex1 than ex2.

There were few interactions between exclosure site and the effects of herbivory on forage quality or tannins. The exceptions were swordfern lignin, which was greater in grazed than enclosed plants in ex3 but greater in enclosed than grazed plants in ex1, and swordfern astringency, which was greater in grazed than ungrazed ferns in ex3, but equal between treatments in ex1. Finally, IVD of salmonberry twigs was greater in grazed than enclosed plants in ex2 and ex3, but not ex1.

Unlike forage quality and tannins, shrub morphology and biomass were significantly effected by herbivory. Leaf area per leaf was less in the grazed than ungrazed salmonberry and red huckleberry ($P < 0.10$), and the trend was consistent in deerfern, wood sorrel and youth-on-age (Table 3a). Leaf weight was less in grazed than ungrazed salmonberry, and appeared to follow the same trend with deerfern, wood sorrel and youth-on-age (Table 3b). The proportion of leaves relative to twigs in CAG was not effected by treatment ($P > 0.10$) (Table 3c).

Herbivory reduced salmonberry BSD, canopy height, and canopy width, and also reduced red huckleberry height ($P > 0.10$) (Table 4). Herbivory appeared to have a similar effect on plant volume, but the difference between grazed and ungrazed plants was not significant ($P > 0.10$). Leaf and twig biomass per plant was greater in ungrazed than grazed plants ($P < 0.10$), as was biomass per unit height and stem diameter ($P < 0.10$). However the reduction in canopy height and width were proportionately greater than the reduction in biomass, resulting in greater biomass/m^3, or biomass concentration, in grazed than ungrazed shrubs ($P < 0.10$) (Table 4).

Discussion

Vine maple, salmonberry, red huckleberry, and swordfern forage quality and astringency were similar to levels measured in old-growth forests in the MFH during the same sampling periods (Happe et al. 1990). The same sampling and analytical techniques were used in both studies. Crude protein levels in this study were either similar to or lower than the amounts reported by Leslie et al. (1984) in the MFH from 1979 - 1981. Lower CP values in the present study were likely related to forage collection techniques; I collected entire shoots of current annual growth whereas Leslie et al. (1984) collected only plant parts that were eaten by cervids, which often did not include the less nutritious lower/older portions of current years growth. Conversely, IVD values in this study tended to be greater than those

Table 3. Seasonal structural characteristics of selected browse, fern, and herbaceous species inside and outside of exclosures in Olympic National Park, Washington, 1985-1986.

Structural characteristic, and plant species	SUMMER Grazed X	(SE)	SUMMER Enclosed X	(SE)	FALL Grazed X	(SE)	FALL Enclosed X	(SE)	WINTER Grazed X	(SE)	WINTER Enclosed X	(SE)	SPRING Grazed X	(SE)	SPRING Enclosed X	(SE)
Leaf area/leaf (cm^2)																
Vine maple[a]	37.30	(2.61)	36.60	(6.56)	42.60	(3.440	42.30	(7.00)								
Salmonberry[bT]	16.92	(3.69)	48.82	(7.20)	16.95	(3.39)	58.67	(6.20)								
Red huckleberry[cTBS]	2.75	(0.39)	2.97	(0.36)	2.17	(0.32)	2.23	(0.38)								
Deerfern[d]	11.64		33.46		10.89		19.83		13.68							
Wood sorrel[d]	10.15		13.77		12.65		10.81		11.89							
Youth-on-age[e]	20.23		21.03		11.95		.		8.87		23.12		9.55		14.49	
Leaf weight (g)																
Vine maple	0.132	(0.007)	0.135	(0.035)	0.127	(0.032)	0.145	(0.005)								
Salmonberry[T]	0.059	(0.014)	0.176	(0.039)	0.057	(0.010)	0.217	(0.021)								
Red Huckleberry	0.008	(0.001)	0.007	(0.000)	0.009	(0.001)	0.007	(0.000)								
Deerfern	0.071		0.2261		0.087		0.158		0.09		.		0.03		0.09	
Wood sorrel	0.033		0.057		0.059		0.055						0.04		0.05	
Youth-on-age	0.099		0.131		0.092		.		0.092		0.17		0.05		0.082	
Leaf/twig ratio (g/g)																
Vine maple	2.350	(0.20)	3.600	(0.50)	1.120		0.760	(0.70)					3.61	(1.01)	9.17	(4.41)
Salmonberry[S]	1.372	(0.246)	1.879	(0.216)	0.524	(0.171)	0.873	(0.156)					6.89		5.37	
Red huckleberry[BSI]	0.874	(0.068)	1.226	(0.063)*	0.365	(0.115)	0.207	(0.040)					3.97		5.58	

[a] Site 1 only; ANOVA treatment season with 3 subsamples per treatment/season
[b] Site 1,2,3; Anova Treatment main plot, Season subplot, site as replication.
[c] Site 1,2; ANOVA same as with b.
[d] Site 2, no subsamples.
[e] Site 3, no subsamples.

[T] Treatment effect significant at $p < 0.10$.
[B] Site effect significant at $p < 0.10$.
[S] Season effect significant at $p < 0.10$.
[I] Treatment*Season interaction significant at $p < 0.10$.
* Grazed significantly different than Enclosed $P < 0.10$ (LSD test conducted if interaction was significant)

Table 4. Salmonberry, red huckleberry, and swordfern size and standing crop biomass (g/plant) inside and outside of cervid exclosures in Olympic National Park, July 1986.

	Salmonberry				Huckleberry				Swordfern			
	Grazed		Exclosed		Grazed		Exclosed		Grazed		Exclosed	
	X	(SE)	X	(SE)	X	(SE)	X	(SE)	X	(SE)	X	(SE)
Plant dimensions												
BSD (mm)[TI]	7.56	(0.55)	20.16	(4.17)*	11.54	(0.34)	19.14	(4.66)				
Height (cm)[T]	57.23	(4.78)	179.96	(15.10)	74.60	(1.77)	130.02	(19.8)				
Length (cm)[TSI]	44.08	(3.56)	145.41	(13.43)*	42.79	(4.86)	78.26	(8.56)				
Volume (m^3)	0.08	(0.02)	3.35	(1.63)	0.10	(0.02)	0.72	(0.34)				
Biomass												
Leaf biomass[T]	3.89	(0.30)	44.84	(10.8)	2.86	(0.40)	11.46	(6.35)	22.56	(13.25)	69.53	(26.79)
Stem biomass[TSI]	2.88	(0.08)	31.65	(6.91)*	2.55	(0.29)	7.35	(3.04)				
Biomass/bsd (g/mm)[TSI]	0.72	(0.09)	2.90	(0.15)*	0.49	(0.05)	0.95	(0.13)				
Biomass/ht (g/cm)[TSI]	0.12	(0.01)	0.38	(0.06)*	0.07	(0.01)	0.14	(0.03)				
Biomass/vol (g/cm^3)[T]	105.00	(23.4)	35.10	(7.12)	69.70	(17.0)	31.10	(5.50)				

[T] Treatment effect significant, $p < 0.10$, 2-way ANOVA.
[S] Species effect significant, $p < 0.10$, 2-way ANOVA.
[I] Treatment*species interaction significant, $p < 0.10$, 2-way ANOVA.
* Grazed significantly different than Enclosed $P < 0.10$ (LSD test conducted if interaction term was significant).

observed by Leslie (1982); these differences were most likely due to differences in inoculum donor or IVD technique (Pearson 1970).

Herbivory often results in increased forage quality, due to the removal of old tissue and stimulation of regrowth; due to its younger age, regrowth of grazed plants provides more nutrients than older plant tissue (Crawley 1983). However, the amount of regrowth caused by herbivory depends on the amount of herbivory, and the plants ability to regrow following tissue removal. Plants will regrow following moderate utilization, but low utilization may be insufficient to stimulate production, and too much herbivory may reduce a plants ability to regrow. Additionally, plants experiencing stress may not have enough resources to regrow following defoliation (Crawley 1983). I observed few indications of increased nutrient content with herbivory, and the grazing effects that were observed were most prevalent with salmonberry, the most heavily grazed shrub (Study 2). Thus, the level of herbivory on the other shrubs and swordfern may not have been sufficient to induce enough regrowth to improve overall plant forage quality. The observation that improved forage quality occurred only during summer most likely reflects cessation of regrowth with the end of the growing season. As plants senesced, and no longer replaced lost tissue, the herbivores continued to remove the most nutritious tissue, leaving behind poorer quality leaves and twigs. Hanley (1987) also observed no difference in forage quality between browsed and unbrowsed *Vaccinium alaskense* and western hemlock growing in old-growth forests in southeastern Alaska.

Plant tannin concentrations typically increase following herbivory, however, as with forage quality, the response is variable. The ability of plants to respond to herbivory with tannin production may depend on the plants' carbon/nitrogen balance (Bryant et al. 1983), for tannins are carbon-based secondary plant compounds. Plants growing in low-light environments, where there is low carbon availability, typically do not respond to herbivory with large increases in tannin content (Larsson et al. 1986, Bryant 1987). I observed few responses of tannins and tannin astringency to herbivory. This lack of response could be due to a combination of several factors. In a related study, I found decreased tannin content in plants growing under old-growth canopies as compared to clear-cuts (Happe et al. 1990). There may not be enough light under the old-growth canopy to allow plants to increase tannin production in response to removal of tissue by herbivores. Additionally, the level of herbivory in the study area may not have been sufficient to induce

a response in plant tannin content. These theories were supported by the observations that the only plants that had greater astringency in grazed plants were salmonberry, which tended to grow in a higher light environment than red huckleberry, and which also sustained the highest level of herbivory (Study 2), and swordfern in ex3 (the only deciduous forest site) during fall and winter. It may also be that although these enclosed plants were protected from cervid herbivory, they were still being consumed by insects and slugs inside the exclosures, and the level of herbivory by the invertebrates was sufficient to stimulate the production of tannin in plants protected from cervids.

Since HT is a smaller molecule and contains less carbon than CT, and is thus 'cheaper' to produce (Zucker 1983), I expected to find a greater response to herbivory in HT than in CT under the forest canopy. This was not observed, in fact only CT responded to herbivory, however this occurred in swordfern, whose tannin was comprised primarily of CT.

Swordfern is heavily used by cervids in winter and mid-spring (Leslie et al. 1984, Study 2), however swordfern had low digestibility in all seasons. During winter the consumption of swordfern may be primarily due to its great availability relative to other forages, however during spring and early summer there is a great availability of alternative forages (Study 2). My swordfern digestibility results may underestimate true swordfern digestibility, due to my use of the *in vitro* technique, and the influence of tannins in depressing *in vitro* digestibility more than *in vivo* (Hanley and McKendrick 1983, Robbins et al. 1987). Swordfern had the highest amount of CT, and CT has been shown to decrease forage digestibility *in vitro* to a greater extent than HT (Van Hoven 1984). Often the inoculum in swordfern samples died before the incubation was complete, while samples of more nutritious/low tannin samples thrived.

Although the level of herbivory in the study areas did not induce many changes in forage quality, it did reduce plant size, standing crop biomass, and leaf area. Under old-growth canopies in southeast Alaska, deer were also observed to have a greater effect on shrub biomass than on forage quality (Hanley 1987).

STUDY II: EFFECTS OF CERVID HERBIVORY ON HERB AND SHRUB PRODUCTION, NUTRIENT QUALITY, AND BIOMASS CONCENTRATION IN OLD-GROWTH SITKA SPRUCE-WESTERN HEMLOCK FORESTS

From March 1987 through March 1989 I investigated ungulate-forage relationships in old-growth forests in the SFH. In that effort I: 1) determined elk and deer diets, 2) measured cervid utilization of herbs, ferns, and shrubs in understories of old-growth stands, and 3) assessed the effects of cervid utilization on herb, fern, and shrub standing crop biomass, production, nutrient content, and biomass and nutrient concentration.

Methods

Cervid Diets

Botanical composition of cervid diets was estimated using microhistological identification of fecal forage fragments. Fresh elk and deer fecal pellets (less than 24 hrs old) were collected monthly, composited, and were air-dried in the field or were frozen until they could be oven dried at 50°C. Composited samples of elk and deer feces consisted of 10 and 20 pellets, respectively, from each of 10 individuals. In this study area, it appeared that all elk were members of 1 herd. Deer were in small family groups; I never sampled from more than 2 members of a group. Diets were determined for 8 sampling periods, which corresponded to a sub-set of the herb utilization sample periods: Fall 1987 (composited October, November, and December 1987 samples), Winter 1988 (composited January, February and March 1988), and monthly from April 1988 through September 1988.

Fecal composition was determined following the frequency conversion technique described by Sparks and Malechek (1968) and reevaluated by Holechek and Gross (1982). Frequencies of occurrence of each plant taxa were determined from 20 microscopic fields (125x) viewed on each of 20 slides prepared from each fecal sample. Forage fragments were identified to genus except for *Rubus* and *Acer*, which were identified to species. Unidentifiable genera were classified as forbs, ferns, shrubs, or grasses. Microhistological determination of the diets was conducted by a technician who had extensive knowledge of the regional and local flora, and who had amassed over 1000 hrs of experience determining cervid diets from fecal analysis of samples collected in the Pacific Northwest. Similarity of elk and deer diets

was estimated using a percent similarity index (Anthony and Smith 1977, Leslie et al. 1984).

Herbaceous Production and Utilization

Sampling

Herbaceous production and utilization was measured from April 1987 through September 1988. Forage utilization and production were measured in 20 sites each year, with 10 sites associated with each of the 2 0.5 ha exclosures in the SFH. Ten sites were allocated the FS and GS strata (5 sites per strata per 0.5 ha exclosure) (Fig. 3). Sampling was stratified into FS and GS because they were the predominant strata on the old-growth terraces, and there appeared to be large differences in species composition and production between strata. I hypothesized that although strata were intermixed within spruce-hemlock forests, the timing, extent, and impacts of herbivory would differ between the strata.

Sample sites were selected using a restricted randomization process. First, a random location along the exterior fence of 1 of the 0.5 ha exclosures was chosen. Second, a distance between 50 and 400 paces was selected and measured perpendicular to the fence. From that spot the closest suitable sample site was located. A suitable site was 1) on an old-growth spruce-hemlock terrace, 2) not visible from a hiking trail, and 3) the strata patch was large enough so that 3 to 5 utilization plots could be installed. In 1987 3 utilization plots were established at each site (total of 60 utilization plots: 30 GS and 30 FS). In 1988 the sample size was increased to 5 plots per site (total of 100 plots: 50 GS and 50 FS).

Herbaceous utilization and production was measured using the cage comparison method (Klingman et al. 1943). At each plot 3 0.25m^2 sub-plots were chosen based on similarities in herbaceous vegetation (Fig. 3). Heights of all herbaceous species were measured and canopy cover was estimated ocularly in each sub-plot and recorded. One sub-plot was randomly assigned to the clip treatment, and was then clipped for determination of initial biomass. Another sub-plot was assigned to the caged treatment, and was protected from herbivory with a 1x1 m^2 portable cage. The third plot was assigned to the grazed treatment, and was exposed to herbivory. At the end of each sampling period, cover and height were re-estimated on the grazed sub-plot, and biomass in the caged and grazed sub-plots was harvested. Two more sub-plots,

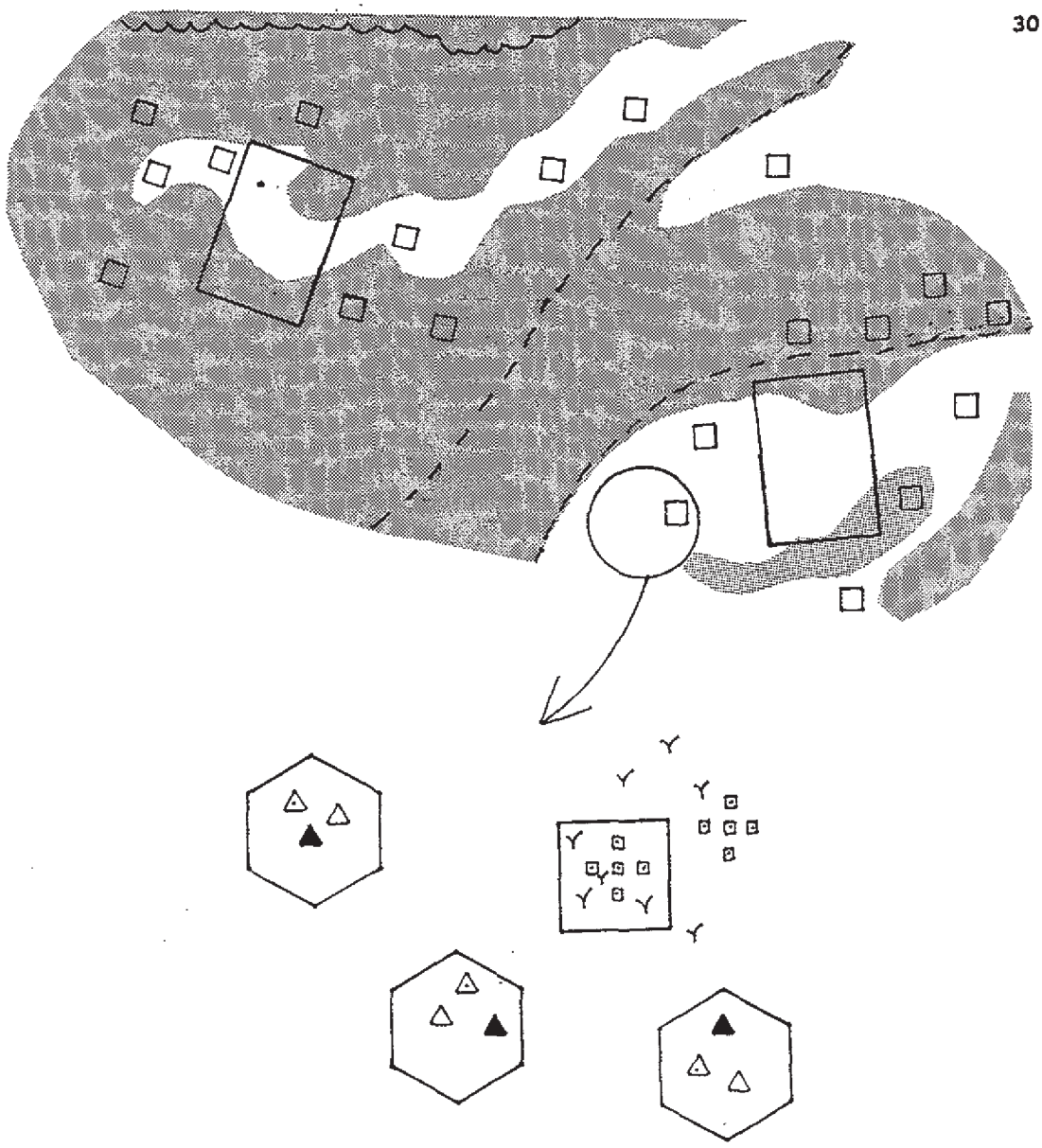


Figure 3. Schematic layout of sampling scheme during 1987, not drawn to scale. □ 0.5 ha exclosure, ○ site, ⬡ utilization plot, ▲ △ △ caged, grazed, and clipped utilization sub-plots, □ annual exclosure, ⊡ annual exclosure sub-plot, Y shrub stem, FS strata, GS strata, ∿∿ valley wall, – – – terrace edge.

similar in species composition, height, and cover to the grazed sub-plot, were selected, and species cover and height estimated and recorded. The grazed sub-plot from the prior sample period was then used as the clipped sub-plot for the subsequent sample period and the 2 newly selected plots were randomly assigned to the grazed or caged treatment. Cervid utilization of the herbaceous layer was measured in this sequential fashion from April 1987 through September 1988. Sampling periods were monthly from April through September in both 1987 and 1988, and once in December 1987. Plots were relocated to new sites in April 1988.

Clipped vegetation was sorted in the field and was later oven dried at 60°C and weighed. Graminoids were separated into grasses, *Carex*, *Scirpus*, and *Luzula*. Ferns were sorted to genus. Major forbs were sorted to species, but uncommon and low biomass forbs were combined into a miscellaneous category. Major forbs included buttercup (*Ranunculus repens*), foamflower, wood sorrel, and strawberry-leaf blackberry (*Rubus pedatus*). Dry weights were multiplied by 4 to convert to a m^2 basis.

Data Analysis

The hypotheses that herbaceous biomass, production and utilization 1) did not differ from 0, and 2) did not vary between years, strata, and sample periods were tested with ANOVA using the Statistical Analysis System (SAS). All hypotheses were tested for total herbaceous species, for forage categories (graminoids, grass, forbs and ferns), and for selected key species. Variables calculated included:

1) Utilization, or biomass consumed, in grams = biomass in caged sub-plot (at t_i) - biomass in grazed sub-plot (at t_i);
2) Actual production (aPn McNaughton 1985) = biomass in caged sub-plot (t_i) - biomass in clipped sub-plot (t_{i-1}).
3) Grazed production, or net production under grazing (gPn McNaughton 1985) =biomass in grazed sub-plot (t_i) - biomass in clipped sub-plot (t_{i-1}): also actual production-utilization.
4) Percent available biomass consumed = utilization (from t_{i-1} to t_i) /biomass cage sub-plot(t_i).
5) Percent actual production consumed = utilization /actual production.

6) Percent production = actual production (from t_{i-1} to t_i) /biomass cage sub-plot(t_i).

Using this manner of measurement, actual production is net production, for it is the sum of new biomass produced minus the weight of old biomass senesced. Similarly, the utilization calculations can not measure the material consumed before it would have senesced, and thus will underestimate utilization over long sample intervals when material is senescing (i.e., fall).

Because it was impossible to match the 3 sub-plots perfectly, initial biomass of forage classes and key species often differed between treatments. Therefore, I used analysis of covariance (ANCOVA) to adjust for initial differences in biomass; monthly estimates of biomass in the 3 treatments (caged, grazed, and clipped) were derived for each site using ANCOVA. In each analysis I tested the effect of 3 covariates (cover, volume, and cover*square root of height) in randomized block ANCOVA, with plot as block and sub-plot type (caged, grazed, or clipped) as treatment. I evaluated the significance of covariates at $P < 0.20$ to guard against unacceptable risks of making Type II errors, because the F test for the covariate had 1/1 degrees of freedom. If more than 1 covariate was significant, the covariate with the greatest P-value was selected. If a covariance was significant, I used the adjusted biomass mean (lsmean), produced by the ANCOVA, as monthly estimates of biomass for each site. Monthly estimates were derived for total herbaceous biomass, forage categories, and key species.

The monthly lsmeans files were combined, estimates converted to a uniform 30-day month basis, and utilization, actual production, grazed production, percent biomass consumed, and percent production calculated for each plot and month. I tested the hypotheses that biomass, utilization, and production did not vary between years or months, using repeated measures ANOVA (year as main plot; model = year site(year) month month*year; year tested with site(year) as an error term). Production and utilization lsmeans were tested for the hypothesis that they were = 0. If a mean was not = 0, then it was concluded that utilization or production was significant. If the year*month interaction term was significant, Fishers' LSD tests were used to compare means within a given month between years. Significance was evaluated at $P < 0.05$.

Total production and utilization were estimated for each site during summer (April-August) and year-round (April-March). Total utilization was determined by summing over all sample periods; total

actual production and grazed production were the sum of positive production values. The hypothesis that year and strata had no effect on standing crop biomass, production, and utilization was tested with ANOVA (model = year strata year*strata).

The Influence of Season-Long Exclusion of Cervids on Herbaceous Forage

Sampling

The influence of season-long exclusion of cervids on herbaceous biomass, production, nutrient content, and biomass concentration was measured using annual exclosures. In 1987 and 1988 I constructed 20 5x5 m^2 cervid exclosures. Each exclosure was 1.83 m tall and was constructed of woven metal fencing and 8 metal T-posts.

The annual exclosures were installed at the same sites as utilization plots (Fig. 3). At each site 2 5x5 m^2 plots were chosen based on similarities in herbaceous and shrub vegetation. Each plot had at least 16 rooted stems of either red huckleberry (FS sites) or salmonberry (GS), and were accessible to herbivores. The paired plots were then randomly assigned to either the enclosed or grazed treatment. Canopy closure at each enclosed plot was estimated using a spherical densiometer during June 1990.

The annual exclosures were constructed from 30 March - 1 April 1987. The annual exclosures were kept in place during the entire 1987-88 growing season and were relocated between 23-25 March 1988. Soon after the exclosures were established each year, initial cover and height of herbaceous species were measured in 0.25 m^2 sub-plots in the enclosed and grazed plots (Fig. 3). In 1987 5 0.25 m^2 sub plots were laid out in a cross pattern in the enclosed and grazed plots. In 1988 the number of sub-plots was increased to 12, laid out in either 2 parallel lines of 6 0.25m^2 plots each, or 3 lines of 4 plots.

Each year during estimated peak standing crop biomass (1987: 13-18 August FS and GS; 1988: 22-26 July FS, 18-25 August GS), plant cover and height were re-measured and biomass harvested on 3 (1987) or 5 (1988) sub-plots on both the enclosed and grazed plots at each site. Plant samples from each sub-plot were sorted in the field, wet weights were recorded, and the samples composited by species over site and treatment. A sub-sample of each composite sample was frozen within 6-36 hours after clipping, and was later lyophilized for use in forage quality analysis. The remaining portions of each composite were oven dried and weighed for percent dry matter and biomass determinations.

All wet weights were multiplied by percent dry matter and converted to a dry matter basis, and then multiplied by 4 to convert to a m^2 basis. In the analysis I omitted the weights of *Pteridium aquilinum* because its distribution was too variable to measure in plots 0.25 m^2 in size.

Prior to the onset of the growing season, at the estimated time of minimum standing crop biomass (1988: 8-13 March; 1989 6-10 March), I reestimated plant cover, measured plant height, and harvested biomass on 2 (1988) or 5 (1989) sub-plots per site and treatment. Once again the samples from each sub-plot were sorted to species and weighed. Selected samples were composited over species/ site/ treatment, and a sub-sample frozen for forage quality analysis.

Laboratory Analysis

Frozen plant tissue was lyophilized at -10 C and ground through a 1 mm screen in a Wiley mill. Total N was assayed on Buchi distillation and control units (models 322 and 343 respectively). Two-stage IVD was determined (Tilley and Terry 1963) with inoculum from a fistulated heifer on a diet of ryegrass hay supplemented with 4.54 kg of grain per day. Forage quality assays were run on samples from each site in which 2 or more grams dry material was available from both treatments. If there was less than 2 grams, plant material was composited (within treatments) with other exclosures that had low biomass availability. Some rare plant species were composited across treatments within a season if there was less than 2 grams available for the sample period (this was more common for winter than summer samples).

Data Analysis

Analysis of variance was used to test the hypotheses that cervid exclusion, year, and strata had no effect on standing crop biomass, mean plant height, biomass concentration, CP, IVD, CP concentration, and IVD concentration of herbaceous forages. All hypotheses were tested for total herbaceous species, forage categories, and key species, during both summer and winter (maximum and minimum standing crop biomass).

New variables calculated included:

1) Biomass concentration per m^3, using plant height and 100% cover to define volume.

2) CP concentration per m^3 = (% CP/100)*biomass concentration.

3) IVD concentration per m^3 =(% IVD/ 100) * biomass concentration.

When calculating CP and IVD concentration for total herbaceous biomass and forage categories, if forage quality was not determined for a species in a particular site and treatment, I used 1) values for that species at the nearest site and treatment within the same sample period and year, 2) values for the same species in another year, but same sample period and treatment, or 3) mean values for the most similar species. Comparisons of CP and IVD between treatments within a species were made only with sites where forage quality was actually measured.

The influence of herbivory, year, and strata on herbaceous forage was examined for each season (summer and winter) using plot means and split plot ANOVAs; year and strata were main plots and treatment was a split plot (MODEL: year strata year*strata plot(year*strata) treatment treatment*year treatment*strata treatment*year*strata treatment*plot(year*strata); the plot(year*strata) term used as the error term for year, strata, and year*strata). Covariance was not used in this model because in addition to adjusting for difference in initial cover between treatments, it also adjusted for initial differences in cover between strata, resulting in an over-estimated of biomass in FS and underestimate in GS. Also, in this analysis I used balanced ANOVAs; i.e. a forage category or species had to be in both treatments in a site for the site to be included. The maximum sample size in this analysis was 40, however sample size was less in some cases because not all species or forage categories occurred in each site.

Effects of Herbivory on Herbaceous Forage

The interactions between varying levels of cervid herbivory and herbaceous production, biomass, and forage quality was examined by ANOVA and regression analysis, using data from herbaceous utilization cages and annual exclosures. Seasonal levels of herbaceous utilization and production were determined for summer 1987 and 1988 (April-August) and winter 1987 (April 1987 - March 1988) by summing monthly estimates obtained from the utilization cages. Seasonal estimates of utilization and production correspond to the sample intervals for the annual exclosures.

The following new variables were calculated:

1) Enclosed production: (cPn McNaughton 1985) = biomass inside the exclosure at maximum standing crop biomass - initial clipped weight (from April clipped utilization plot).

2) S: effect of grazing on production (McNaughton 1985) = actual production - enclosed production.

The hypotheses that herbivory and year had no effect on herbaceous production was tested with a split plot ANCOVA, using initial canopy cover as a covariate if it was significant (model=year plot(year) treatment year*treatment covariate) for each strata. Herbivory treatments were actual production, grazed production, and enclosed production; if the treatment effect was significant, then Fisher's LSD tests were run to test for over (actual production > enclosed production), exact (actual production = enclosed production), or undercompensation (actual production < enclosed production) in grazed plant production.

Relationships between biomass, production, and utilization were examined with regression analysis. The relationships examined include:

1) The correlation between enclosed production, actual production, and utilization with canopy cover, to test the influence of forest canopy on production and utilization.

2) The correlation between actual production and enclosed production, to see how actual production is influenced by intrinsic productivity.

3) The correlation between utilization and enclosed production, to see how herbivory is influenced by intrinsic productivity.

4) The relationships between utilization and percent biomass consumed with actual production, to see if the cervids consumed greater amounts, or greater portions, of biomass in productive sites.

5) The relationships between utilization and percent biomass consumed with S, to see if herbivory had a stimulatory or depressing effect on production.

6) The relationship between percent production and percent biomass consumed to examine the relationship between production and herbivory on an equal biomass basis.

If scatter plots of the data revealed that the relationship was non-linear, I tested both linear and polynomial models, and selected the

best model using MAXR in SAS (the model chosen was a significant model ($P < 0.05$) with the highest r^2).

Shrub Production, Utilization, and Nutrient Content

Sampling

Shrub production, utilization, biomass, nutrient content, and morphology were measured on shrubs growing within and adjacent to the annual exclosures. In May of 1987 and 1988, soon after the shrubs set forth new shoots, I randomly selected 4 (1987) to 8 (1988) rooted stems within each of the annual exclosures and assigned them to the manipulated treatment. The presence and location of similar plants within the exclosure, which would serve as ungrazed controls, were noted. In GS sites I selected salmonberry stems, and in the FS sites I selected red huckleberry and blue huckleberry stems, however blue huckleberry was not available in all 10 FS sites. Shrub basal stem diameter (BSD) and height were measured and recorded, and each plant was tagged. Outside the exclosures, shrubs as similar as possible to the manipulated plants (in BSD, height, growth form, and vigor) were found, measured, tagged, and assigned to the grazed treatment. The amount of utilization on each grazed plant was then recorded. Utilization was recorded by tallying the total number of new shoots in each of the following size categories: <1 cm, 1-5 cm, 5-10 cm, 10-15 cm, 15-20 cm, and >20 cm. If a twig was browsed, I recorded the length of twig remaining and its pre-browsed size class, estimated through use of position on the plant, length of twig remaining, and twig BSD. For twigs on which only leaves were consumed, I recorded the number of leaves removed. Plant tissue from stems within the annual exclosures assigned to the manipulated treatment was then removed in a fashion to mimic the utilization observed on the grazed treatment stems. First I counted number of twigs in each size class, then clipped a similar proportion of leaves and twigs in each size-class to the same remaining twig length as was observed on the paired plant outside the exclosure. Twig numbers, length, and manipulation (estimated utilization) were recorded. Tissue removed from each plant was labeled, oven dried, sorted into leaf and stem components, and weighed. In later months I recorded the availability and utilization of regrowth. Shrub utilization measurements were repeated monthly until the plants were harvested at the end of the growing season, at maximum standing crop biomass. The end of the growing season was

determined when 1) regrowth shoots ceased to appear and 2) prior to the onset of leaf abscission.

For each shrub species, a rooted stem was designated as the experimental unit, but I manipulated all connected rooted stems on shrubs inside the annual exclosure, in case that if a stem was not browsed, it would affect the regrowth potential of connected, browsed stems. Manipulated stems within the annual exclosures were not independent, however the degree of connectiveness was often hard to determine; often more than 1 species grew in 1 clump. Grazed stems usually were on separate plants, scattered around all sides of the annual exclosure.

At the end of the growing season (1987: red huckleberry and blue huckleberry 26/08 - 2/09, salmonberry 3 - 6/09. 1988: red huckleberry, blue huckleberry 11-18/08, salmonberry 18-27/08) I measured the following shrub dimensions: BSD, height of current years growth, height of last years growth, rooted height, distance from soil to lowest portion of the crown, and crown length (max diameter) and width (diameter perpendicular to the length). I then harvested all the current annual growth (CAG) on the grazed, manipulated, and ungrazed control shrubs. In 1987 plant tissue from each of the 3 treatments was separated into leaf and twig components, oven dried, and weighed. In 1988 plant tissue was weighed in the field, and a sub-sample frozen within 6-48 hours after collection. The sub-samples were later lyophilized at -10, separated into leaf and twig components, weighed, and composited over site/ treatment/ plant part. Composite samples were ground through a 1 mm screen, and analyzed for CP and IVD following the methods used for analyzing herbaceous forage quality.

Data Analysis

The hypotheses that cervid herbivory had no effect on shrub biomass, production, forage quality, or morphology was tested using ANOVA and regression analyses. The following variables were calculated:

1) Utilization = sum of the weight of tissue removed monthly from the manipulated plants. This is an estimate of utilization during the growing season only.
2) Actual production = end of season weight of CAG on manipulated plant + utilization.
3) Enclosed production = weight of control plant CAG.

4) Grazed production = weight of grazed plant CAG (also = weight of the end of season CAG on the manipulated plant.)

5) Plant volume (m^3) = 3.14159*length*width*(height-beginning of crown))/4)/1000000

6) Biomass concentration = weight CAG/vol (g/m^3).

7) CP concentration= biomass concentration*(CP/100)

8) IVD concentration= biomass concentration*(IVD/100)

9) Leaf twig ratio=biomass or production of leaves/biomass or production of twigs.

The hypotheses that herbivory and year had no effect on shrub maximum standing crop biomass, production, height, height growth, biomass concentration, CP, IVD, CP concentration, and IVD concentration were tested using split plot ANOVA (model = year plot(year) treatment year*treatment) on plot means, using BSD or height in the prior year as a covariate if it was significant ($P < 0.20$). The effect of year on utilization and percent production consumed was also tested with one-way ANCOVA (model= year BSD). In analyses of production, biomass, and morphology, plot means were determined using only those shrubs which were grazed. For tests on utilization and percent production consumed, plot means were derived using all shrubs. All analyses were conducted for leaves, stems, and combined biomass. Additionally, in 1988 the effect of herbivory on red huckleberry berry production was also measured.

Finally, I used regression analyses to examine the relationships between canopy closure, plant size, production, and utilization. Regression analyses were similar to those run for herbaceous biomass. If the scatter plot indicated a curvilinear relationship, I tested polynomial equations using MAXR on SAS, and selected the best significant model.

Swordfern Production, Utilization and Nutrient Content

Sampling

Swordfern production and utilization, and the influence of cervid herbivory on swordfern biomass, production, morphology, and forage quality was also examined using plants in and adjacent to the annual exclosures. Because of its large size, clumped distribution, and dietary importance, swordfern was treated like a shrub. Swordfern grew in both strata, and was sampled in each exclosure in which it occurred.

In May of each year, when I initiated measurements of shrub utilization, I randomly selected one-half (up to 4) of the swordferns inside each annual exclosure to serve as manipulated plants. Number and mean length of the previous years fronds were recorded. I then sought pairs outside the exclosure, based on frond number, size, vigor, strata, and past browsing level. The number of previous years fronds on the grazed plants were recorded, as were the numbers of current years fronds, partial fiddleheads, and fiddleheads. I then recorded the number of each frond category that was browsed, and the amount of frond tissue that remained after herbivory. I returned to the manipulated plants, counted the numbers of current years fronds in each category, and mimicked the utilization observed on the outside plants. Tissue removed from each plant was bagged, oven-dried, and weighed. Utilization was recorded monthly throughout the growing season.

At the end of the growing season (1987: 21-22/09, 1988: 7-12/09) I harvested the manipulated plants, grazed plants, and ungrazed controls inside the annual exclosure. Fern fronds were separated into current and previous years fronds (the determination was made based on appearance, and records of frond number recorded at the onset and during the growing season). I then tallied the number of current years and previous years fronds for all 3 treatments. In addition, the number of browsed and unbrowsed current and previous years fronds were separated in the grazed and control treatments. In 1988 I also separated out weights of fiddleheads at the end of the season. After sorting, weights were recorded separately for each category for all 3 treatments.

In 1988 samples were frozen soon after collection, and later lyophilized. Plants were composited over site/ treatment/ frond type, and CP and IVD from control and grazed plants were determined.

Data Analysis

The hypotheses that cervid herbivory had no effect on swordfern biomass, production, forage quality, or morphology was tested using ANOVA and regression analyses. Data from swordfern were treated in a similar fashion as shrub data. The following variables were calculated:

1) Utilization = sum of utilization over growing season.
2) Actual production = utilization + end of season biomass of current years fronds of the manipulated plant.

3) Enclosed production = end of season (maximum standing crop) biomass current years fronds of control plant.
4) Grazed production = end of season biomass of current years fronds of grazed plant.
5) Percent production consumed = utilization/actual production.
6) Percent biomass consumed = utilization/weight control plant.
7) S = actual production - grazed production.
8) Weight CP per plant = mean swordfern biomass per plot (%CP/100)
9) Weight IVD per plant = biomass * (IVD/100)
10) Number of current years fronds
11) Number of previous years fronds
12) Mean frond weight = plant biomass/ number of current years fronds.
13) Mean unbrowsed frond weight = weight unbrowsed fronds/ number of unbrowsed fronds.

The hypotheses that strata, year, and herbivory had no effect on swordfern biomass, production, and frond number was tested with split-plot ANOVAs, using previous years number of fronds as a covariate if it was significant (model =year strata y*s plot(year*strata) treatment t*s t*y t*s*y). The hypotheses that strata and year had no effect on utilization and percent production consumed was tested with ANOVA (model =strata year strata*year). Because I did not measure plant volume, I could not calculate biomass concentration. The effect of utilization on production, biomass and forage quality was examined using plot means derived only from browsed plants. Tests on utilization and percent production consumed were done using plot means derived from both browsed and unbrowsed plants.

Regression analysis was used to examine the relationships between utilization and production, forage quality, canopy closure, and number of fronds per plant. Relationships examined were similar to those run for herbaceous forage.

Results

Cervid Diets

A total of 64 genera were identified in deer and elk feces in the SFH, from fall 1987 through summer 1988 (Table 5). The unknown forb category was comprised primarily of fragments too small to determine genus, but which were identifiable as forbs. The majority

Table 5. Elk and deer diets (percent) in the South Fork Hoh, Olympic National Park, as determined from fecal analysis, October 1987 - September 1988.

	ELK									DEER								
Plant	Fall	Wint.	Apr.	May	June	July	Aug.	Sept.	MEAN	Fall	Wint.	Apr.	May	June	July	Aug.	Sept.	MEAN
Boykinia			0.2		0.8	3.1		1.3	0.7	0.1	0.6	0.6		1.5	2.7	0.2	0.3	0.7
Cerastium	1.6	1.1	1.8	0.3	1.8	1.4	1.4	2.0	1.4	0.7	0.7	0.8	1.2	1.1	1.0	0.3		0.7
Cirseae			0.8	2.6	1.8	2.5	1.1		1.1	0.2			2.2	0.5	1.7	1.2	0.3	0.8
Cornus	0.9	0.6	0.5		1.9	0.4		1.6	0.7	1.6	2.4	0.5	1.3	1.2	2.0		1.8	1.3
Fragaria	0.1			1.7	1.7	1.7	1.3	1.5	1.0	2.3			3.6	1.9	3.1	2.3	2.0	1.9
Hypocharus		0.2	0.5	2.2	4.3	2.1	4.1	1.2	1.8	1.0	0.4	0.7	0.9	1.7	0.8	3.0	2.4	1.4
Oxalis	2.7	0.2	1.9	10.4	10.3	7.8	4.1	6.6	5.5	1.6	1.1	13.5	6.5	11.9	8.0	7.0	9.3	7.3
Ranunculus	1.5	0.7	0.6	1.0	1.9	2.7	1.2	2.7	1.5	1.5	1.5	0.5	1.1	1.2	2.9	1.9	2.5	1.6
Rubus pedatus	2.4	1.9	1.8	3.0	0.7	1.0	1.4	0.6	1.6	5.7	4.8	3.4	6.8	1.1	7.9	2.1	7.4	4.9
Tiarella	1.3	0.7	1.5	1.1	1.5	0.9	0.7	2.0	1.2	4.4	2.2	1.6	1.9	3.0	2.0	0.9	4.4	2.5
Tolmiea	0.9	1.3	0.7	0.2	1.6	0.7	0.3	1.5	0.9	2.6	5.0	3.3	2.0	5.4	1.1	1.4	1.5	2.8
Trifolium	4.6	0.6		1.8	2.5	5.6	2.0	1.6	2.3	1.6	0.4	1.9	2.5	2.3	1.3	0.7	2.4	1.6
Misc. forbs[a]	3.7	3.2	1.7	4.4	3.4	4.6	4.9	4.4	3.8	3.7	2.6	3.0	3.4	1.7	4.8	2.5	4.4	3.2
Unknown Forbs	7.5	9.1	8.8	13.9	11.4	10.7	11.3	9.1	10.2	7.9	13.2	11.6	16.4	10.1	8.9	9.0	7.7	10.6
TOTAL FORBS	27.1	19.6	20.7	42.6	45.4	45.1	33.8	36.2	33.8	34.9	34.7	41.4	49.8	44.3	48.1	32.4	46.3	41.5
Agrostis	5.3	5.7	2.9	5.2	10.0	8.2	13.3	7.3	7.2	0.8	1.9	0.3	0.4	0.9	0.7	2.8	1.2	1.1
Dactylis	0.8	2.2	0.6	1.8	2.4	2.3	0.4	2.0	1.6	0.1	0.2	0.4		0.3		1.1	0.3	0.3
Elymus	0.2			0.1	0.2	1.0	3.0	0.2	0.6					0.1		0.3		0.1
Poa	0.4		1.1	1.2	1.4	2.9	6.9	1.4	1.9	0.3		0.3	0.4		0.2	1.3	0.2	0.3
Misc. grasses[b]	1.6	1.7	4.0	1.5	1.9	3.4	1.1	5.7	2.6	0.4	0.9	1.0	0.1	1.2	0.4	0.1	0.2	0.5
Unknown grass	2.0	4.0	3.5	3.9	3.9	4.9	4.9	6.7	4.2	0.7	1.0	2.6	1.1	1.5	0.6	1.2	1.5	1.3
TOTAL GRASSES	10.3	13.5	12.1	13.6	19.7	22.7	29.6	23.3	18.1	2.3	4.0	4.5	2.1	3.9	1.8	6.8	3.4	3.6
Carex	1.6	2.2	3.5	3.5	2.6	2.1	4.4	3.9	3.0	1.0	2.1	1.9	1.5	0.9	0.7	0.1	0.7	1.1
Luzula	0.5	1.6	2.2	1.1	0.9	1.1	1.5	1.2	1.3	0.2	0.1	0.2	1.1	0.2	0.3	0.3	0.4	0.4
Scirpus	1.7	2.3	7.3	1.5	0.7	2.1	0.1	2.4	2.3	0.2	3.4	3.7	0.5	0.5	0.2	0.2	0.6	1.2
TOTAL SEDGES[c]	3.9	6.4	13.0	6.1	4.2	5.3	6.0	7.5	6.6	1.3	5.6	5.8	3.6	1.6	1.2	0.7	1.7	2.7
Athyrium	0.1	0.4	0.9		0.5	0.2		3.7	0.7	0.2	1.0	1.0		2.1	0.9	0.2	0.2	0.7
Blechnum	3.1	2.5	2.1	0.1		0.1		0.4	1.0	0.1	0.7	0.5	0.1	0.4	0.1			0.2
Polystichum	1.4	9.8	6.2	12.6	3.6	1.2	0.5	1.0	4.5	0.8	6.9	1.2	7.6	1.5	1.1	0.6	0.9	2.6
Misc. Ferns[d]	1.3	0.8	0.7	2.8	2.4	1.5	0.7	2.3	1.5	1.0	0.5	1.7	1.9	3.0	1.5	0.3	1.3	1.4
TOTAL FERNS	5.9	13.4	9.9	15.5	6.4	3.1	1.2	7.4	7.8	2.1	9.1	4.4	9.6	6.9	3.7	1.1	2.4	4.9

Table 5. Continued.

	ELK									DEER								
Plant	Fall	Wint.	Apr.	May	June	July	Aug.	Sept.	MEAN	Fall	Wint.	Apr.	May	June	July	Aug.	Sept.	MEAN
Acer circinatum	1.3	0.2	1.0	1.6	3.1	2.4	3.7	2.6	2.0	0.4	1.1	0.7	1.2	2.6	0.4	0.7	1.3	1.1
Alnus rubra	17.9	0.3	1.9	1.2	1.5	2.5	8.3	5.1	4.8	21.5	3.0	1.8	7.7	3.1	11.7	28.0	12.3	11.1
Populus	1.1	0.2		1.0	0.3	0.1	0.3	0.2	0.4				3.9	2.1	0.2	0.2	0.2	0.8
Rubus spectabilis	4.0	0.4	0.3	0.9	4.9	4.5	2.4	2.4	2.5	5.9	4.2	3.5	2.2	9.1	9.2	4.8	8.6	5.9
Rubus ursinus		0.4	0.1	0.7	0.4	0.1	1.4	1.1	0.5		1.0	0.4	5.5	2.0	3.6	2.9	1.1	2.1
Salix	2.7		0.1	1.2	0.5	5.0	3.9	2.3	2.0	2.5		0.2	1.2	3.8	5.4	12.5	5.8	3.9
Vaccinium	2.0	1.2	2.0	3.8	1.2		0.5	0.1	1.3	0.9	3.5	6.2	3.0	5.3	0.5	2.2	0.3	2.7
Misc. Shrubs[a]	0.0	0.0	0.1	1.0	3.1	0.9	0.3	0.2	0.7	0.3	0.2	0.0	1.7	1.7	3.0	0.5	1.0	1.1
Unknown shrub	5.3	6.6	6.4	4.2	5.4	5.0	5.0	5.0	5.4	6.1	7.0	9.5	5.9	5.5	7.4	5.4	8.5	6.9
TOTAL SHRUBS	34.4	9.3	11.9	15.5	20.4	20.5	25.7	19.0	19.6	37.7	20.1	22.4	32.4	35.1	41.3	57.2	39.2	35.7
Picea	3.3	9.1	7.6	1.1	1.0	1.2	1.0	1.4	3.2	2.9	8.1	5.5		2.1	1.4	0.4	1.3	2.7
Pseudotsuga	2.0	4.1	1.8	0.4	0.2	0.4			1.1	2.3	0.8	1.5	0.2	1.0			0.5	0.8
Thuja	6.7	7.2	12.0	0.4	0.9	1.1		1.5	3.7	11.1	8.4	4.8	0.6	2.5	1.9	0.5	3.8	4.2
Tsuga	6.5	17.5	11.1	4.8	1.8	0.7	1.7	3.4	6.0	5.5	9.2	9.8	1.9	2.7	0.7	0.6	1.4	4.0
TOTAL CONIFERS	18.6	37.9	32.4	6.7	3.8	3.4	2.7	6.4	14.0	21.8	26.4	21.6	2.7	8.2	4.1	1.5	6.9	11.6
% DIET OVERLAP	72.0	65.0	60.0	58.0	60.0	57.0	50.0	57.0	62.8									

[a] Includes: Artemesia, Cirsium, Dicentra, Disporum, Epilobium, Galium, Lystichum, Maianthemum, Mimulus, Mitella, Montia, Oenanthe, Polygonum, Prunella, Smilacina, Stachys, Stellaria, Veronica, Viola
[b] Includes: Bromus, Deschampsia, Festuce, Holcus, Phleum, Tricetum
[c] also includes Juncus
[d] Includes: Dryopteris, Equisetum, Gymnocarpium, Pteridium
[e] Includes: Acer macrophyllum, Pyrus, Rosa, Rubus leucodermis, Symphoricarpus

of the unknown shrub category was twig tissue. Dietary overlap between elk and deer averaged 63%, and was greatest in the fall (72%) and least in July (50%) (Table 5).

Both elk and deer diets were usually dominated by forbs (Fig. 4, Table 5); forbs comprised 34 and 41%, respectively, of elk and deer annual diets. Key forb species included wood sorrel, buttercup, strawberry-leaf blackberry, and foamflower (Table 5). Use of forbs was lowest in the fall and winter for both deer and elk, increased during spring, and decreased during August.

Elk tended to consume more graminoids than deer; grass comprised 18.1% of elk and 3.6% of deer annual diets and sedges were 6.6% of elk and 2.7% of deer annual diets (Fig. 4, Table 5). Key grass genera included bentgrass (*Agrostis*), orchardgrass (*Dactylis*), wildrye (*Elymus*), and bluegrass (*Poa*) (Table 5). For both herbivores, use of grasses was greatest in August, and use of sedges greatest in the winter and April.

Ferns comprised 7.8 and 4.9% of annual elk and deer diets (Fig. 4). Ladyfern (*Athyrium filix-femina*), deerfern, and swordfern were seasonally important components of cervid diets. Ladyfern was consumed primarily in the summer, and deerfern in the fall and winter. Swordfern comprised 9.8 and 6.9% of elk and deer winter diets, respectively, and in May it again was important, comprising 12.6 and 7.6% of elk and deer diets (Table 5).

Deciduous browse comprised 19.6 and 35.7% of elk and deer diets respectively (Fig. 4). For both species, use of browse was least in the winter. Elk use of deciduous browse was greatest in the fall, whereas deer use of browse was greater than 33% of their diet from June through the fall. In both ungulate diets red alder was the most important deciduous browse species, and was consumed primarily in late summer and fall. Salmonberry was the second most important browse: it was 2.5% of elk and 5.9% of deer diet. Use of salmonberry by both species was greatest in June and July. Huckleberry (*Vaccinium* species) was used by both cervids, but it was only 1.3% of elk and 2.7% of deer diets. Use of huckleberry by both ungulates occurred primarily in spring and early summer (Table 5).

Coniferous browse, particularly western cedar (*Thuja plicata*) and hemlock, was also an important component of both species diets (Fig. 4). Although it was consumed throughout the year, use of coniferous browse peaked during winter for both species, when it was 37.9 and 26.4% of elk and deer diets respectively. Coniferous browse was also important during fall and early spring (Table 5).

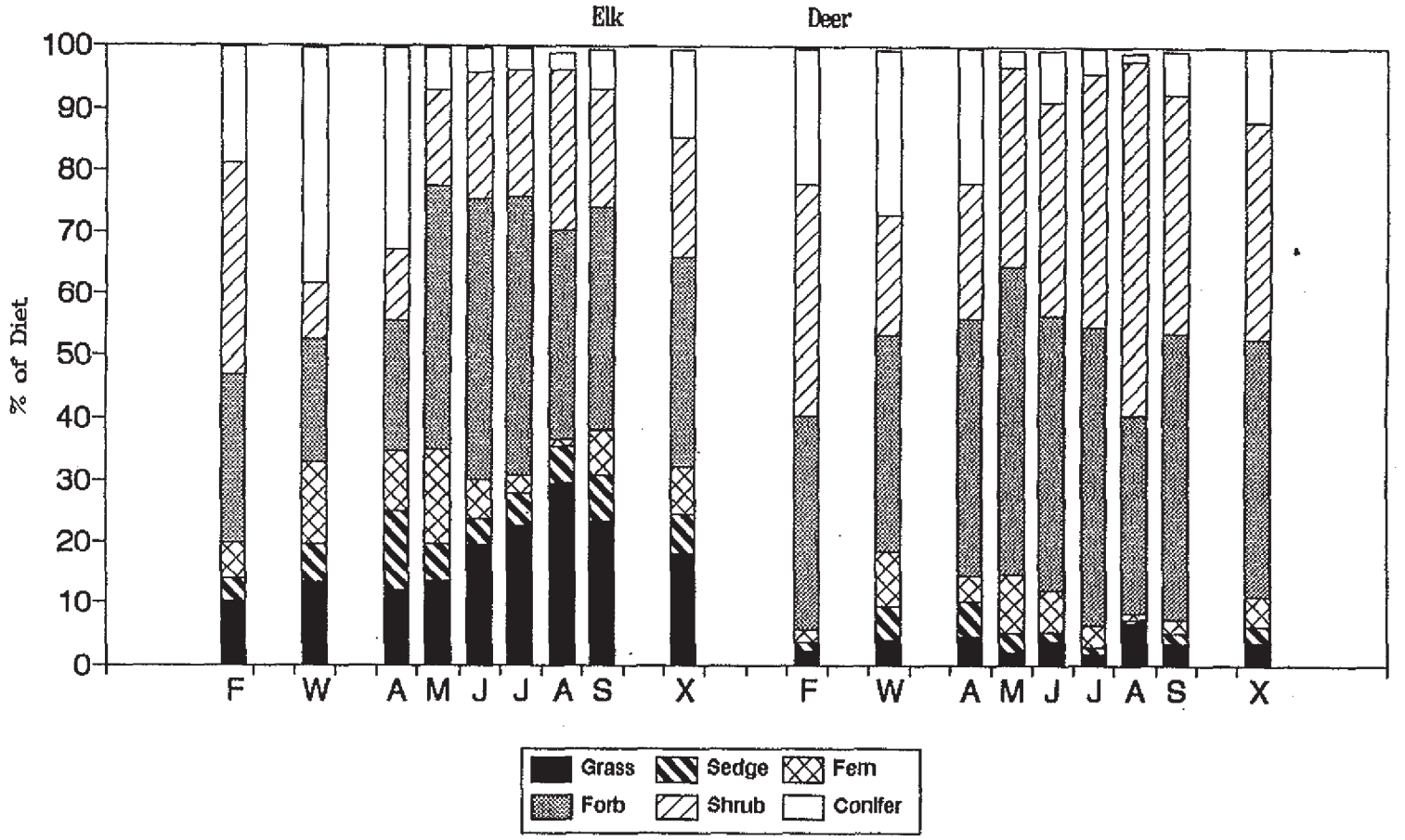


Figure 4. Percent composition of elk and deer diets in the South Fork Hoh during fall (F) and winter (W) seasons and monthly between April and September, 1987-1988.

Herbaceous Forage

Standing Crop Biomass and Species Composition

More herbaceous biomass was available in GS than in FS ($P = 0.0001$), however the degree of difference varied with the seasons (Fig. 5a). Difference in biomass between strata was greatest in late summer (September) and was least during spring (April). Both strata had similar patterns of increasing biomass throughout the growing season, however biomass in the FS was more uniform over the seasons; the difference in peak versus low biomass was much greater in GS sites (126 versus 39 grams per square meter (g/m^2) than in FS sites (22 versus 9 g/m^2). There was no significant difference in mean biomass between years in each strata ($P > 0.05$). In GS, however, available biomass was less in June and July 1988 than in 1987 ($P < 0.05$). In FS, there was less biomass available in July and September 1988 than 1987 ($P < 0.05$). In both years of study, peak standing crop biomass occurred in September in GS and in July in FS. However, in 1987 there were 2 peaks, during July and September, in both strata (Fig. 5a).

Herbaceous biomass in GS was dominated by grass and other graminoids in all seasons (Fig. 5b); grass comprised from 52% (April) to 78% (September) of standing crop biomass in the GS. *Carex* and other sedges comprised about 5% of GS biomass in all months. Ferns comprised on average 8.5% of GS biomass. The dominant fern in GS May through August was ladyfern, which comprised an average of 3% of GS biomass, but senesced in September. Deerfern was also present in GS in small amounts. Deerfern comprised 12% of biomass in GS during fall and winter, when forb and grass biomass decreased. The remaining biomass in GS (mean = 21%) consisted of forbs (Fig. 5b), predominantly buttercups (primarily *Ranunculus repens*, but *Ranunculus uncinatus* was also present) (2 to 12% monthly biomass) and foamflower (1 to 9% monthly biomass).

On an annual basis, 67% of biomass in FS was forbs (Fig. 5c). The forb component was dominated by 3 species: foamflower, wood sorrel, and strawberry-leaf blackberry. Foamflower and strawberry-leaf blackberry were available throughout the year, however wood sorrel senesced during fall and winter. Graminoids comprised an average of 26% of the FS biomass; the graminoid component was dominated by grasses. Ferns were present in small amounts in FS throughout the year (mean = 7%). Several fern species were present in the summer, but winter fern biomass was primarily deerfern.

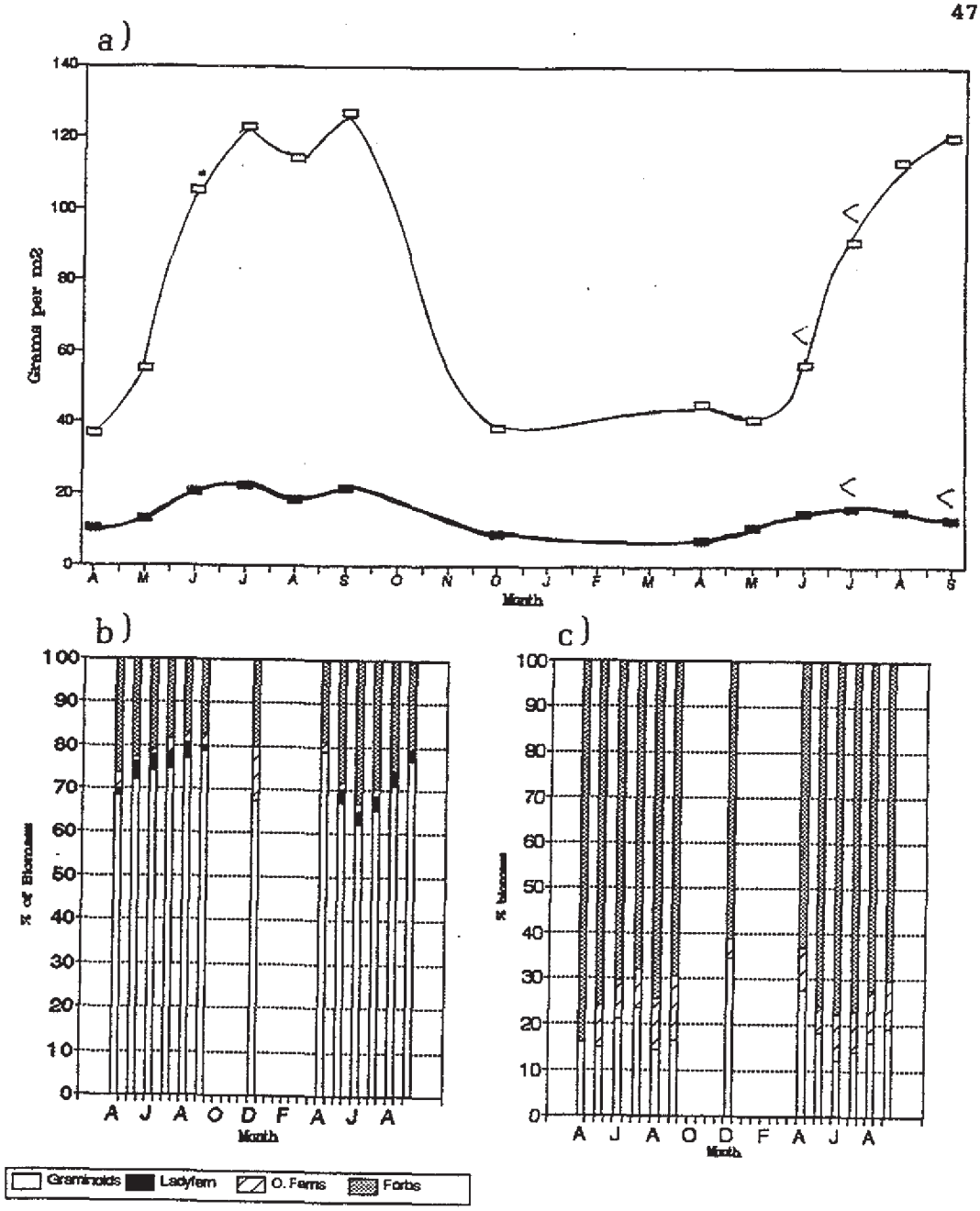


Figure 5. a) Mean monthly herbaceous standing crop biomass (g/m^2) in grass (□) and forb (■) dominated strata, and percent composition of herbaceous biomass in b) grass, and c) forb strata in the South Fork Hoh, April 1987-September 1988. < indicates values was less ($P < 0.05$) in 1988 than during same month in 1987.

Herbaceous Production and Utilization

Total Herbaceous Biomass

Total actual production during summer (April through August) differed between strata ($P = 0.0001$); actual production averaged 133.7 g/m^2 in GS and 20.59 g/m^2 in FS. Actual production was greater in 1987 (90.9 gm^2) than 1988 (63.4 gm^2) ($P = 0.0238$). The amount of herbaceous biomass consumed (utilization) was also greater in GS (74.1 g/m^2/year) than FS (13.0 g/m^2/year) ($P = 0.0047$). However, there was no difference between strata, on an annual basis, in percent biomass consumed (GS = 9.22, FS = 8.00, SERR=2.07, $P = 0.6786$), or percent production consumed (GS = 35.35, FS = 39.94, SERR = 9.33, $P = 0.7430$). There was no difference in utilization, percent biomass consumed, or percent production consumed between years ($P > 0.05$).

Throughout the year, actual production in GS varied among months ($P = 0.0001$). During 1987, actual production in GS peaked at 51.2 g/m^2 in June and again at 52.7 g/m^2 in August. In 1988, actual production in GS again peaked in June, at 46.9 g/m^2, but there was no additional peak in late summer. Actual production in GS was negative during fall due to the large amount of senescing plant tissue. During winter 1988, actual production in GS was positive, but not significantly greater than zero ($P > 0.05$) (Fig. 6a).

In GS herbaceous utilization did not differ among plots, years, or months (ANOVA $P = 0.2018$). In both years utilization in GS peaked slightly during April, June, and August. Percent biomass consumed in GS never exceeded 20% of available biomass, however, percent production consumed was greater than 40% of actual production in 5 out of 11 sample periods. Utilization during April was high in both years, however it was greatest in April 1988, when utilization exceeded production. Although actual production in GS continued to increase into May during both years, utilization dropped off during that month (Fig. 6a).

Herbaceous actual production in FS varied among months ($P = 0.0001$). Actual production peaked during May in both 1987 and 1988, at 9.2 and 6.4 g/m^2 respectively. In 1987, actual production was positive in FS through August, however actual production stopped earlier in 1988. During winter 1988 (Dec 1987-March 1988) production was positive, but not significant ($P > 0.05$) (Fig. 6b).

Although the monthly actual production pattern in FS did not differ between 1987 and 1988 (year* month interaction $P = 0.8876$), the

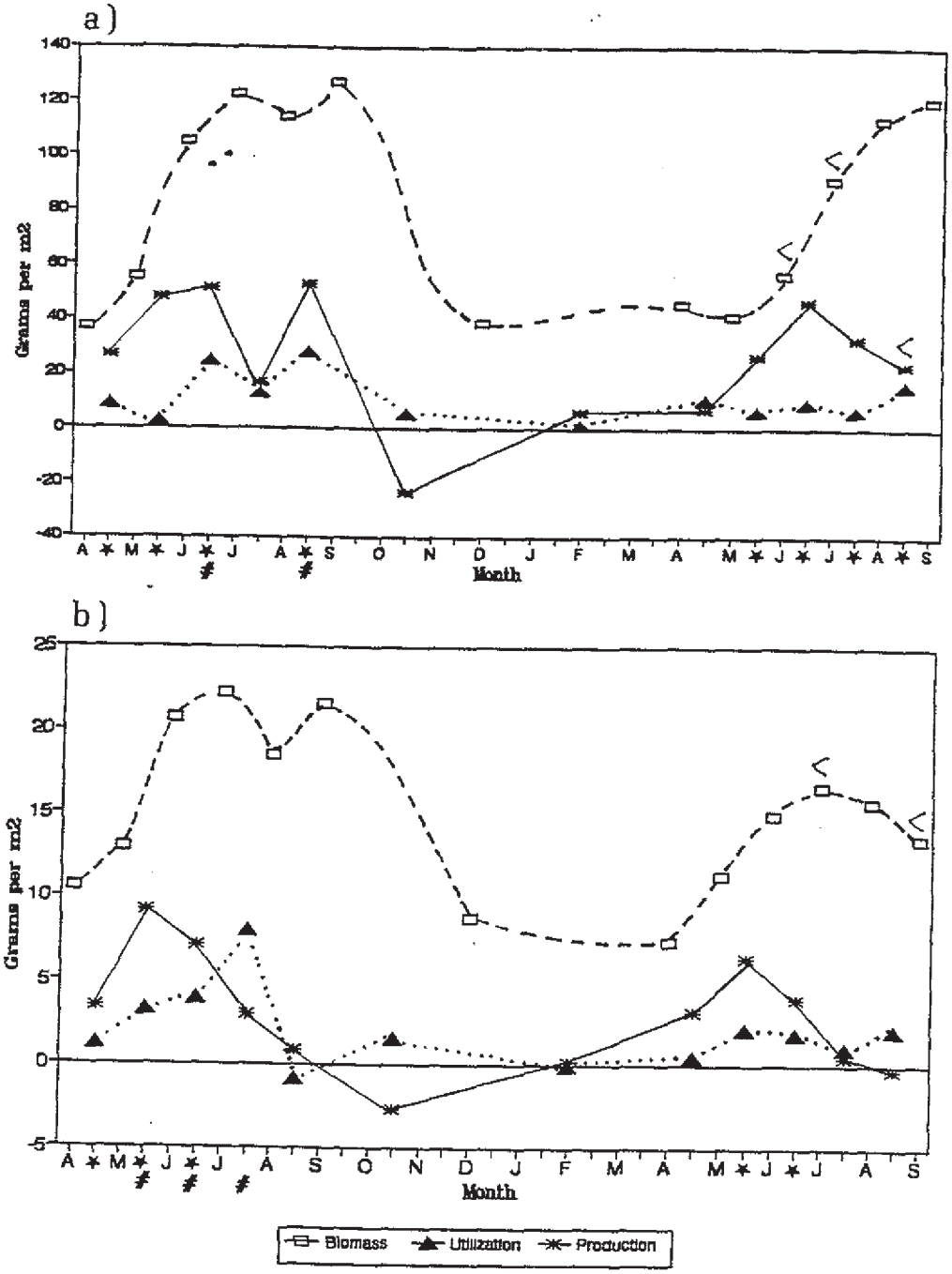


Figure 6. Mean monthly standing crop biomass, utilization, and production (g/m^2) of herbaceous forage in a) grass and b) forb dominated strata in the South Fork Hoh, April 1987-September 1988. < indicates value was less ($P < 0.05$) in 1988 than during same month in 1987. * indicates production was greater than 0 ($P < 0.05$) during sample period. # indicates utilization was greater than 0 ($P < 0.05$) during sample period.

monthly pattern of herbivory did (year*month $P = 0.0074$ utilization and $P = 0.0171$ percent biomass consumed). In 1987 there was a sharp peak in utilization in July, followed by no utilization in August. Whereas, during 1988 utilization was relatively stable May through August. Monthly utilization averaged 1.55 g/m^2 from September through December 1987, but was not detectable from January through March 1988 (Fig. 6b). The pattern of percent production consumed was very similar between years; in both years percent production consumed started at a low in April, and steadily increased to about 50% of actual production in June and greater than 100% actual production in July (when utilization in GS was low). Utilization was significantly greater in July in 1987 than in July 1988 ($P = 0.0003$), however, and resulted in a decrease in standing crop biomass during July 1987 (Fig. 6b).

Grass

Since graminoid biomass in both strata was dominated by grasses, and the distribution of other graminoids was too variable for adequate replication, the following analysis and discussion of graminoids is limited to grasses. Grass actual production in GS was greater in 1987 (121.8 g/m^2) than 1988 (61.7 g/m^2) ($P < 0.05$). In addition, GS grass actual production peaked later in 1988 than in 1987; in 1987, actual production peaked in May, with a lower peak in August. During 1988, however, actual production was significantly less in May ($P < 0.05$), did not peak until June, and there was very little increase in actual production in August (Fig. 7a).

Utilization of GS grasses was low: utilization averaged 36 g/m^2/year and percent biomass consumed 6.6% biomass/month. Grass utilization and percent biomass consumed did not differ between years or among months ($P > 0.05$), but varied among plots ($P = 0.0006$). In both years, utilization and percent biomass consumed for grasses in GS had slight peaks in April, June, and August (Fig. 7a), and appeared to parallel patterns in actual production, with the exception that utilization decreased in May of both years (grass utilization was not significant in May of both years, and undetectable in May 1988). However, the pattern of percent production consumed differed between years, a consequence of the different pattern of actual grass production that existed between years. Overall, percent GS grass production consumed averaged 37% actual production, but peaked at

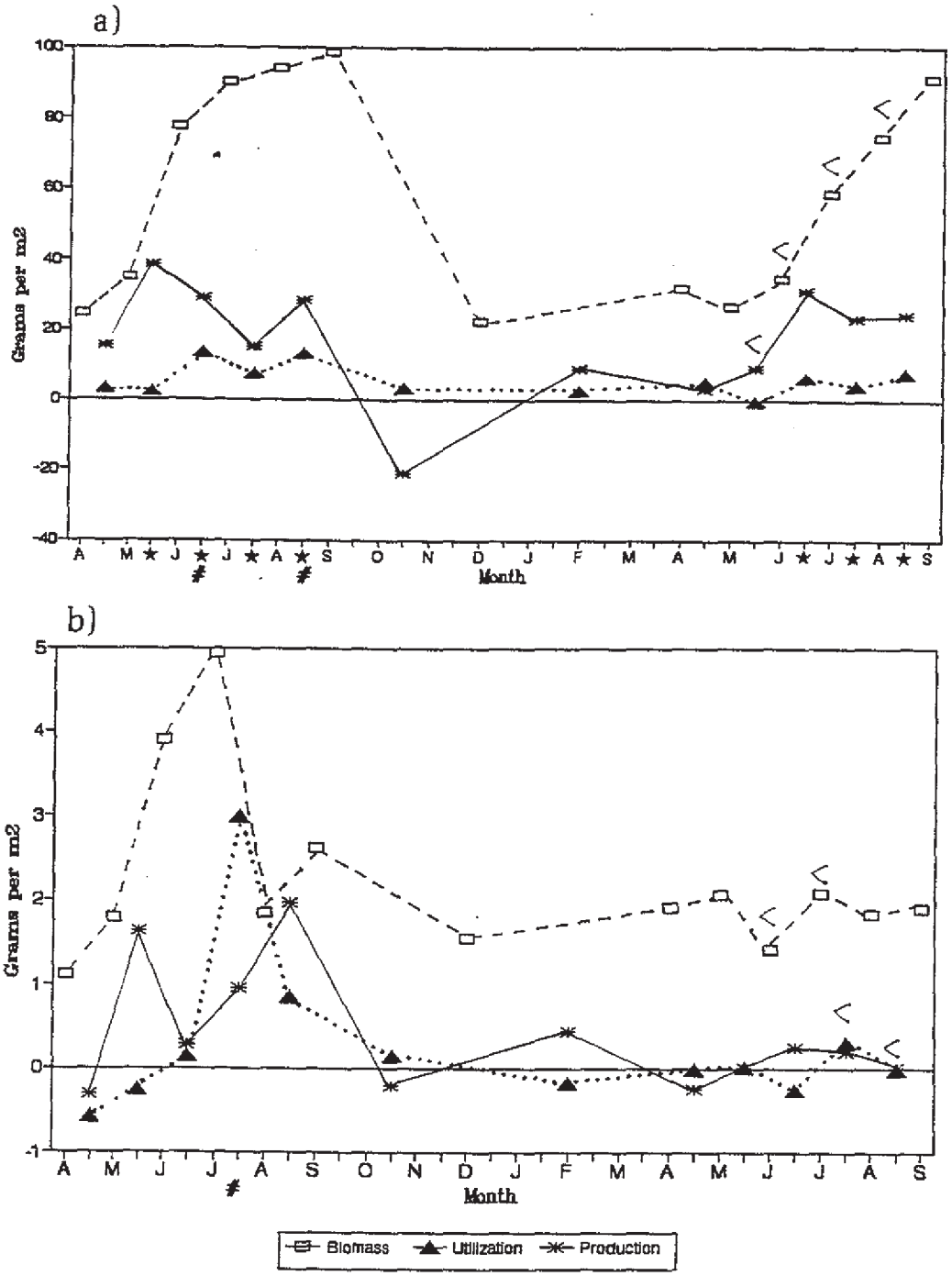


Figure 7. Mean monthly standing crop biomass, utilization, and production (g/m^2) of grasses in a) grass and b) forb dominated strata in the South Fork Hoh, April 1987-September 1988. < indicates value was less ($P < 0.05$) in 1988 than during same month in 1987. * indicates production was greater than 0 ($P < 0.05$) during sample period. # indicates utilization was greater than 0 ($P < 0.05$) during sample period.

greater than 100% of actual production in April 1988, and exceeded 40% of actual production from June - August 1987 (Fig. 7a).

Grass actual production in FS did not differ between months, plots, or years ($P = 0.1210$); yearly actual production averaged 3 g/m^2. Yearly and seasonal patterns of actual production of FS grasses parallelled the pattern for grasses in GS, although at lower levels (Fig. 7).

The use of grasses in FS varied between months and years ($P = 0.0231$). Annually, utilization averaged 1.6 g/m^2/year, 6% biomass consumed/month, and 53% production consumed/year. Although the seasonal pattern of grass actual production in FS is similar to grass actual production in GS, monthly grass utilization patterns in FS appeared different from GS. In both years grass utilization in FS peaked in July (when grass utilization in GS was low), and was greater than 100% of actual production (Fig. 7b). Use of FS grasses continued into the fall, even though actual production was negative. Grass utilization in FS was not detectable in winter, although there was some actual production of grasses.

Fern

In GS, actual production of ladyfern averaged 10.1 g/m^2. In both years ladyfern actual production peaked in early spring and declined sharply in mid summer (Fig. 8a). Although there was no difference in ladyfern actual production between years ($P = 0.531$), the growing season started later and lasted longer in 1988 than in 1987. Consequently, ladyfern biomass peaked later in 1988 than in 1987 (Fig. 8a).

Although ladyfern comprised a small percentage of both cervid diets and available GS biomass, its level of utilization in GS sites was high (mean 5.18 g/m^2/year, 28% biomass consumed/month, 51% production consumed/year). In both years the pattern of ladyfern utilization paralleled the pattern of ladyfern actual production, i.e., cervids consumed the most ladyfern when it was most actively growing (Fig. 8a). Utilization and actual production of ladyfern peaked in April 1987 and May 1988; during both peaks use was greater than 60% of biomass and 70% of actual production. In 1988, when regrowth of ladyfern occurred in late summer, percent production consumed was greater than 100% actual production, but percent biomass consumed was only 20% of the available ladyfern biomass (Fig. 8a).

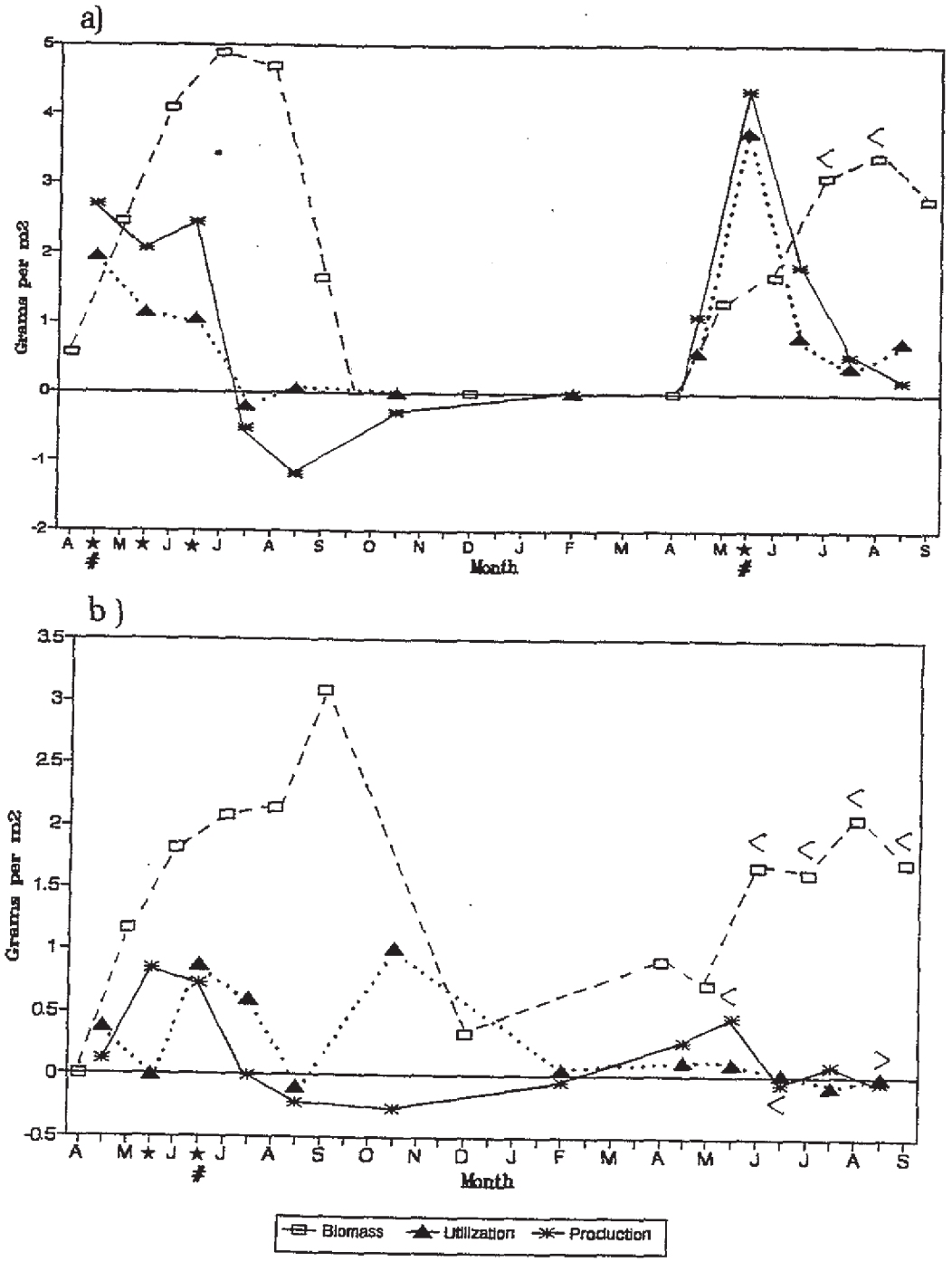


Figure 8. Mean monthly standing crop biomass, utilization, and production (g/m^2) of a) ladyfern in grass dominated strata and b) ferns in forb dominated strata in the South Fork Hoh, April 1987-September 1988. < indicates value was less ($P< 0.05$) in 1988 than during same month in 1987. > indicates value was greater ($P< 0.05$) in 1988 than during same month in 1987. * indicates production was greater than 0 ($P< 0.05$) during sample period. # indicates utilization was greater than 0 ($P < 0.05$) during sample period.

Fern actual production in FS did not differ between years, plots, or months ($P = 0.7485$), and averaged 2.5 g/m^2. Biomass and actual production of ferns in FS varied widely throughout the year, and between years (Fig. 8b). Part of this variation may be due to sampling error, since fern biomass was low and variable. Moreover, it was difficult to pair sub-plots on the basis of fern biomass and species composition. In 1987, there were only 2 FS sites that had ferns present in the plots during all sample periods, and in both plots the fern biomass was primarily comprised of deerfern, an evergreen fern. In 1988, due to increased replication at each site, I was able to sample ephemeral forest ferns more effectively (primarily oakfern (*Gymnocarpium dryopteris*), woodfern (*Dryopteris species*), and ladyfern) and increase sample size of FS sites with ferns. This resulted in decreased variation in biomass, and, with decreased dominance of deerfern in the sample, decreased actual production in late summer 1988.

The use of ferns in FS plots was also highly variable between months and years (Fig. 8b), and showed no relation to either actual production in FS, or use of ferns in GS. Part of this variation is most likely a result of shifts in species composition within each forage category, both between plots and months (i.e., a lot of ladyfern in forest plots in the summer, and deerfern in the fall).

Forbs

Forb actual production in GS averaged 38.26 g/m^2, and did not differ between years ($P = 0.279$). In both years actual production of forbs in GS increased steadily from April through June, and then declined in July. As with grasses in GS, actual production of forbs in GS increased again in August only during 1987 (Fig. 9a). However, the pattern of monthly actual production varied widely across individual species (Appendices 1-2).

The monthly pattern of forb use in GS paralleled that of grasses, however forb utilization was greater than grasses (utilization = 26 g/m^2/year, percent biomass consumed = 11% /month, percent production consumed = 68% /year.) Forb use in GS did not differ between years ($P = 0.771$), but did vary among plots ($P = 0.0005$) and months ($P = 0.0046$). Forb percent biomass consumed in GS rarely exceeded 20% of available biomass, but percent production

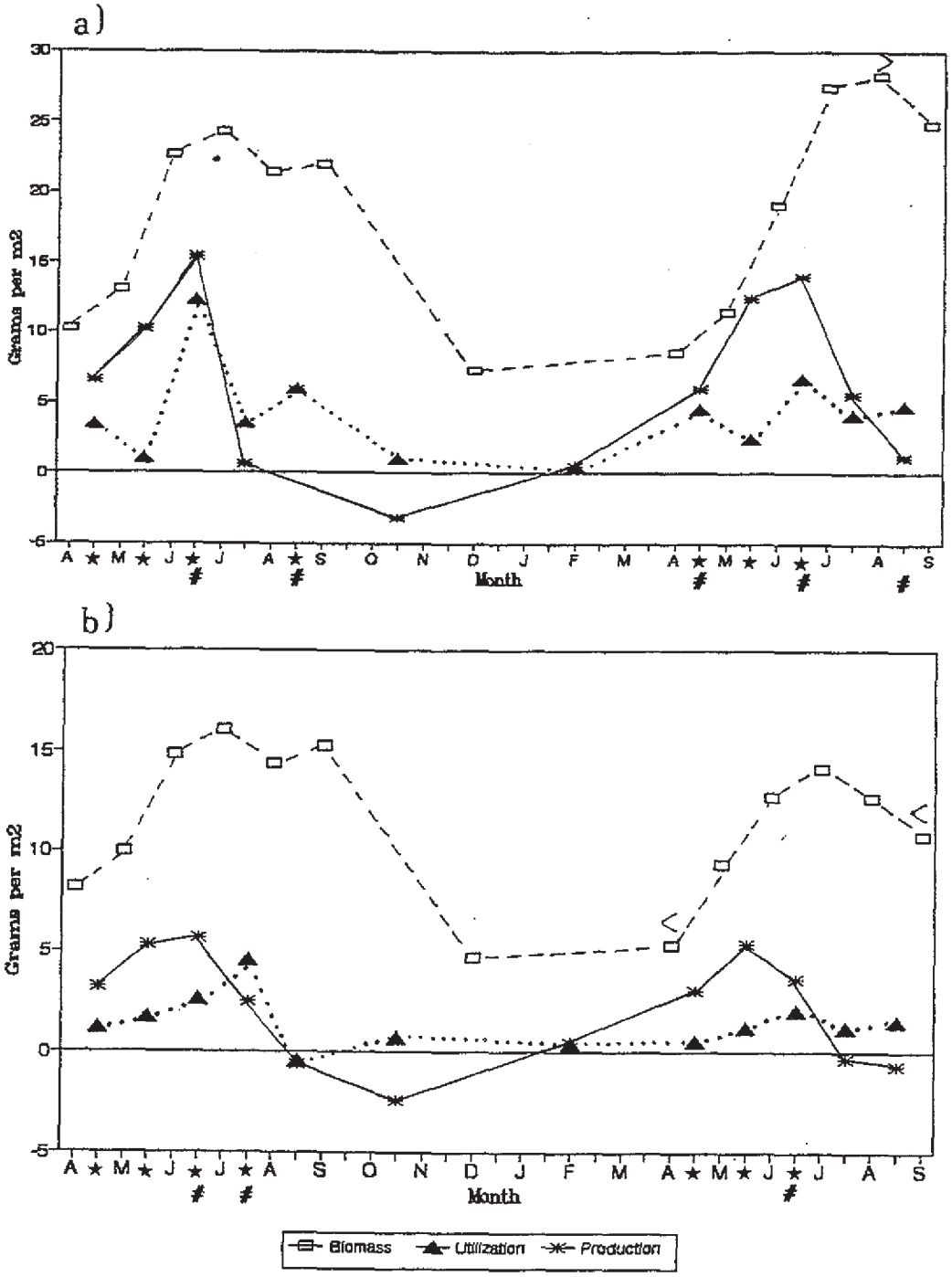


Figure 9. Mean monthly standing crop biomass, utilization, and production (g/m^2) of forbs in a) grass and b) forb dominated strata in the South Fork Hoh, April 1987-September 1988. < indicates value was less ($P < 0.05$) in 1988 than during same month in 1987. > indicates value was greater ($P < 0.05$) in 1988 than during same month in 1987. * indicates production was greater than 0 ($P < 0.05$) during sample period. # indicates utilization was greater than 0 ($P < 0.05$) during sample period.

consumed often was greater than 50%, and was greater than 100% of actual production in late summer both years (Fig. 9a).

Forb actual production in FS averaged 15.9 g/m^2, and varied among months ($P = 0.0001$), but not between plots or years ($P > 0.05$). Forb actual production peaked in May and June each year, and then quickly declined (Fig. 9b). There was no regrowth of forbs in FS during late summer of either year. Actual production of forbs in FS declined earlier in 1988 (July) than in 1987 (August). Forb actual production was negative in fall 1987, but was slightly positive in winter 1988 (Fig. 9b).

Because forbs dominated the herbaceous layer at FS sites, patterns of overall forb utilization were nearly identical to that of total biomass in FS sites (Figs. 6b, 9b). Forb utilization in FS averaged 8.7 g/m^2/year, 8.2% biomass consumed/month, and 55% production consumed/year. Forb utilization did not differ among plots ($P = 0.1441$) or years ($P = 0.737$), but did differ among months ($P = 0.0415$). Use of forbs in FS peaked during July 1987 at 24% biomass consumed and greater than 100% production consumed, and during June 1988 at 12.6% biomass consumed and 58% production consumed. The pattern of monthly actual production and utilization of forbs in FS varied widely across individual forb species (Appendices 1,3,4,5).

Effects of Herbivory on Herbaceous Biomass, Structure, Production, and Forage Quality

Total Herbaceous Biomass

As in the utilization plots, there was significantly less standing crop biomass available in FS than GS, in both the enclosed and grazed 5x5 m^2 plots, and during both seasons and years ($P = 0.0001$) (Table 6a). Although plant height was usually greater in GS than FS (Table 6b), the greater difference between strata in biomass over-rode differences in plant height. Consequently there was greater biomass concentration (g/m^3) in GS than FS during both seasons and years ($P = 0.0001$) (Table 6c).

Differences between strata in forage quality were inconsistent. Herbaceous biomass contained higher CP in FS than GS during summer ($P = 0.0008$), but herbs had greater CP in GS than FS during winter ($P = 0.0001$) (Table 6d). Herbaceous plants had lower IVD in FS than GS plants during both summer and winter ($P < 0.05$) (Table 6e). Differences between strata in biomass concentration were so large that

Table 6. Means and P values from three-way ANOVAs on effects of strata, year, and herbivory, by season, on herbaceous forage in old-growth forests in the South Fork Hoh, Olympic National Park.

	GS[a]		FS[b]								
SEASON YEAR	E[c]	G[d]	E	G	Stderr	Year	Str	Y*S	Tmt	Y*T	S*T	Y*S*T
a) Biomass (g/m^2)												
SUMMER[e]						0.0479	0.0001	0.5951	0.0475	0.2256	0.1218	0.3990
1987	173.9[g]	164.2	16.22	15.67	8.826							
1988	202.1	166.4	20.76	15.48								
WINTER[f]						0.0400	0.0001	0.0370	0.0253	0.2131	0.1939	0.1750
1987	88.2	73.6	6.54	4.48	3.270	1987>1988 for GS only						
1988	58.6	56.2	7.03	4.43								
b) Plant Height (cm)												
SUMMER						0.4899	0.0001	0.7791	0.0001	0.7337	0.0005	0.3914
1987	28.0	19.0	9.99	9.43	1.255	E>G for GS only						
1988	28.8	21.7	11.14	9.65								
WINTER						0.0001	0.0028	0.0004	0.0001	0.0001	0.1027	0.4216
1987	12.1	7.9	8.53	5.86	0.438	GS>FS 1987 only						
1988	6.1	5.2	6.09	5.78		E>G 1987 only						
c) Biomass Concentration (g/m^3)												
SUMMER						0.8323	0.0001	0.9204	0.0417	0.0294	0.0264	0.1264
1987	643.8	922.3	152.04	168.93	47.690	G>E in GS, 1987 only						
1988	781.0	800.9	197.79	167.18								
WINTER						0.2128	0.0001	0.3412	0.0249	0.1360	0.0042	0.3888
1987	741.0	962.2	78.54	76.73	40.006	G>E GS only						
1988	1010.9	1095.7	124.41	85.67								
d) Percent Crude Protein												
SUMMER						0.9709	0.0008	0.2270	0.0298	0.0525	0.0034	0.3920
1987	9.7	10.2	10.97	10.50	0.266	G>E GS only						
1988	8.8	10.3	11.06	11.20								
WINTER						0.7184	0.0001	0.2277	0.6579	0.7025	0.0662	0.3654
1987	12.2	12.4	9.95	9.74	0.319							
1988	12.9	13.8	9.52	9.07								
e) Percent In Vitro Digestible Dry Matter												
SUMMER						0.0411	0.0001	0.3597	0.2097	0.5494	0.2535	0.6627
1987	51.5	52.9	40.94	40.89	1.398							
1988	52.6	56.1	46.16	46.43								
WINTER						0.4369	0.0346	0.3597	0.1091	0.1341	0.3217	0.8908
1987	44.7	45.7	43.23	42.45	1.077							
1988	43.9	47.0	38.78	40.54								
f) Crude Protein Concentration (g/m^3)												
SUMMER						0.9212	0.0001	0.7897	0.0069	0.2141	0.0040	0.4121
1987	61.7	93.2	16.68	17.57	5.537	G>E GS only						
1988	68.7	83.7	21.10	18.59								
WINTER						0.1105	0.0001	0.1596	0.0195	0.5757	0.0068	0.8807
1987	90.7	117.5	7.88	7.84	6.267	G>E GS only						
1988	128.2	148.6	11.94	8.23								
g) In Vitro Digestible Dry Matter Concentration (g/m^3)												
SUMMER						0.5576	0.0000	0.9143	0.0116	0.0828	0.0056	0.1872
1987	329.4	484.5	60.81	63.54	25.109	G>E GS only						
1988	412.1	456.0	87.33	74.45								
WINTER						0.2337	0.0001	0.3113	0.0044	0.4120	0.0010	0.6659
1987	332.7	434.8	34.23	32.34	18.320	G>E GS only						
1988	429.0	498.4	45.92	33.77								

[a]GS: grass dominated strata.
[b]FS: forb dominated strata
[c]E: enclosed, or ungrazed, treatment
[d]G: grazed treatment
[e]SUMMER: samples collected July - August.
[f]WINTER: samples collected in early March.
[g]sample size for each cell was 10.

they either over-rode differences in forage quality, or were accentuated by them, resulting in consistently greater CP and IVD concentration in GS than in FS ($P = 0.0001$). Greater concentration of nutrients in GS than FS was consistent during both seasons, and over both years of the study (Table 6 f,g).

There were few significant differences in herbaceous characteristics between years. During winter, biomass of GS was greater in 1987 then 1988 ($P = 0.0044$), and plant height was greater in 1987 than 1988 in both strata. The only difference between years during summer was greater IVD in 1988 than 1987 ($P = 0.0411$).

Herbivory had variable effects on herb biomass and forage quality. Herbivory reduced maximum standing crop biomass in both strata, ($P < 0.05$). This pattern was consistent in both seasons and years (Table 6a). Plant height was also reduced by herbivory during both seasons ($P = 0.0001$). However, during summer, treatment effects were influenced by strata (treatment*strata $P = 0.0005$); treatments were not different in FS ($P = 0.4198$) but were different in GS ($P = 0.0001$). During winter, treatment effects were affected by year (treatment*year $P = 0.0001$); plant height was greater inside the exclosures in 1987 ($P = 0.0001$) but not in 1988 ($P = 0.1909$) (Table 6b). The reduction in plant height resulted in either increased biomass concentration in grazed than in ungrazed GS sites, or no difference in biomass concentration between treatments in FS. The difference in biomass concentration between treatments was significant only during summer 1987 (Table 6c).

Herbivory increased CP content ($P = 0.0298$) during summer, however the effect varied with strata (T*S $P = 0.0034$). Herbivory had no effect on CP in FS ($P = 0.5403$), but CP was greater in grazed than enclosed plots in GS ($P = 0.0005$). Herbivory did not influence CP during winter ($P = 0.6579$), and did not influence IVD during either season in either strata($P > 0.05$) (Table 6d,e).

When forage quality and biomass concentration effects were combined, the result was greater concentration of nutrients in grazed than ungrazed plots in GS ($P < 0.05$). This result was consistent over both seasons, and for both CP and IVD concentration. However, differences between treatments in FS sites were not significant ($P < 0.05$) (Table 6f,g).

Summer (April through August) production of herbaceous biomass in GS varied between treatments; grazed production was significantly less than both actual and enclosed production ($P < 0.05$), but there was no difference between enclosed and actual production ($P = 0.9359$),

thus there was exact compensation in production of grazed herbs. Overall, herbaceous production in GS did not vary between years ($P = 0.1905$). The effects of herbivory on production (S) did not vary over the years, and did not differ from zero ($S = -12.82$, $P = 0.2928$). Thus, on average, season-long herbivory did not influence herbaceous production in GS.

In GS during summer, there was a negative correlation between enclosed production and coniferous canopy cover (Fig. 10a) ($P = 0.0007$, $r^2 = 0.5013$), and to a lesser degree between enclosed production and total (coniferous and deciduous) canopy cover ($P = 0.0228$, $r^2 = 0.2692$), however neither actual production nor utilization were correlated with canopy cover ($P > 0.05$). Neither utilization nor actual production were correlated with enclosed production ($P < 0.05$) (Fig. 10b,c). However, utilization and percent biomass consumed were positively correlated with actual production ($P = 0.0001$, $r^2 > 0.6182$), and percent biomass consumed was positively correlated with percent production (Fig. 11) ($P = 0.0002$, $r^2 = 0.5585$). All 3 relationships were linear, i.e., herbaceous production in GS increased linearly with increasing utilization, however there was no observation of utilization greater than 30% of mean monthly available biomass. Because herbivory was not correlated with the intrinsic productivity of the site (enclosed production), and there was no correlation between actual production and enclosed production, and actual production increased with increasing utilization, it appeared that production was stimulated by herbivory. However, the relationship between both utilization and percent biomass consumed with S (actual production - enclosed production) was significant during 1987 only (1987: $P < 0.05$ $r^2 > 0.69$; 1988 $P > 0.16$; combined years $P > 0.06$). During 1987 production was stimulated with increasing levels of herbivory up to an 18% biomass consumed asymptote, and depressed production at levels greater than 22% biomass consumed (Fig. 11 d,e). When herbivory was summed over the year during 1987, the relationship between utilization and percent biomass consumed with actual production and percent production in GS was enhanced ($P = 0.0057$, $r^2 > 0.79$) (Fig. 12), but this correlation was strongly influenced by 1 observation of 25% biomass consumed.

In summary, when all GS herbaceous species were combined there was exact compensation in GS sites during summer, but grazed production was less than both actual and enclosed production. Cervid herbivory reduced peak standing crop biomass in GS, but it either increased biomass concentration (1987) or caused no change in biomass

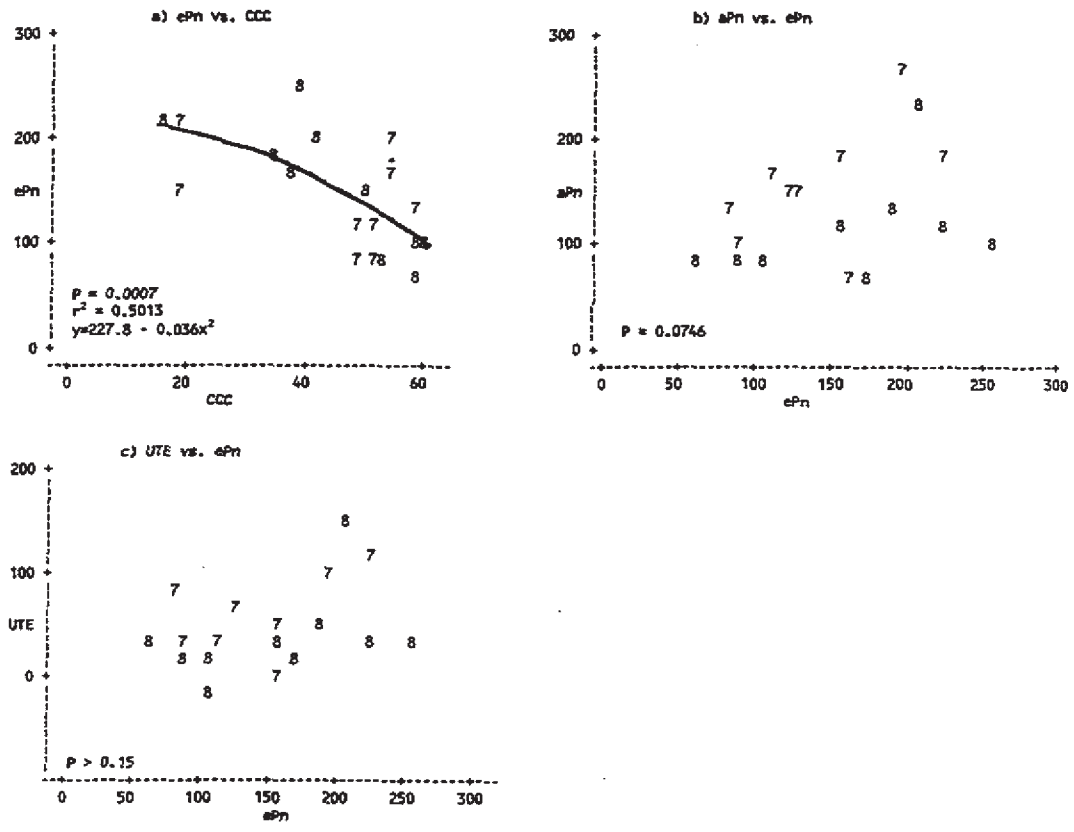


Figure 10. Relationship between herbaceous enclosed production (ePn, g/m^2) during summer in grass dominated strata and a) percent coniferous canopy closure (CCC), b) actual production under herbivory (aPn, g/m^2), and c) utilization (UTE, g/m^2). Value for observation indicates sample year (7=1987, 8=1988). One outlier was omitted from the regression analysis.

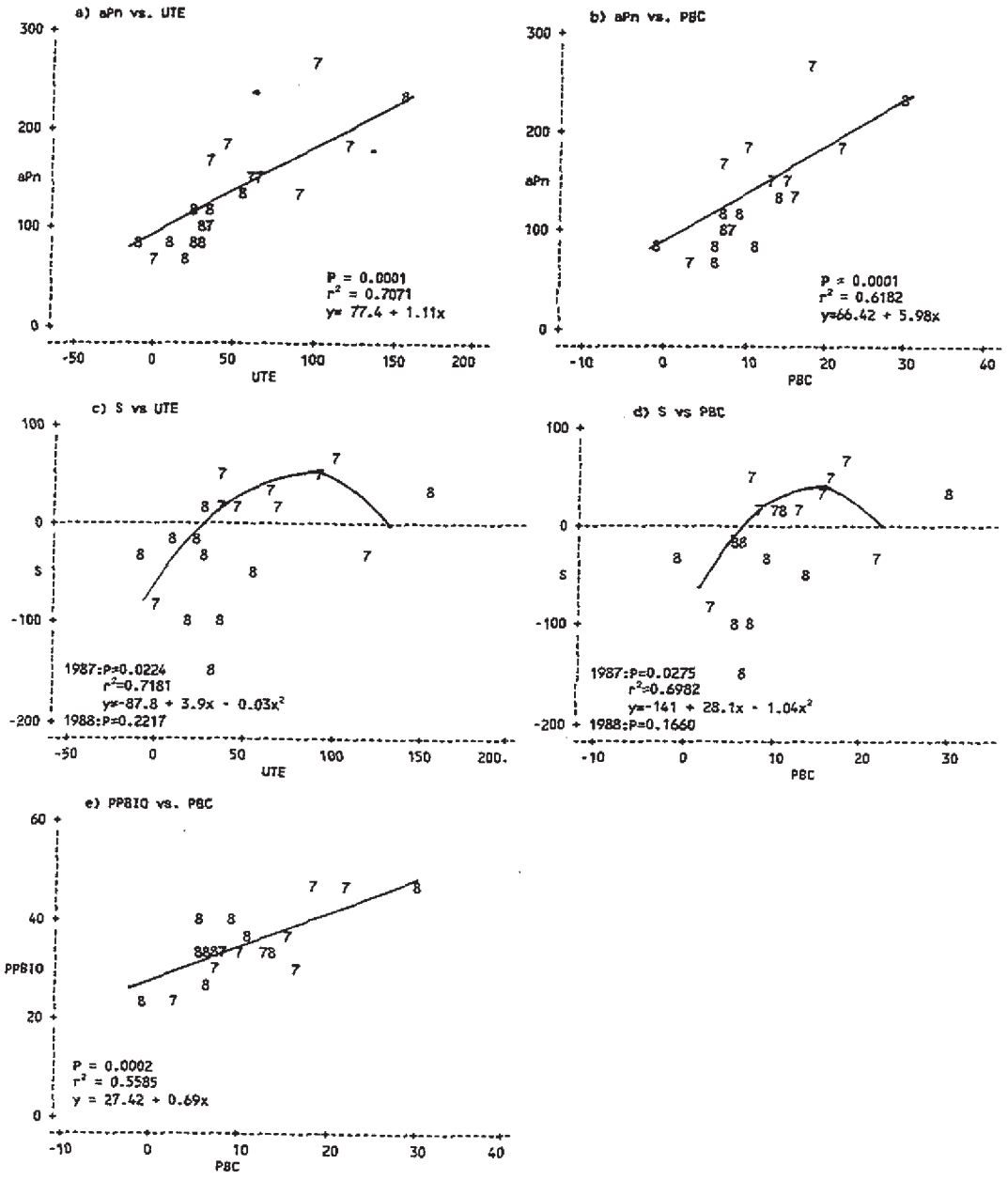


Figure 11. Relationships between herbaceous production and utilization in grass dominated strata during summer; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), c) effect of herbivory on production (S, or aPn - ungrazed production) (g/m^2) and UTE, d) S and PBC, and e) production as percent of biomass (PPBIO) and PBC. Value of observation indicates sample year (7=1987, 8=1988). One outlier was omitted from the regression analysis.

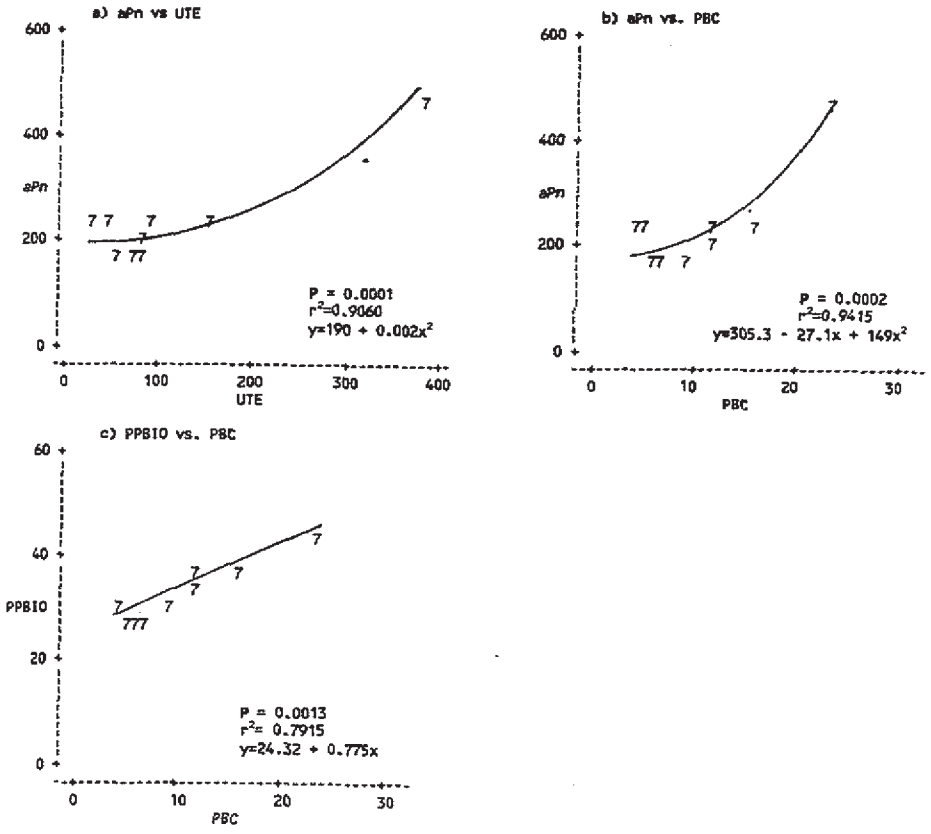


Figure 12. Relationships between production and utilization of herbaceous forage in grass strata on annual (March 1987 - March 1988) basis; a) actual production under herbivory (aPn) (g/m^2) and utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), and c) production as percent of biomass (PPBIO) and PBC. One outlier was omitted from the regression analysis. Data point value reflects sample year (7=1987).

concentration (1988), increased forage CP content, and increased concentration of nutrients. Herbivory was positively correlated with actual production in GS, indicating that cervids ate more at productive sites, but herbivory stimulated production during 1987 only, and utilization greater than the 22% biomass consumed asymptote depressed production.

The effect of herbivory on herbaceous production in FS during summer varied between treatments ($P = 0.0001$), but the effect of treatment varied with year (year*treatment $P = 0.0026$). During 1987 both actual production and grazed production were greater than enclosed production ($P < 0.01$), thus there was overcompensation in grazed herbs in FS. During 1988 there was no difference in production between treatments ($P > 0.20$), or exact compensation. S did not vary between years ($P > 0.05$), and did not differ from zero ($S = 11.09$, $P = 0.209$).

Although the year*treatment interaction was significant, scatter plots revealed that the data points were interspersed between years, thus regression analysis consisted of combined 1987 and 1988 data. As in GS, utilization and actual production in FS were not correlated with enclosed production ($P > 0.05$), but unlike in GS, enclosed production in FS was not correlated with coniferous canopy cover ($P > 0.05$) (Fig. 13). Herbaceous utilization and percent biomass consumed were positively correlated with actual production in FS ($P < .05$) (Fig. 14 a,b). As in GS during 1987, utilization and percent biomass consumed were correlated curvilinearly with S in FS (Fig. 14c,d); utilization had a stimulatory effect on production, which peaked at 25% of percent biomass consumed. Percent biomass consumed was also positively correlated with percent production ($P =0.0041$) (Fig. 14e). On a year-round basis, utilization and actual production were highly correlated during 1987 in FS ($P = 0.0001$), but the relationship between percent biomass consumed and actual production was not significant (Fig. 15). Production as a percent of biomass increased exponentially with percent biomass consumed ($P = 0.0337$, $r^2 = 0.4501$); but no FS observation was greater than 20% biomass consumed (Fig. 15c).

In summary, although percent biomass consumed was similar between GS and FS, herbivory had a different affect in FS than in GS. In both strata herbivory reduced standing crop biomass, during both summer and winter, but unlike GS, in FS herbivory had no effect on herb CP, IVD, or biomass and nutrient concentration in summer or winter. Herbivory stimulated production in FS during 1987, but had no

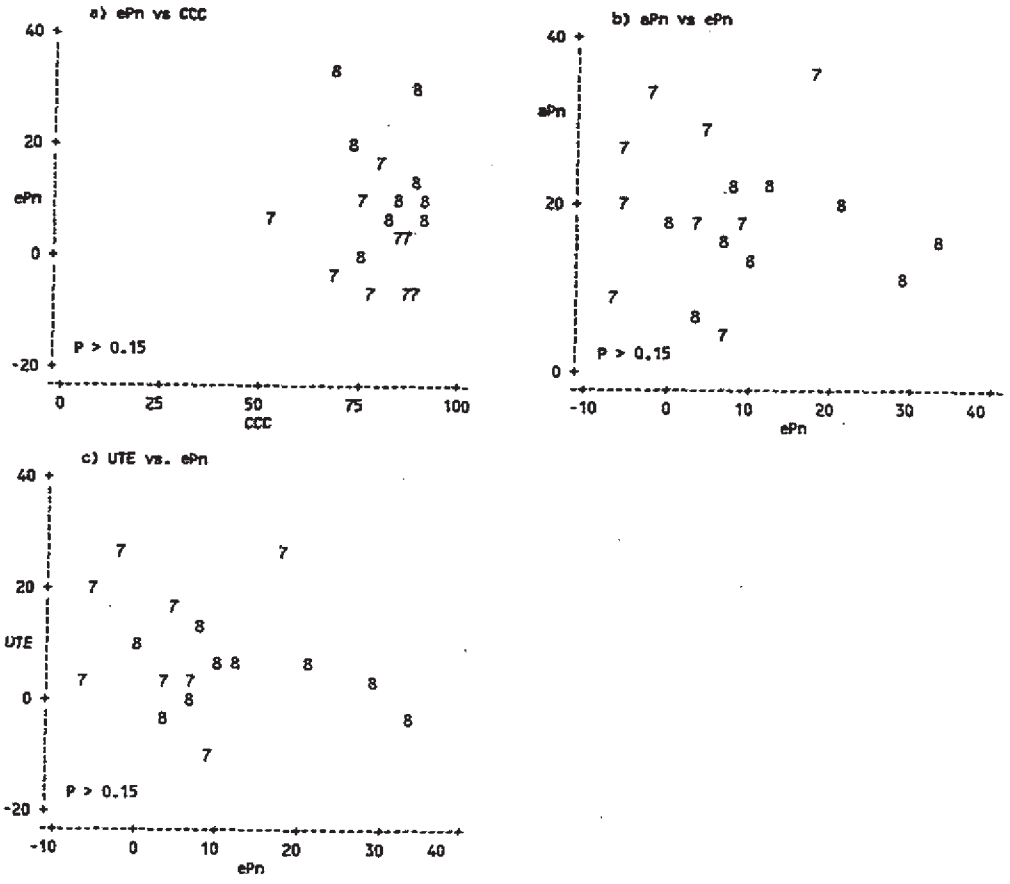


Figure 13. Relationship between herbaceous enclosed production (ePn, g/m^2) during summer in forb dominated strata and a) percent coniferous canopy closure (CCC), b) actual production under herbivory (aPn, g/m^2), and c) utilization (UTE, g/m^2). Value for observation indicates sample year (7=1987, 8=1988). One outlier was omitted from the regression analysis.

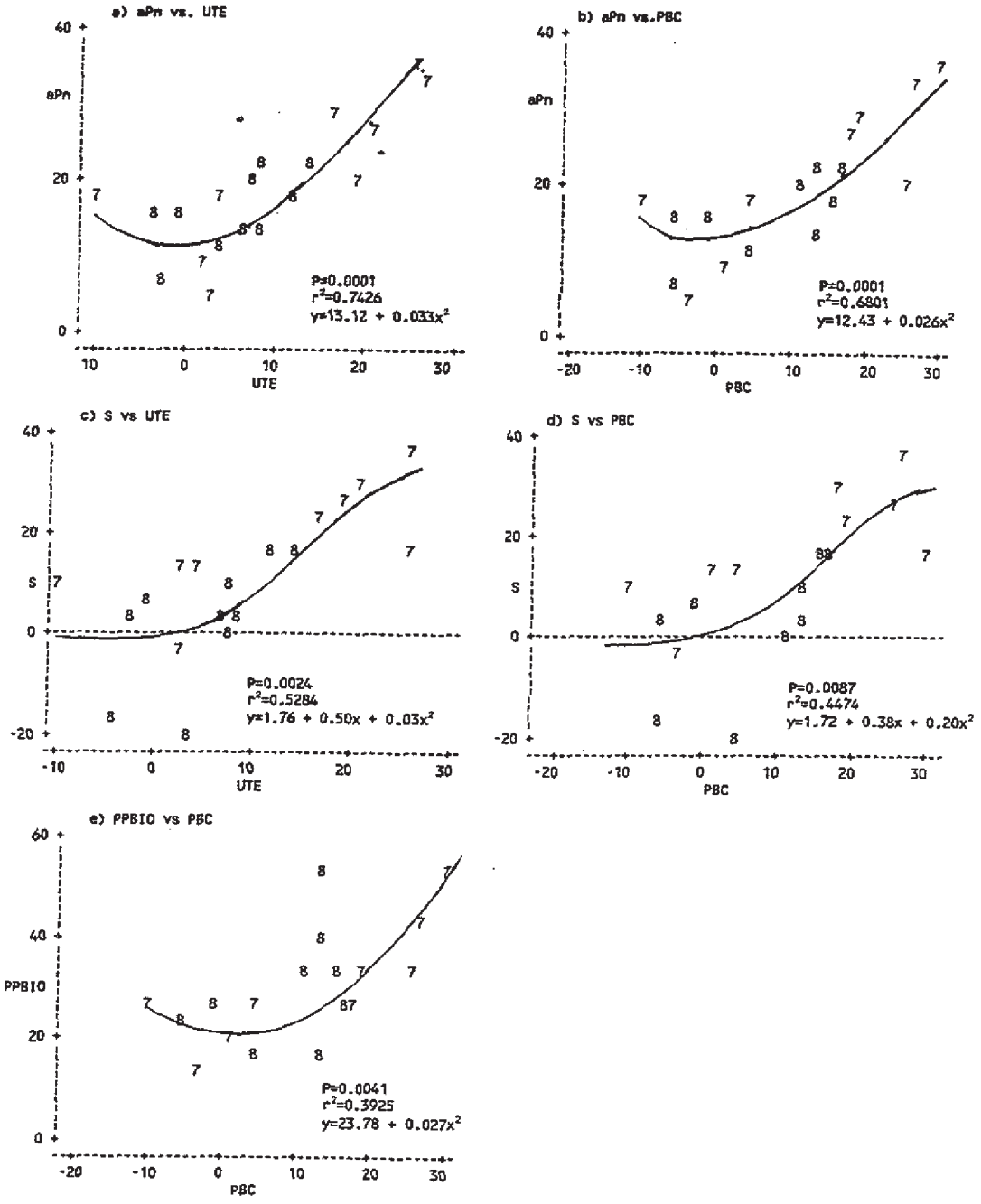


Figure 14. Relationships between herbaceous production and utilization in forb dominated strata during summer; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), c) effect of herbivory on production (S, or aPn - ungrazed production) (g/m^2) and UTE, d) S and PBC, and e) production as percent of biomass (PPBIO) and PBC. Value of observation indicates sample year (7=1987, 8=1988). One outlier was omitted from the regression analysis.

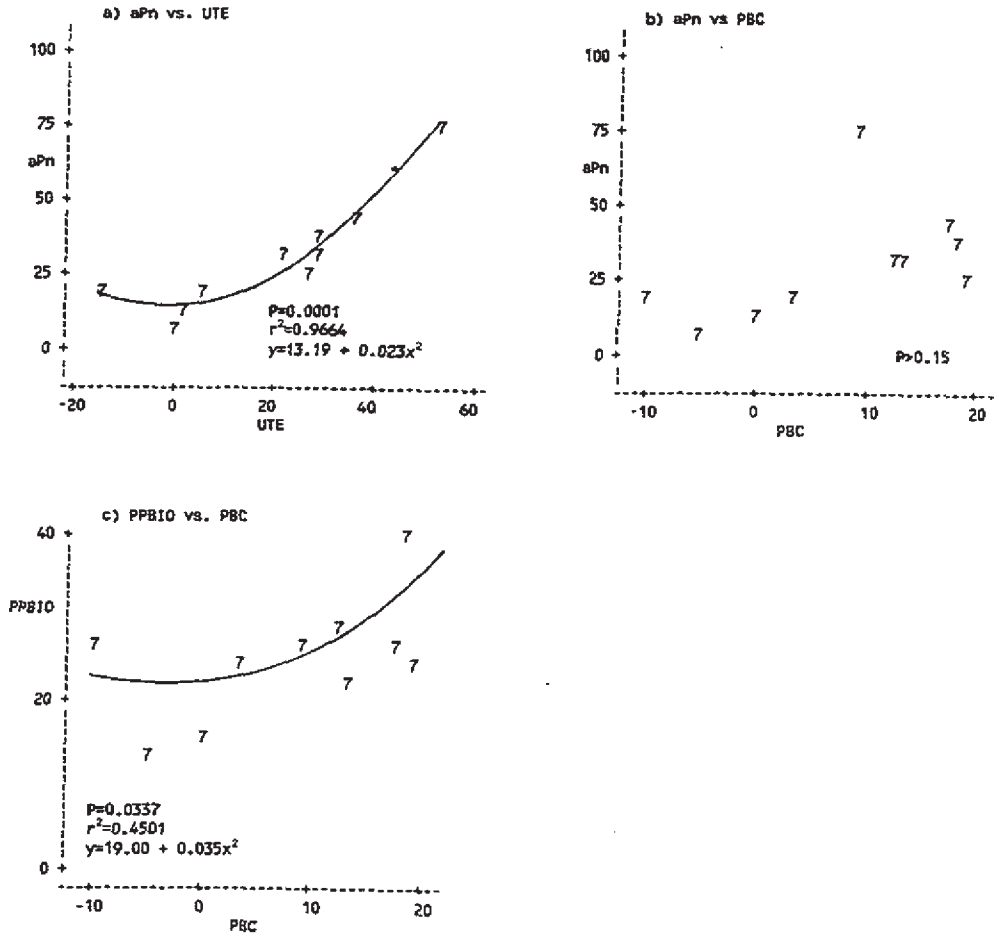


Figure 15. Relationships between production and utilization in forb strata on annual (March 1987 - March 1988) basis; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), and c) production as percent of biomass (PPBIO) and PBC. Data point value reflects sample year (7=1987).

effect on production in 1988. As in GS, herbivory in FS was positively correlated with actual production and S, indicating that the stimulatory effect of herbivory on production increased as herbivory increased, up to about 25 to 30% biomass consumed.

Grass

Biomass, biomass concentration, and nutrient concentration of grasses were greater in GS than FS in both seasons ($P < 0.001$) (Table 7). Grass CP content was greater in FS than GS during both summers, and during winter 1987 ($P < 0.05$). Grass IVD content was greater in GS than FS during summer 1987, however the reverse was true in summer 1988. Grass biomass and height were greater in 1987 than 1988 during winter, and grass IVD was greater in 1988 than 1987 during summer (Table 7).

Herbivory had a similar effect on grasses in both strata; in both GS and FS biomass did not differ between grazed and ungrazed plots during either season ($P > 0.05$), but grass height was significantly reduced in grazed plots during both summer and winter ($P < 0.0001$) (Table 7a,b). Biomass concentration of grasses was greater in grazed than ungrazed plots in summer 1987, and during winter of both years ($P < 0.05$). Grass CP responded differently to herbivory in GS than in FS; during summer CP was greater in grazed than ungrazed plants in GS ($P= 0.0004$), but there was no difference between treatments in FS ($P=0.6990$). During winter there was no difference in CP between grazed and ungrazed plots ($P = 0.3180$). Grass IVD was significantly greater in grazed than ungrazed plants during summer ($P = 0.0295$), but not winter ($P =0.0721$). During summer, nutrient concentration was greater in grazed than ungrazed grasses, but this trend was stronger in 1987 than 1988 (Y*T interaction $P < 0.05$). During winter nutrient concentration was greater in grazed grasses in both years ($P < 0.05$) (Table 7).

Unlike results for GS total herbaceous biomass, the influence of herbivory on grass production during summer in GS varied between years (Year*Treatment $P = 0.0013$). Actual production was greater than enclosed production during 1987, and less than enclosed production in 1988; indicating there was overcompensation in grazed grasses during summer 1987, and undercompensation during 1988. Grazed production was intermediate to actual production and enclosed production during 1987, and less than enclosed production during 1988. Enclosed production was equal between the years, but both actual production and grazed

Table 7. Means and P values from three-way ANOVAs on effects of strata, year, and cervid herbivory, by season, on grass forage in old-growth forests in the South Fork of the Hoh, Olympic National Park.

Season / Year	GS[a] E[c]	GS[a] G[d]	GS[a] n	GS[a] Stderr	FS[b] E	FS[b] G	FS[b] n	FS[b] Stderr	Year	Strata	Y*S	Tmt	Y*T	S*T	Y*S*T
a) Biomass (g/m^2)															
SUMMER[e]									0.3232	0.0001	0.8556	0.9022	0.0721	0.7399	0.1108
1987	114.2	134.0	10	8.591	3.65	3.58	6	11.092							
1988	137.6	114.5	10	8.591	0.86	1.42	8	9.056							
WINTER[f]									0.0071	0.0001	0.1916	0.2603	0.2362	0.4595	0.4182
1987	71.1	62.2	10	3.133	0.35	0.68	3	4.954							
1988	46.5	46.2	10	3.133	0.21	0.28	7	3.746							
b) Plant Height (cm)															
SUMMER									0.9186	0.0009	0.7359	0.0001	0.5937	0.1955	0.3704
1987	28.9	20.0	10	1.709	15.7	14.4	3	3.120							
1988	30.4	24.0	10	1.709	18.1	13.6	7	2.042							
WINTER									0.0001	0.2844	0.1180	0.0001	0.0046	0.1129	0.3712
1987	12.8	8.3	10	0.522	10.4	8.5	4	0.824	E>G 1987 only						
1988	6.3	5.4	10	0.522	6.5	6.1	2	1.166							
c) Biomass Concentration (g/m^3)															
SUMMER									0.1010	0.0001	0.9316	0.0333	0.0095	0.3274	0.0987
1987	466.6	718.2	10	49.16	45.87	44.93	3	89.74	G>E 1987 only						
1988	532.3	514.0	10	49.16	5.48	12.15	7	58.75							
WINTER									0.1249	0.0003	0.6355	0.0273	0.4051	0.1823	0.5920
1987	569.5	771.6	10	52.62	3.49	7.21	3	83.2							
1988	804.4	883.5	10	52.62	8.38	13.77	6	117.6							
d) Percent Crude Protein															
SUMMER									0.7645	0.0001	0.3445	0.0023	0.4422	0.0189	0.4946
1987	8.90	9.65	10	0.263	11.70	11.55	4	0.589	G>E GS only						
1988	8.10	9.55	10	0.263	12.38	12.13	4	0.416							
WINTER									0.3115	0.0560	0.0328	0.3180	0.3130	0.1792	0.8715
1987	12.00	12.11	3[g]	0.734	19.98	18.34	1	1.272	FS>GS 1987 only						
1988	12.17	13.16	10	0.402	13.16	11.93	1	1.272							
e) Percent In Vitro Digestible Dry Matter															
SUMMER									0.0002	0.1152	0.0007	0.0295	0.4269	0.3607	0.1784
1987	50.93	53.13	10	0.881	44.07	47.91	2	1.971	GS>FS in 1987, FS>GS in 1988						
1988	54.04	56.32	10	0.881	63.87	62.45	4	1.393							
WINTER									0.1103	0.1156	0.6193	0.0721	0.3815	0.5839	0.3831
1987	45.72	48.26	3	2.431	59.28	54.59	1	4.211							
1988	41.37	45.16	10	1.332	46.21	51.21	1	4.211							
f) Crude Protein Concentration (g/m^3)															
SUMMER									0.0857	0.0001	0.9352	0.0052	0.0276	0.1074	0.1761
1987	38.9	67.0	10	4.600	5.70	5.17	3	8.399							
1988	44.3	50.1	10	4.600	0.67	1.46	7	5.498							
WINTER									0.0665	0.0002	0.5170	0.0204	0.7825	0.1834	0.8125
1987	65.2	91.5	10	7.825	0.70	1.32	3	12.37							
1988	96.8	115.2	10	7.825	1.09	1.64	6	17.50							
g) In Vitro Digestible Dry Matter Concentration (g/m^3)															
SUMMER									0.1477	0.0001	0.9744	0.0091	0.0099	0.1862	0.1147
1987	222.5	370.6	10	23.356	19.29	21.56	3	42.64							
1988	279.8	289.5	10	23.356	3.47	7.50	7	27.92							
WINTER									0.1341	0.0001	0.6893	0.0044	0.5828	0.0901	0.6707
1987	245.0	348.9	10	23.087	2.07	3.93	3	36.50							
1988	320.7	382.6	10	23.087	3.84	7.05	6	51.62							

[a]GS: grass dominated strata.
[b]FS: forb dominated strata.
[c]E: enclosed, or ungrazed, treatment.
[d]G: grazed treatment.
[e]SUMMER: samples collected July - August.
[f]WINTER: samples collected in early March.
[g]due to low biomass, grass samples were composited into 3 samples for forage quality analyses.

production were less in 1988 than 1987. S varied between years; it did not differ from zero in 1987 (S = 16.2, P = 0.1665), and was negative in 1988 (-37.7, P = 0.0023).

Because the year*treatment interaction term was highly significant, data on GS grasses from 1987 and 1988 were not combined for the regression analyses. During both 1987 and 1988, enclosed grass production in GS was negatively correlated with coniferous canopy closure ($P < 0.05$, $r^2 = 0.64$) (Fig. 16a), but not with total canopy closure ($P > 0.05$). Utilization was not correlated with enclosed production during either year, and there was no relationship between actual production and enclosed production in 1987. During 1988, however, actual production and enclosed production were positively correlated ($P = 0.0222$, $r^2 = 0.5000$) (Fig. 16 b,c). During 1987 only, actual production of grasses in GS was positively correlated with utilization ($P = 0.0002$, $r^2 = 0.6464$) and percent biomass consumed ($P = 0.0287$, $r^2 = 0.6939$). In both cases, the relationship between utilization and production was curvilinear; the rate of increase of actual production leveled off at 20% biomass consumed (Fig. 17a,b). At no point did utilization appear to decrease actual production, but I did not observe utilization levels greater than 30% of available biomass per month. S and percent production were also positively correlated with utilization in 1987 only ($P < 0.05$, $r^2 > 0.55$); both relationships were linear throughout the observed range of utilization (Fig. 17 c,d,e). On a year-round basis during 1987, the correlation between grass actual production and percent production with percent biomass consumed improved; actual production continued to increase up to the maximum observed level of 30% biomass consumed (Fig. 18).

In summary, during summer 1987, grass production and nutrient and biomass concentration in GS were stimulated or enhanced by cervid herbivory. Throughout the observed range of herbivory, actual production increased with increased utilization, therefore no asymptote of optimum grass utilization was observed. Although utilization did not differ between years, during 1988 there were no correlations between utilization and production, and on average utilization decreased production.

Production of grasses in FS during summer did not differ between grazed and ungrazed plots, thus there was exact compensation. None of the regressions for grass in FS were significant (Figs. 19,20), probably a consequence of low grass biomass, poor pairing between treatments, low levels of replication, and low levels of herbivory.

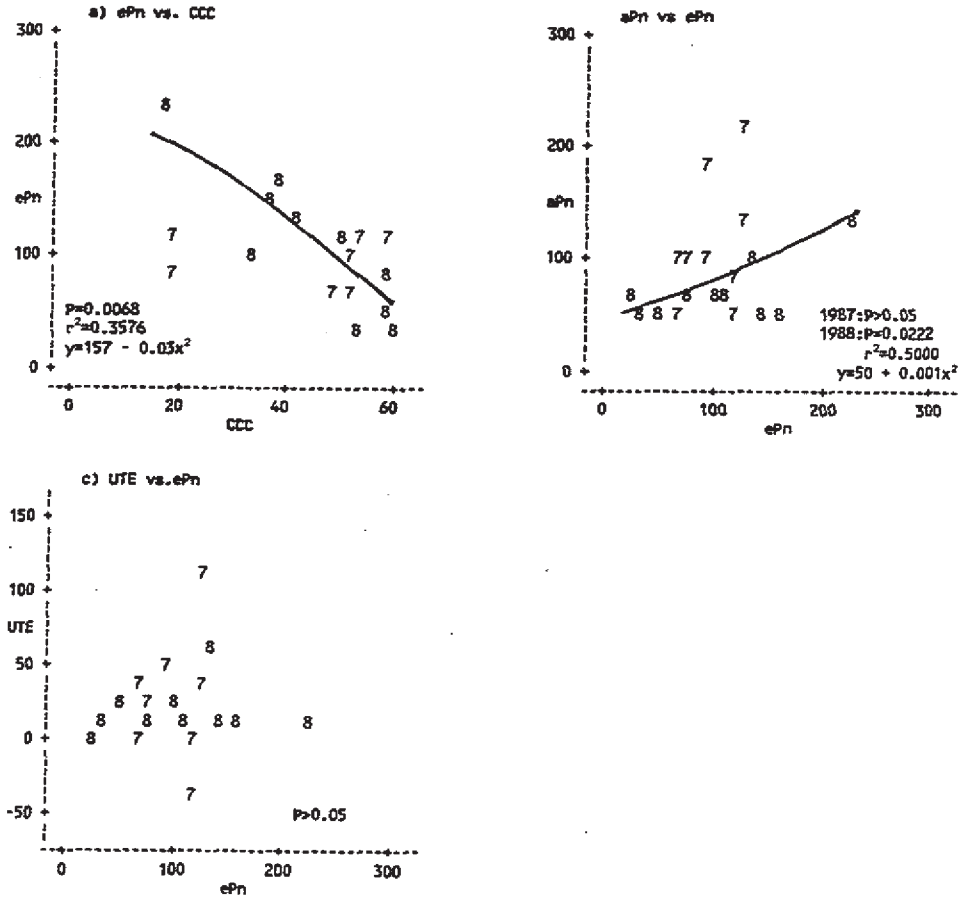


Figure 16. Relationship between enclosed grass production (ePn, g/m^2) during summer in grass dominated strata and a) percent coniferous canopy closure (CCC), b) actual production under herbivory (aPn, g/m^2), and c) utilization (UTE, g/m^2). Value for observation indicates sample year (7=1987, 8=1988). One outlier was omitted from the regression analysis.

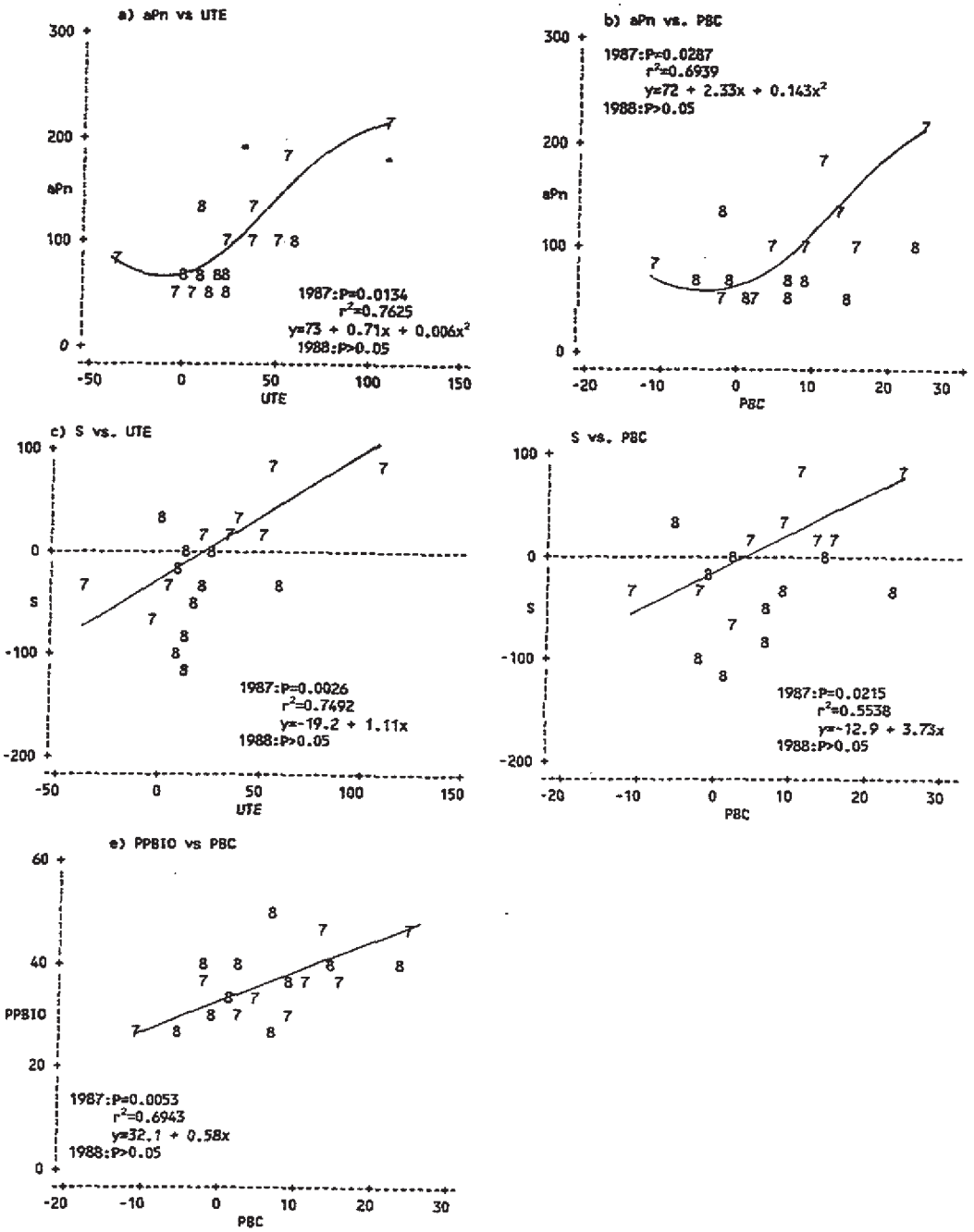


Figure 17. Relationships between grass production and utilization in grass dominated strata during summer; a) actual production under herbivory (aPn) (g/m^2) and utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), c) effect of herbivory on production (S, or aPn - ungrazed production) (g/m^2) and UTE, d) S and PBC, and e) production as percent of biomass (PPBIO) and PBC. Value of observation indicates sample year (7=1987, 8=1988). Since the herbivory*year interaction term was significant ($P < 0.05$), regressions were run separately for each year. One outlier was omitted from the 1987 regression analysis.

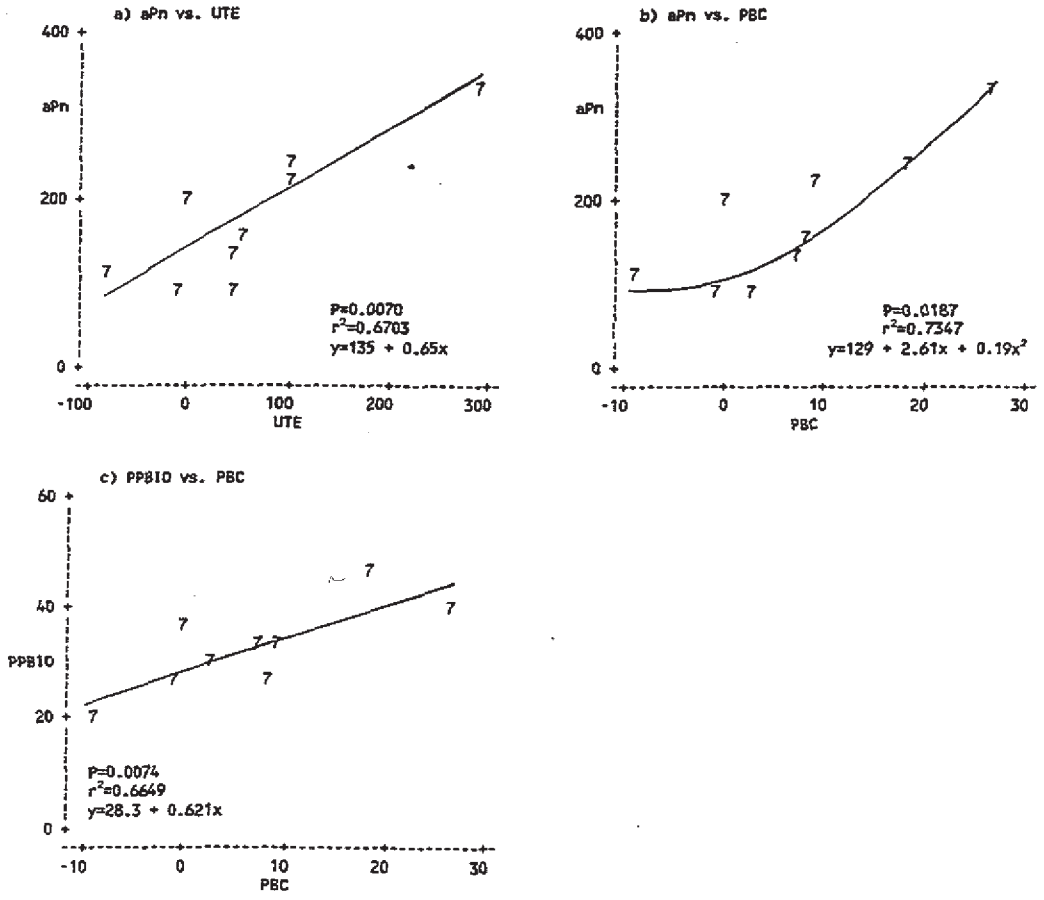


Figure 18. Relationships between grass production and utilization in grass strata on annual (March 1987 - March 1988) basis; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), and c) production as percent of biomass (PPBIO) and PBC. Data point value reflects sample year (7=1987).

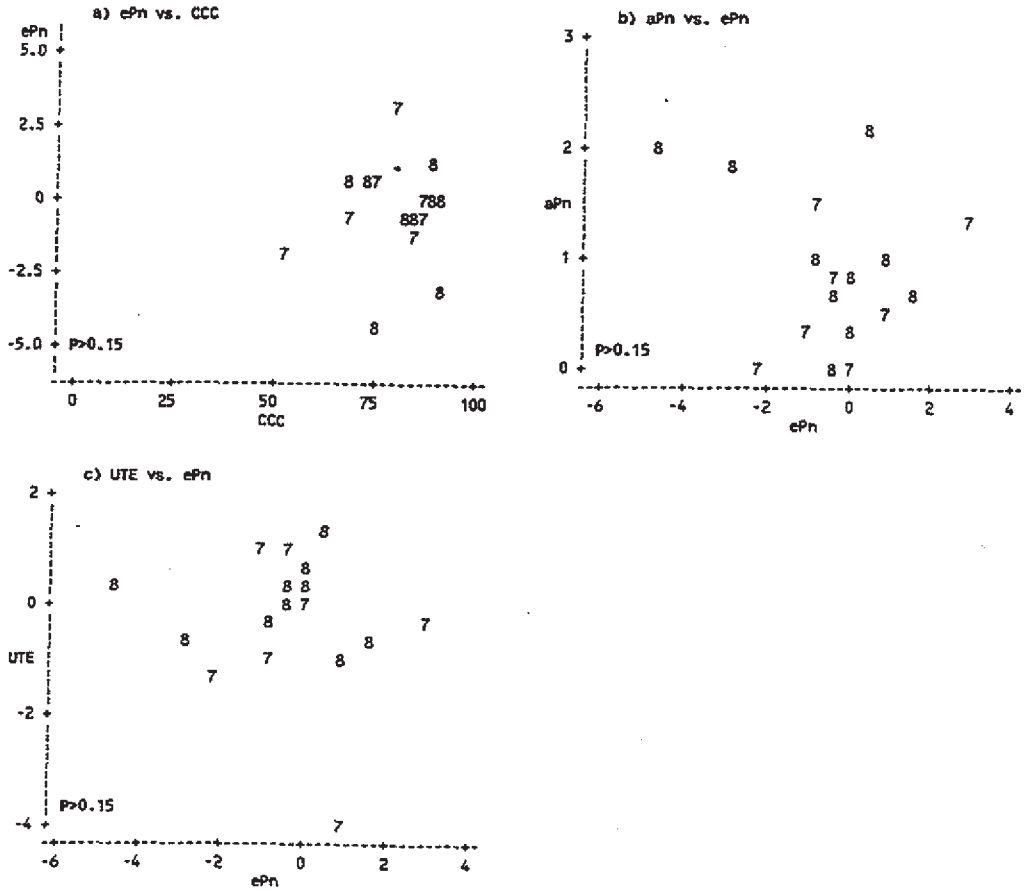


Figure 19. Relationship between enclosed grass production (ePn, g/m^2) during summer in forb dominated strata and a) percent coniferous canopy closure (CCC), b) actual production under herbivory (aPn, g/m^2), and c) utilization (UTE, g/m^2). Value for observation indicates sample year (7=1987, 8=1988). One outlier was omitted from the regression analysis.

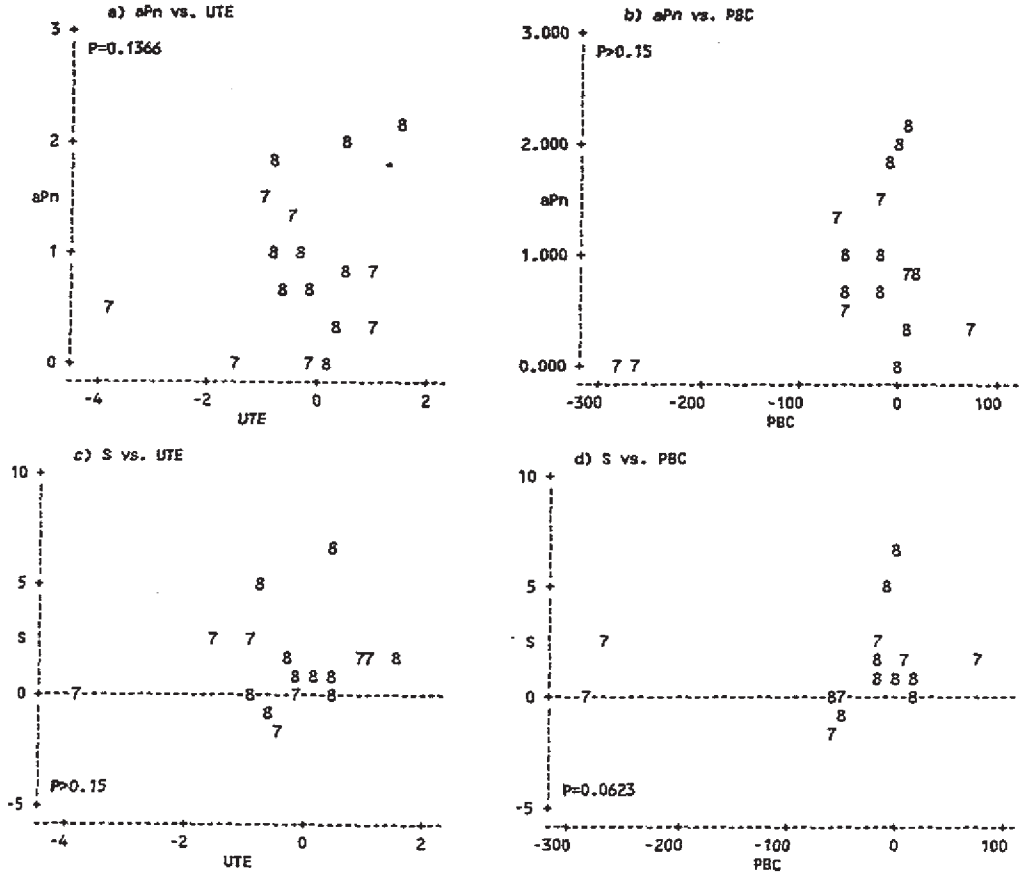


Figure 20. Relationships between grass production and utilization in forb dominated strata during summer; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), c) effect of herbivory on production (S, or aPn - ungrazed production) (g/m^2) and UTE, d) S and PBC. Value of observation indicates sample year (7=1987, 8=1988). One outlier was omitted from the regression analysis.

Ferns

Fern biomass, height, and biomass and nutrient concentration were usually less in FS than in GS ($P < 0.05$) (Table 8). However, there was no difference between strata in nutrient content of ferns ($P > 0.05$). During summer, fern biomass in GS was mainly ladyfern, whereas fern biomass in FS was comprised of a variety of species, including ladyfern, oakfern, woodfern, and deerfern. During winter, fern biomass in both strata was predominantly deerfern.

Herbivory affected fern biomass and nutrient content, but the effects generally were only significant during summer, and only in GS. Differences between grazed and ungrazed plots in GS were generally related to trends in ladyfern; biomass and height of ladyfern in GS was less in grazed plots ($P < 0.05$) during both years (Table 9). Unlike other forage categories, herbivory also reduced biomass concentration of ladyfern ($P = 0.0230$). Cervid herbivory also resulted in increased CP and IVD in grazed as compared to ungrazed ladyfern, but this was significant only during 1988. The increase in forage quality counteracted the decrease in biomass concentration, and resulted in no significant difference in ladyfern nutrient concentration between treatments (Table 9).

Ladyfern production in GS did not vary between years or treatments ($P > 0.15$), thus there was exact compensation. Overall, S did not differ from zero ($P > 0.05$). Utilization and actual production were not correlated with enclosed production, and enclosed production was not correlated with coniferous canopy closure ($P > 0.05$) (Fig. 21). Actual production and S of ladyfern were positively correlated with utilization ($P < 0.001$, $r^2 > 0.56$), but not percent biomass consumed (Fig. 22).

In summary, herbivory decreased ladyfern maximum standing crop biomass and plant height, but the effect on biomass was so great that it overrode the height reduction and resulted in greater biomass concentration inside the exclosures. Although herbivory influenced ladyfern biomass and structure, herbivory had no effect on production. The cervids ate more ladyfern at the more productive sites, but actual production, biomass and forage quality were not correlated with percent biomass consumed.

There also was exact compensation in fern production in FS during summer. Fern utilization and actual production were not correlated with enclosed production, and enclosed production was not correlated with canopy closure ($P > 0.05$) (Fig. 23). Fern actual

Table 8. Means and P values from three-way ANOVAs on effects of strata, year, and cervid herbivory, by season, on ferns in the South Fork Hoh, Olympic National Park.

	GS[a]				FS[b]								
SEASON YEAR	E[c]	G[d]	n	Stderr	E	G	n	Stderr	Year	Strata	Y*S	Tmt	Y*T	S*T	Y*S*T
a) Biomass (g/m^2)															
SUMMER[e]									0.7655	0.0013	0.2537	0.0047	0.4717	0.0369	0.3014
1987	11.3	5.8	8	2.341	4.34	2.50	6	2.703	E>G in GS only						
1988	17.1	5.8	9	2.207	1.38	1.11	9	2.502							
WINTER[f]									0.0323	0.0001		0.1754	0.2011	0.0036	
1987					0.70	0.50	3	0.406							
1988	2.6	6.0	2	0.497	0.69	0.43	5	0.314							
b) Plant Height (cm)															
SUMMER									0.5378	0.0055	0.6879	0.0005	0.1310	0.3165	0.1591
1987	23.6	19.4	7	2.974	17.42	10.39	4	3.933							
1988	32.1	16.0	9	2.622	16.75	11.42	5	3.518							
WINTER										0.5940		0.9729		0.9323	
1987															
1988	7.5	7.4	2	0.955	6.51	6.62	4	0.941							
c) Biomass Concentration (g/m^3)															
SUMMER									0.5753	0.0578	0.2438	0.1504	0.7691	0.2564	0.9776
1987	50.6	30.9	7	9.621	34.90	33.19	4	12.73							
1988	51.3	36.4	9	8.484	11.57	13.73	5	11.38							
WINTER										0.0011		0.1528		0.0246	
1987									G>E in GS only						
1988	33.9	83.7	2	0.293	12.91	7.56	4	0.148							
d) Percent Crude Protein															
SUMMER									0.4787	0.7266	0.0859	0.0397	0.1639	0.4253	0.2587
1987	11.3	12.0	8	0.43	10.82	10.27	6	0.500							
1988	10.0	11.1	9	0.41	10.59	11.79	9	0.463							
WINTER									0.0001	0.2163		0.0002	0.0010	0.0621	
1987					14.75	10.37	3	0.369							
1988	9.1	9.3	2	0.453	10.39	8.90	5	0.286							
e) Percent In Vitro Digestible Dry Matter															
SUMMER									0.0001	0.2141	0.6477	0.0003	0.0003	0.0009	0.0030
1987	32.3	32.2	8	1.191	33.34	32.79	6	1.375	G>E in GS in 1988 only						
1988	31.6	43.8	9	1.123	39.37	39.65	9	1.273							
WINTER									0.0973	0.1598		0.0579	0.0445	0.6695	
1987					54.16	40.75	3	2.774							
1988	39.3	39.9	2	3.398	45.37	43.25	1	2.403							
f) Crude Protein Concentration (g/m^3)															
SUMMER									0.3045	0.0254	0.3684	0.2270	0.4488	0.3012	0.7865
1987	5.7	3.4	7	0.987	3.47	3.24	4	1.305							
1988	4.7	3.8	9	0.870	1.20	1.59	5	1.167							
WINTER										0.0030		0.2256		0.0392	
1987									G>E in GS only						
1988	3.1	7.9	2	0.341	1.27	0.68	4	0.105							
g) In Vitro Digestible Dry Matter Concentration (g/m^3)															
SUMMER									0.8238	0.0981	0.2031	0.4271	0.5007	0.4311	0.6584
1987	16.5	10.1	7	3.339	12.14	2.52	4	4.417							
1988	16.7	15.4	9	2.945	4.56	5.41	5	3.951							
WINTER										0.0007		0.1302		0.0145	
1987									G>E in GS only						
1988	13.4	33.0	2	0.253	5.86	3.27	4	0.129							

[a]GS: grass dominated strata.
[b]FS: forb dominated strata
[c]E: enclosed, or ungrazed, treatment
[d]G: grazed treatment
[e]SUMMER: samples collected July - August.
[f]WINTER: samples collected in early March.

Table 9. Means and P values from two-way ANOVA on effect of year and herbivory on ladyfern in grass dominated strata during summer (August) in old-growth forests in the South Fork Hoh, Olympic National Park.

YEAR	E[a]	G[b]	n	Stderr	Year	Tmt	Tmt*Year
a) Biomass (g/m^2)							
1987	9.62	4.29	8	2.752	0.5119	0.0046	0.2300
1988	15.08	3.05	9	2.595			
b) Plant Height (cm)							
1987	23.94	19.81	7	3.185	0.4294	0.0032	0.0768
1988	32.88	17.28	9	2.809			
c) Biomass Concentration (g/m^3)							
1987	42.73	23.28	7	9.161	0.6778	0.0230	0.8072
1988	41.16	17.42	9	8.079			
d) Crude Protein (%)							
1987	11.59	11.89	6	0.372	0.6341	0.0083	0.0099
1988	9.70	12.79	4	0.455	G>E in 1988 only		
e) In Vitro Digestible Dry Matter (%)							
1987	32.05	31.42	6	1.629	0.0107	0.0652	0.0158
1988	30.69	41.18	4	1.995	G>E in 1988 only		
f) Crude Protein Concentration (g/m^3)							
1987	5.01	2.76	7	0.969	0.3577	0.0517	0.7571
1988	3.86	2.19	9	0.854			
g) In Vitro Digestible Dry Matter Concentration (g/m^3)							
1987	13.29	7.38	7	2.976	0.8799	0.0670	0.9035
1988	12.54	7.32	9	2.625			

[a]E: enclosed, or ungrazed, treatment
[b]G: grazed treatment

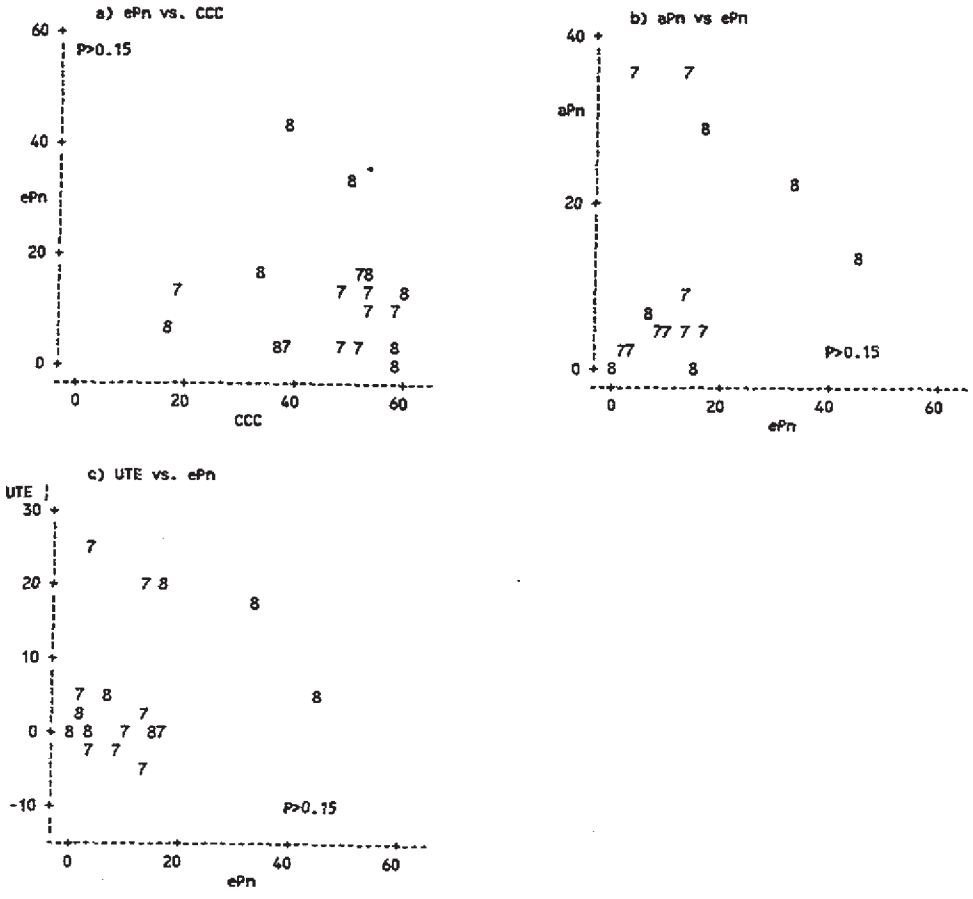


Figure 21. Relationship between enclosed ladyfern production (ePn, g/m^2) during summer in grass dominated strata and a) percent coniferous canopy closure (CCC), b) actual production under herbivory (aPn, g/m^2), and c) utilization (UTE, g/m^2). Value for observation indicates sample year (7=1987, 8=1988).

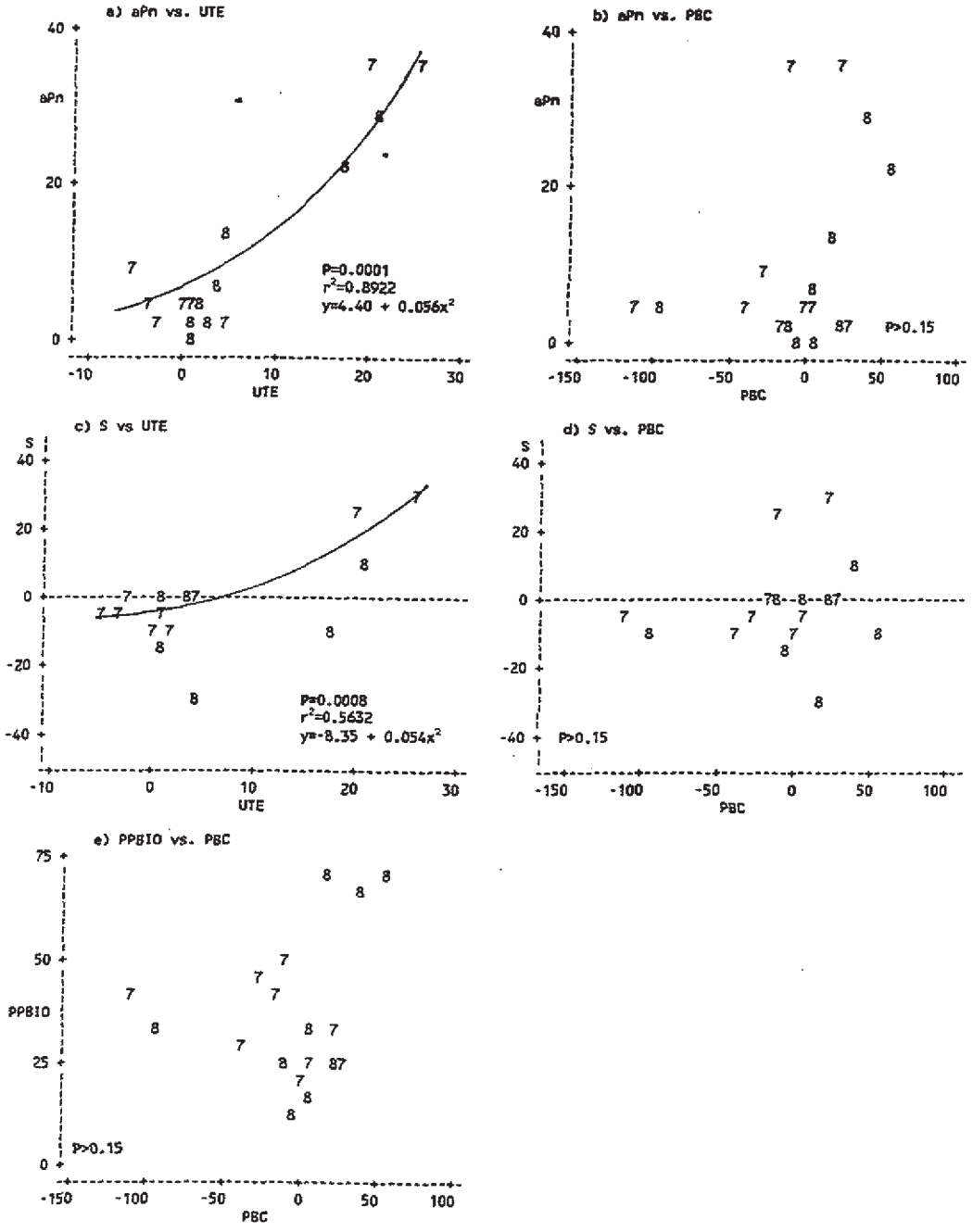


Figure 22. Relationships between ladyfern production and utilization in grass dominated strata during summer; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), c) effect of herbivory on production (S, or aPn - ungrazed production) (g/m^2) and UTE, d) S and PBC, and e) production as percent of biomass (PPBIO) and PBC. Value of observation indicates sample year (7=1987, 8=1988).

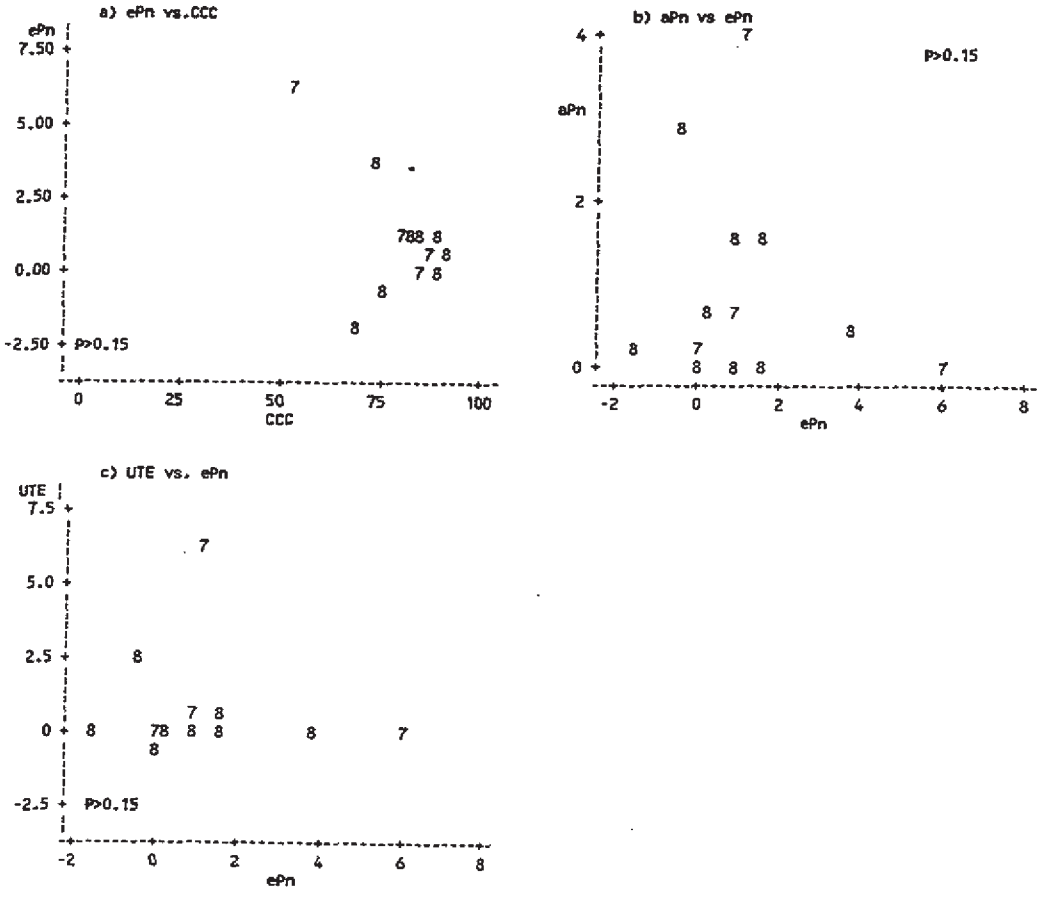


Figure 23. Relationship between enclosed fern production (ePn, g/m^2) during summer in forb dominated strata and a) percent coniferous canopy closure (CCC), b) actual production under herbivory (aPn, g/m^2), and c) utilization (UTE, g/m^2). Value for observation indicates sample year (7=1987, 8=1988).

production in FS was positively correlated with utilization (P = 0.0001) (Fig. 24a). There was no relationship between percent biomass consumed and actual production, or between S and utilization or percent biomass consumed (Figs. 24 b,c,d,e).

Forbs

Forb biomass, biomass concentration, forage quality, and concentration of nutrients were greater in GS than FS during both seasons (P < 0.05) (Table 10). Forage quality differences between strata appeared to be related in part to differences in species composition. Nutrient quality of forbs found in GS tended to be higher than nutrient quality of dominant forbs in FS (Appendices 1-5), and there was no difference between strata in CP of foamflower (Appendix 1). Forb height was greater in FS than GS during winter, and forb IVD did not differ between strata in winter 1987 (P >= 0.05) (Table 10).

Herbivory reduced forb biomass during both seasons in both strata (P <0.05), however that difference was not significant during summer in GS in 1988 or FS in 1987 (T*S*Y interaction P = 0.0199). Forb height also was reduced by herbivory during both seasons and years, however the effect was stronger in GS than FS during summer (Treatment*Strata interaction P = 0.0042). Reductions in biomass were counteracted by reductions in forb height, resulting in no difference in biomass concentration of forbs between treatments (P > 0.05). During summer, CP of forbs in GS was greater in grazed than ungrazed plants (P = 0.0001), however during winter CP of forbs in GS was either greater in ungrazed forbs (1987) or not different between treatments (1988). Forb CP did not differ between grazing treatments in FS during either season (P > 0.05). Forb IVD did not differ between grazing treatments in either strata or season. The only difference in forb nutrient concentration between grazed and enclosed plots occurred during summer in GS, when forb CP and IVD concentration were greater in grazed than ungrazed forbs (P <0.01) (Table 10).

Forb production during summer in GS differed between grazing treatments (P = 0.0007) but not years; grazed production was less than both actual and enclosed production (P < 0.01), but actual and enclosed production did not differ (P = 0.3851) thus there was exact compensation in grazed GS forbs. S also did not differ from zero (P = 0.6594).

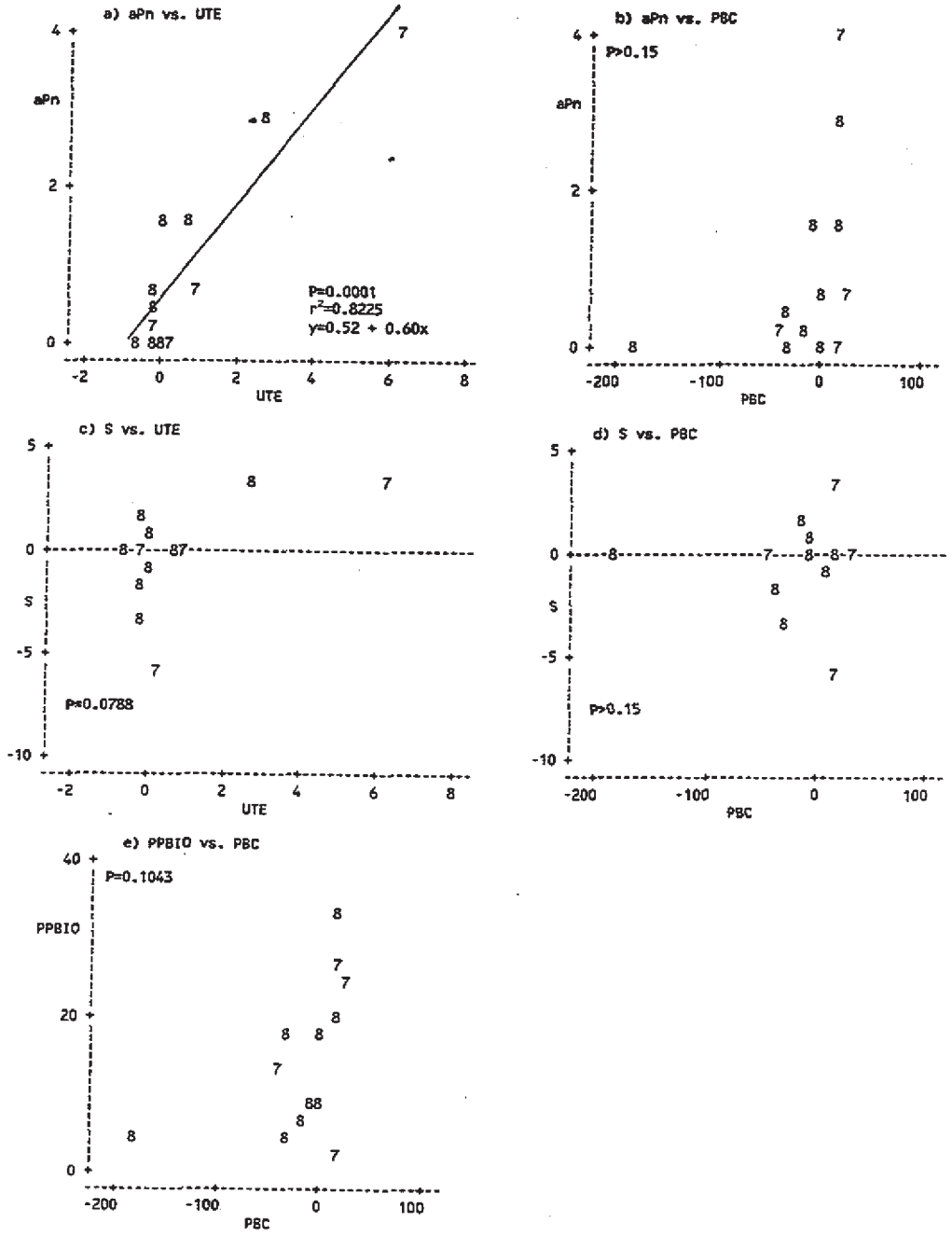


Figure 24. Relationships between fern production and utilization in forb dominated strata during summer; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), c) effect of herbivory on production (S, or aPn - ungrazed production) (g/m^2) and UTE, d) S and PBC, and e) production as percent of biomass (PPBIO) and PBC. Value of observation indicates sample year (7=1987, 8=1988). One outlier omitted from the regression analysis.

Table 10. Means and P values from three-way ANOVAs on effects of strata, year, and herbivory, by season, on forbs in old-growth forests in the South Fork Hoh, Olympic National Park.

SEASON / YEAR	GS[a] E[c]	GS[a] G[d]	FS[b] E	FS[b] G	Stderr	Year	Strata	Y*S	Tmt	Y*T	S*T	Y*S*T
a) Biomass (g/m^2)												
SUMMER[e]						0.2376	0.0001	0.5790	0.0014	0.1929	0.0816	0.0199
1987	45.23[g]	24.29	11.01	11.62	3.602	E>G in GS during 1987 and in FS during 1988						
1988	46.61	44.85	17.84	12.78								
WINTER[f]						0.6112	0.0159	0.5569	0.0366	0.7734	0.8301	0.5437
1987	12.56	8.48	5.70	3.67	1.752							
1988	9.37	7.54	6.24	3.42								
b) Plant Height (cm)												
SUMMER						0.6178	0.0001	0.1189	0.0001	0.0413	0.0001	0.0042
1987	23.2	12.3	8.7	8.5	0.846	E>G in both strata and years, but stronger in GS						
1988	18.0	13.1	10.5	9.1								
WINTER						0.0020	0.0027	0.6716	0.0001	0.0567	0.5785	0.3417
1987	6.9	4.6	8.1	5.5	0.527							
1988	5.1	3.5	5.9	5.5								
c) Biomass Concentration (g/m^3)												
SUMMER						0.0752	0.0132	0.3326	0.1475	0.9152	0.0523	0.1155
1987	177.4	206.9	126.9	144.6	21.000							
1988	252.8	326.9	181.9	148.5								
WINTER						0.7676	0.0007	0.7102	0.8809	0.6453	0.1367	0.3459
1987	195.0	213.5	71.9	73.7	21.652							
1988	181.6	215.0	112.3	69.5								
d) Percent Crude Protein												
SUMMER						0.9694	0.0225	0.2270	0.0169	0.3931	0.0009	0.5226
1987	11.35	12.74	11.05	10.43	0.333	G>E in GS only						
1988	10.84	12.33	11.12	11.22								
WINTER						0.1834	0.0001	0.1146	0.0874	0.0199	0.8480	0.0113
1987	15.81	14.33	9.53	9.25	0.296	E>G in GS during 1987 only						
1988	16.80	17.47	9.39	9.02								
e) Percent In Vitro Digestible Dry Matter												
SUMMER						0.3384	0.0023	0.6898	0.7218	0.6716	0.7687	0.9165
1987	54.98	54.06	41.11	39.60	2.188							
1988	55.97	56.69	45.53	46.01								
WINTER						0.0485	0.0001	0.0014	0.7578	0.0949	0.3618	0.4744
1987	46.58	43.08	42.49	42.12	1.347	GS>FS during 1988 only						
1988	57.85	58.99	38.04	39.57								
f) Crude Protein Concentration (g/m^3)												
SUMMER						0.1316	0.0060	0.4834	0.0194	0.8311	0.0068	0.2631
1987	19.7	28.1	13.91	14.97	2.991	G>E in GS only						
1988	26.4	40.5	19.41	16.57								
WINTER						0.6767	0.0001	0.9993	0.7725	0.5914	0.2689	0.1865
1987	33.2	31.9	6.95	6.91	3.445							
1988	30.2	38.3	10.61	6.62								
g) In Vitro Digestible Dry Matter Concentration (g/m^3)												
SUMMER						0.0930	0.0011	0.4278	0.0968	0.6048	0.0141	0.1692
1987	101.0	121.4	51.35	51.39	12.216	G>E in GS only						
1988	139.6	193.2	79.14	63.96								
WINTER						0.6166	0.0003	0.7882	0.9221	0.5871	0.3497	0.1689
1987	107.6	99.2	30.75	30.80	11.784							
1988	104.1	129.0	40.52	26.31								

[a]GS: grass dominated strata.
[b]FS: forb dominated strata
[c]E: enclosed, or ungrazed, treatment
[d]G: grazed treatment
[e]SUMMER: samples collected July - August.
[f]WINTER: samples collected in early March.
[g]sample size for each cell was 10.

Unlike grasses and ferns, utilization and actual production of forbs in GS were positively correlated with enclosed production ($P < 0.005$) (Fig. 25). However, enclosed production was not correlated with canopy closure ($P > 0.05$). As with other forage categories, forb actual production in GS was positively correlated with utilization and percent biomass consumed ($P < 0.001$, $r^2 > 0.52$), and percent biomass consumed was positively correlated with percent production ($P = 0.0039$, $r^2 = 0.3950$) (Fig. 26). Utilization, however, was not significantly correlated with S (Fig. 26). Year-round GS forb percent biomass consumed during 1987 was not correlated with actual or percent production, however actual production was positively correlated with utilization ($P = 0.0029$, $r^2 = 0.8112$), and percent production was correlated with percent production consumed. Percent production was maximized at utilization equalling 60% production consumed (Fig. 27).

Herbivory had less effect on forbs than grasses in GS; herbivory reduced forb biomass, but had little effect on biomass and nutrient concentration, and had no effect on forb production. Additionally, although forb use in GS was positively correlated with production, herbivory did not stimulate forb production. Instead, the cervids ate more forbs at the more productive sites. Unlike what was observed with total herbaceous species, for forbs the relationship between production and utilization was consistent for both actual and enclosed production.

Forb production during summer in FS was affected by herbivory ($P = 0.0015$), but the effects of herbivory varied between years ($T*Y$ $P = 0.0029$). During summer 1987 there was overcompensation; actual production was greater than both enclosed and grazed production, and grazed production was greater than enclosed production ($P < 0.05$). During summer 1988 there was exact compensation; there was no difference between treatments. Overall S was positive (8.256, $P = 0.0441$).

Because there was good interspersion between the 1987 and 1988 FS forb data points, the regression analysis was conducted with the years combined. In FS, forb enclosed production was not correlated with coniferous canopy closure, and utilization and actual production were not correlated with enclosed production ($P > 0.05$) (Fig. 28). As with herbs in FS, forb actual production, S, and percent production in FS were positively correlated with utilization and percent biomass consumed ($P < 0.01$, $r^2 > 0.47$) (Fig. 29). However, all relationships were linear, thus there was no asymptote of optimum forb utilization in FS. On a year-round basis, during 1987 utilization and percent

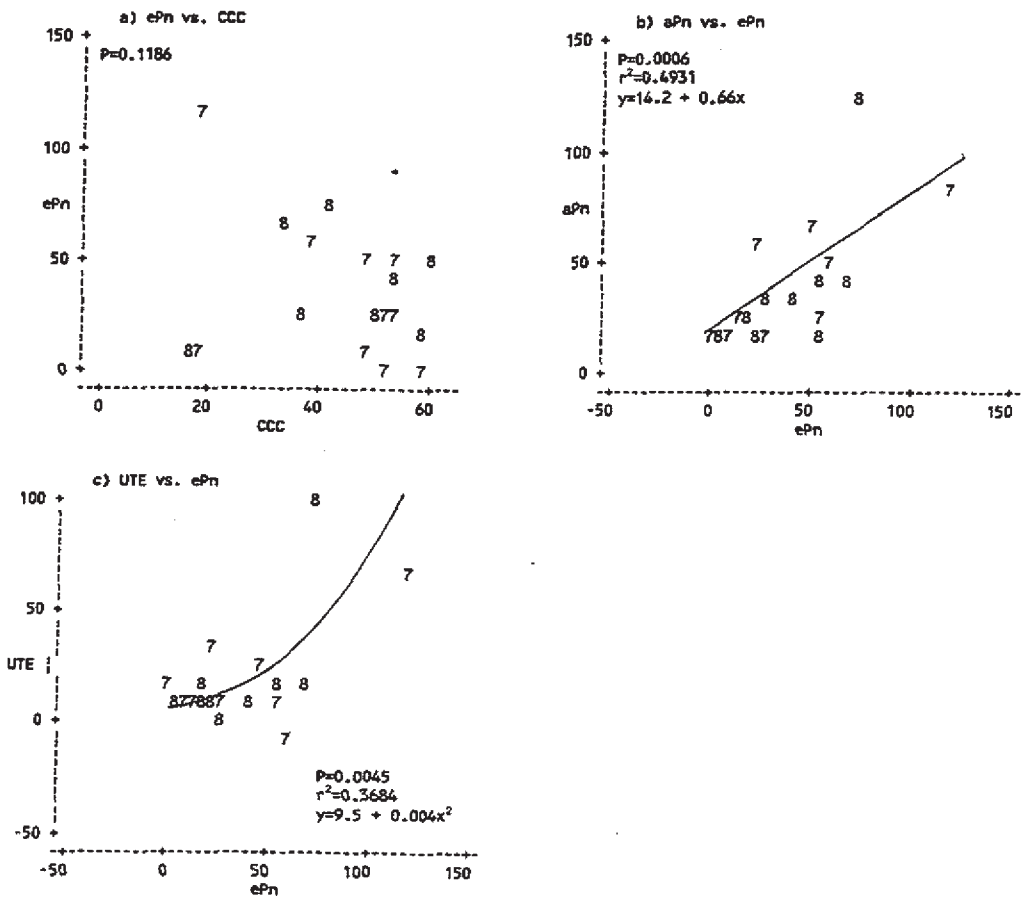


Figure 25. Relationship between enclosed forb production (ePn, g/m^2) during summer in grass dominated strata and a) percent coniferous canopy closure (CCC), b) actual production under herbivory (aPn, g/m^2), and c) utilization (UTE, g/m^2). Value for observation indicates sample year (7=1987, 8=1988).

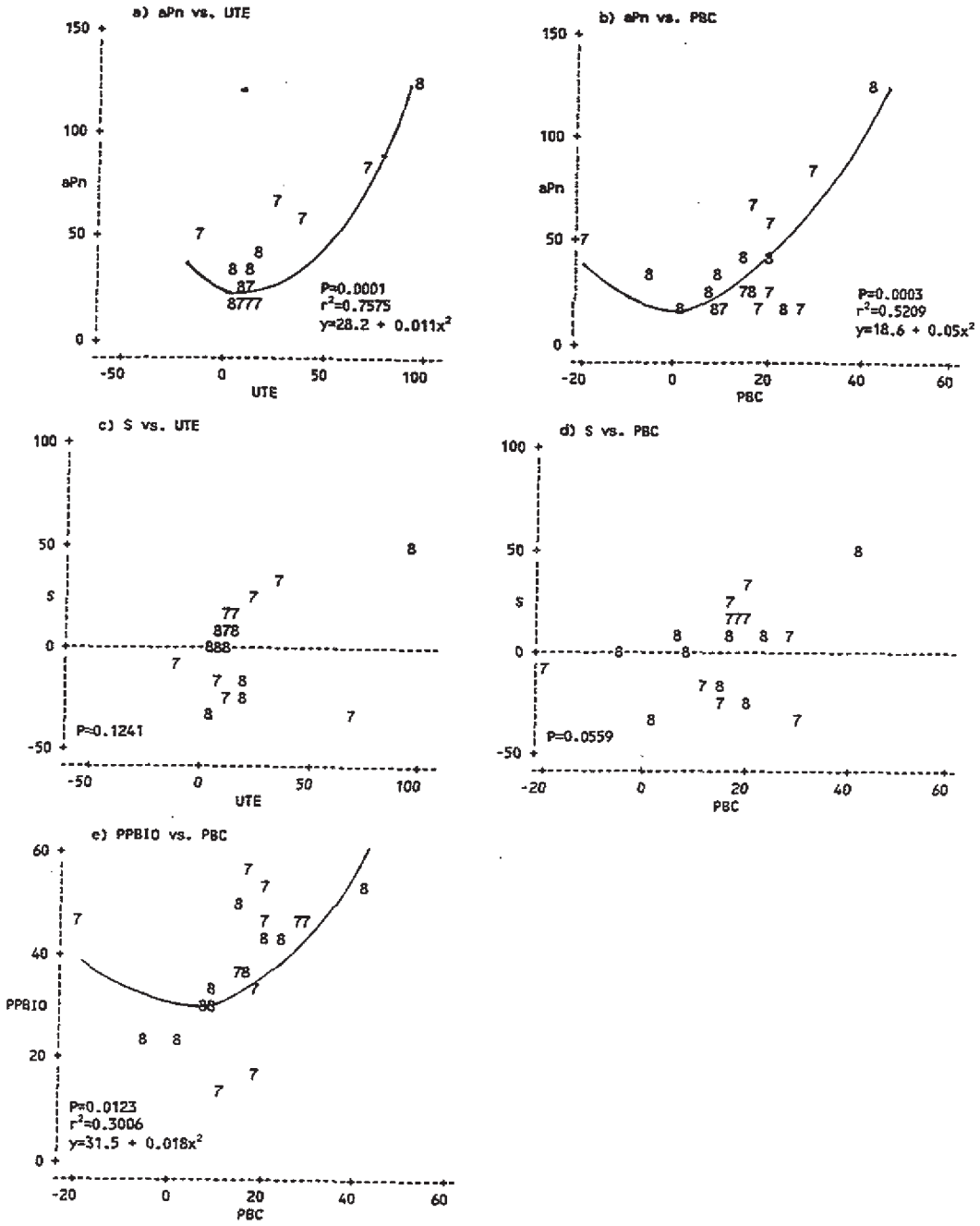


Figure 26. Relationships between forb production and utilization in grass dominated strata during summer; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), c) effect of herbivory on production (S, or aPn - ungrazed production) (g/m^2) and UTE, d) S and PBC, and e) production as percent of biomass (PPBIO) and PBC. Value of observation indicates sample year (7=1987, 8=1988).

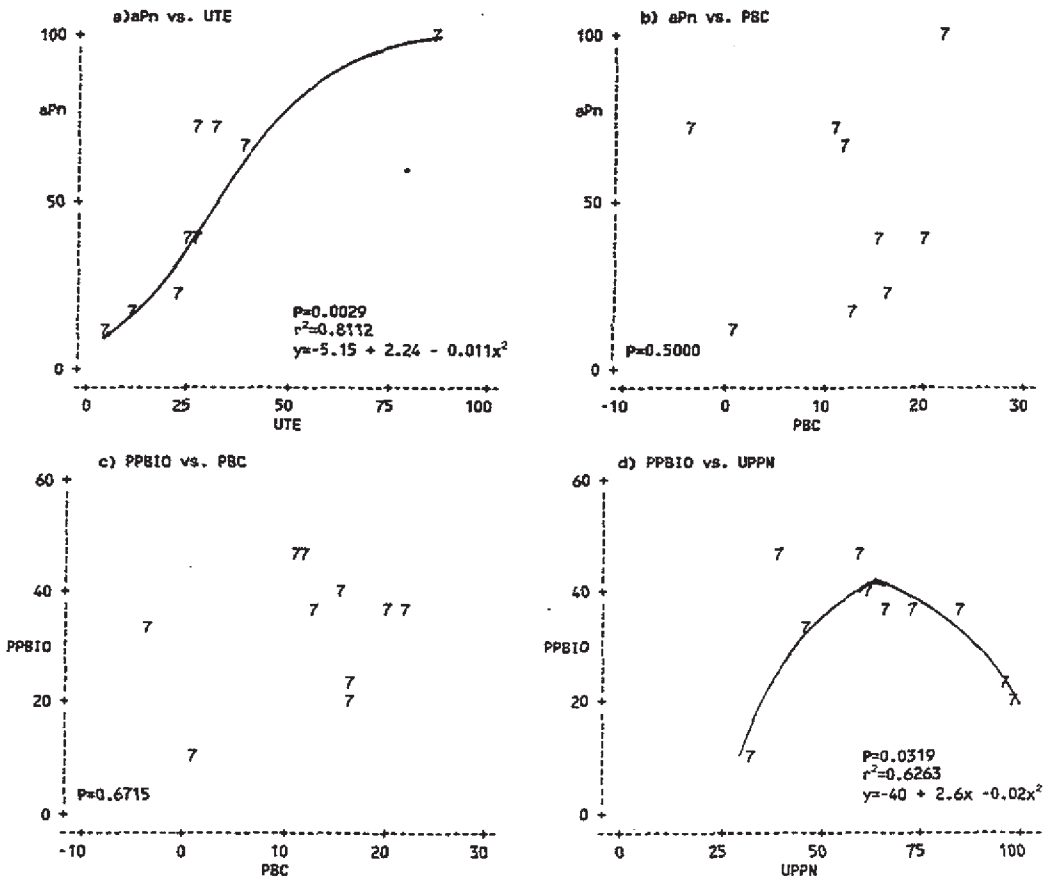


Figure 27. Relationships between forb production and utilization in grass strata on annual (March 1987 - March 1988) basis; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), c) production as percent of biomass (PPBIO) and PBC, and d) PPBIO and utilization as percent of aPn (UPPn). Data point value reflects sample year (7=1987).

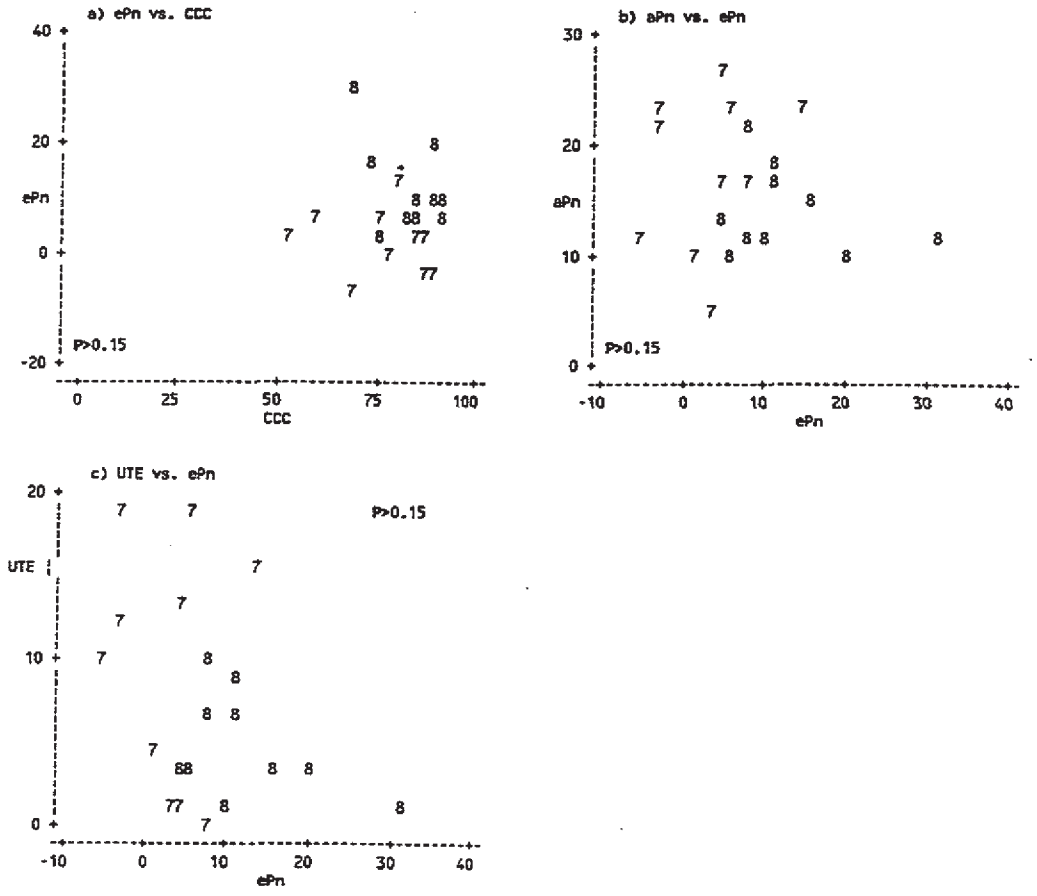


Figure 28. Relationship between enclosed forb production (ePn, g/m^2) during summer in forb dominated strata and a) percent coniferous canopy closure (CCC), b) actual production under herbivory (aPn, g/m^2), and c) utilization (UTE, g/m^2). Value for observation indicates sample year (7=1987, 8=1988).

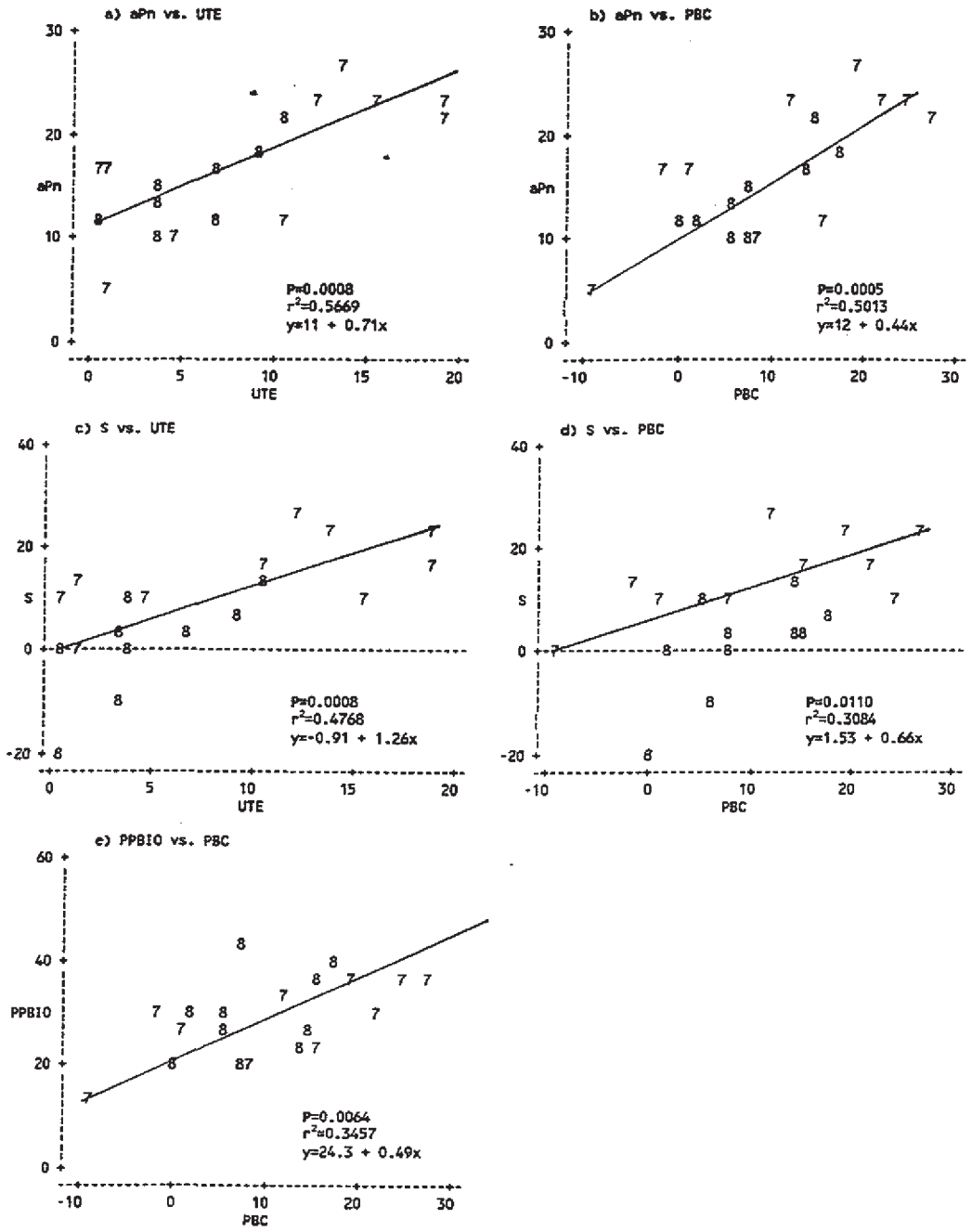


Figure 29. Relationships between forb production and utilization in forb dominated strata during summer; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), c) effect of herbivory on production (S, or aPn - ungrazed production) (g/m^2) and UTE, d) S and PBC, and e) production as percent of biomass (PPBIO) and PBC. Value of observation indicates sample year (7=1987, 8=1988).

biomass consumed of forbs in FS continued to be linearly correlated with actual production ($P > 0.01$), and percent production peaked at 25% biomass and 15-20% percent biomass consumed (Fig. 30).

Although herbivory reduced forb biomass in FS, it had no other effects on forb forage quality or biomass and nutrient concentration. Unlike what was observed for GS forbs, however, herbivory stimulated FS forb production, and there was overcompensation in FS forbs during summer 1987.

Shrub Utilization, Production, Biomass, and Forage Quality

Salmonberry

Forty-eight salmonberry stems were monitored in 1987, and 80 in 1988. During both years use of salmonberry increased throughout the growing season, peaked in July, and dropped off sharply in August. Monthly patterns of salmonberry use did not parallel herbaceous use in GS (Fig. 31). During each year, 98% of the tagged plants were browsed. There was no difference in utilization between years ($P > 0.05$). Leaf and twig utilization averaged 2.12 and 0.29 g/plant, or 69 and 26% of actual production respectively (56.7% total actual production).

At the end of the growing season, cervid herbivory had a significant effect on maximum standing crop biomass of both the leaf and twig component ($P < 0.0001$). Biomass of both leaves and twigs in the control salmonberry plants was greater than on the grazed plants (Table 11a). There was no difference in biomass between grazed and manipulated salmonberry plants, indicating that manipulations of salmonberry stems closely mimicked actual cervid herbivory. Crude protein of leaves and twigs was greater in grazed than ungrazed salmonberry ($P < 0.05$), however, there was no difference in IVD between treatments ($P > 0.50$) (Table 11b,c). At the end of the growing season, both plant height, incremental increase in height (height of current years growth - height of last years growth), and plant volume were reduced by herbivory ($P < 0.0001$) (Table 11d,e,f); grazed plants only grew an average of 7.5 cm, whereas control plants grew 24.2 cm. Although biomass was greater in ungrazed than grazed salmonberry, the reduction in volume in grazed plant was greater, resulting in greater biomass concentration in grazed than in ungrazed salmonberry shrubs at the end of the growing season ($P < 0.01$) (Table 11g). The effect of herbivory on biomass concentration was greater

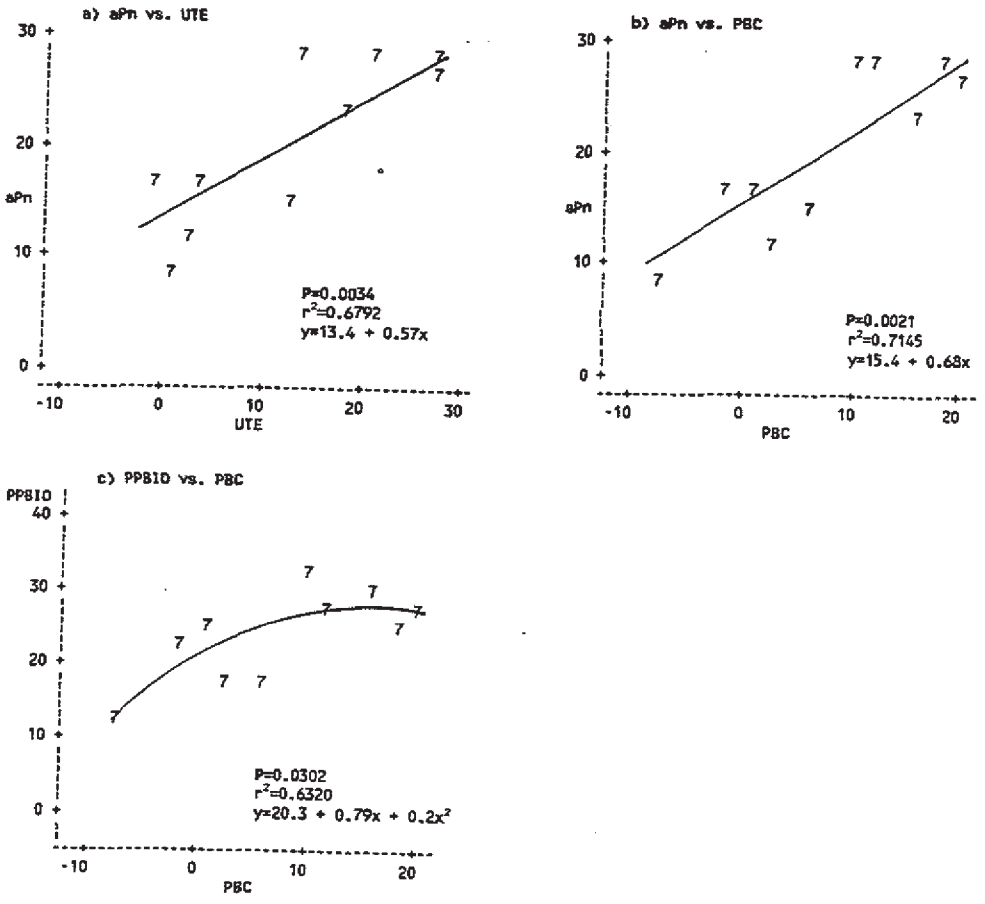


Figure 30. Relationships between forb production and utilization in forb strata on annual (March 1987 - March 1988) basis; a) actual production under herbivory (aPn) (g/m^2) and herbivory, or utilization (UTE) (g/m^2), b) aPn and percent biomass consumed (PBC), and c) production as percent of biomass (PPBIO) and PBC. Data point value reflects sample year (7=1987).

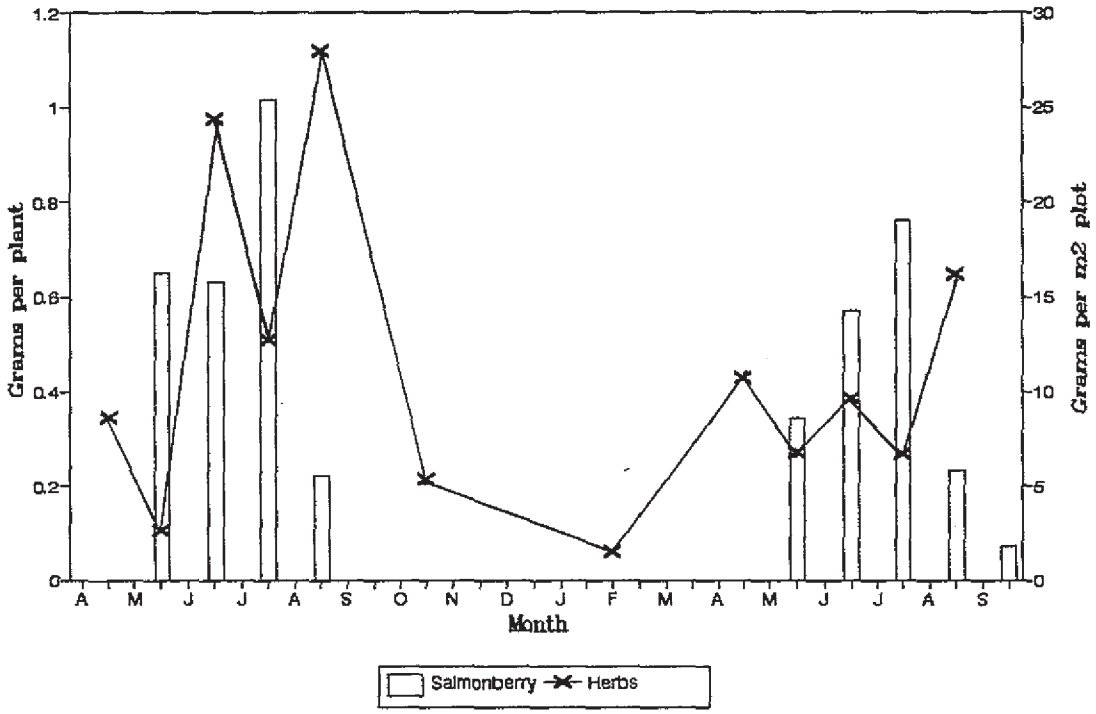


Figure 31. Year-round utilization of herbaceous biomass (g/m^2) and summer utilization of salmonberry (g/plant) in grass-dominated strata in the South Fork Hoh, April 1987-September 1988.

Table 11. Means and P values from two-way ANOVAs on the effect of cervid herbivory and year on current years growth of salmonberry leaves, twigs, and total combined biomass in old-growth forests in the South Fork Hoh, Olympic National Park, during summer 1987 and 1988.

	E[a]	A[b]	G[c]	Stderr	Year	Tmt	Y*Tmt	COVAR[d]
a) Maximum Standing Crop Biomass of Current Years Growth (g/plant)								
Leaves[e]	3.14[a]	1.04[b]	0.89[b]	0.191	0.7282	0.0001	0.5333	
Twigs	2.05[a]	1.05[b]	0.89[b]	0.156	0.7032	0.0001	0.2004	0.1654
Total	5.24[a]	2.12[b]	1.74[b]	0.311	0.7305	0.0001	0.1944	
b) Percent Crude Protein[f]								
Leaves	12.89[a]		14.48[b]	0.346		0.0102		
Stems	3.73[a]		5.75[b]	0.117		0.0001		
c) Percent In Vitro Digestible Dry Matter								
Leaves	23.09		23.71	0.653		0.5214		
Twigs	18.48		18.92	0.810		0.7074		
d) Plant Height (cm)								
Total	50.05[a]	32.93[b]	33.41[b]	1.047	0.6794	0.0001	0.0895	0.0001
e) Height Growth (cm) during year								
Total	24.41[a]	6.06[b]	7.41[b]	1.077		0.2114	0.0001	0.1621
f) Volume (g/m^3/plant)								
1987	0.0403[a]	0.0171[b]	0.0174[b]	0.00607	0.8069	0.0001	0.0236	
1988	0.0633[a]	0.0108[b]	0.0089[b]					
g) Biomass Concentration (g/m^3/plant)								
Leaves	86.07[a]	118.05[b]	102.51[ab]	6.997	0.3262	0.0094	0.4219	0.0242
Twigs	49.67[a]	108.59[b]	98.40[b]	6.395	0.4076	0.0001	0.7710	
Total	138.15[a]	227.72[b]	199.50[b]	11.358	0.3705	0.0001	0.7574	0.0356
h) Crude Protein Concentration (g/m^3/plant)								
Leaves	844.9[a]		1436.6[b]	83.49		0.0007		
Twigs	157.4[a]		553.4[b]	59.64		0.0011		
Total	1002.3[a]		1990.0[b]	132.59		0.0005		
i) In Vitro Digestible Dry Matter Concentration (g/m^3/plant)								
Leaves	1568.1[a]		2145.7[b]	145.24		0.0407		0.1794
Twigs	790.3[a]		1707.1[b]	117.06		0.0004		
Total	2235.6[a]		3975.4[b]	226.15		0.0004		
j) Production (g/plant)[g]								
Leaves	3.14[a]	3.23[a]	0.89[b]	0.230	0.4560	0.0001	0.1429	
Twigs	2.05[a]	1.35[b]	0.89[c]	1.589	0.6274	0.0001	0.1331	0.1678
Total	5.23[a]	4.55[a]	1.82[b]	0.344	0.5282	0.0001	0.1082	0.1981
k) Leaf/Twig ratio								
Biomass	1.68[a]	1.08[b]	1.17[b]	0.093	0.7538	0.0001	0.3017	
Production	1.68[a]	2.77[b]	1.17[c]	0.115	0.7671	0.0001	0.5389	

[a]E: enclosed, or ungrazed control, treatment. Plants were protected by an enclosure from March through August each year.
[b]A: manipulated treatment; plant was enclosed with the control treatment, but herbivory was simulated monthly matching use on paired plant in G treatment.
[c]G: grazed treatment. Plant was exposed to cervid herbivory.
[d]Covar: covariant use in ANOVA. Was basal stem diameter in all analyses except for height, where last years' height was used
[e]values with same letter superscript were not different ($P < 0.05$)
[f]forage quality measurements were made during 1988 only, and for only the C and G treatments
[g]production for E treatment was weight of current years growth (CYG) at maximum standing crop biomass, for A (actual production under herbivory) was biomass plus sum of weight removed by simulated utilization, for G (apparent production under herbivory) was weight of CYG at maximum standing crop biomass.

for twigs than for leaves. Those differences in biomass concentration resulted in greater CP concentration and IVD concentration in grazed than ungrazed plants ($P < 0.05$) (Table 11h,i).

Cervid herbivory also affected salmonberry production ($P < 0.0001$), however the effect differed between leaves and twigs. There was no difference between leaf enclosed and actual production, thus there was exact compensation in leaf production (even at an average of 69% percent production consumed). Leaf enclosed and actual production were both greater than leaf grazed production. Actual production of salmonberry twigs was less than enclosed production, indicating undercompensation. Both twig actual production and enclosed production were greater than twig grazed production. There was no difference between salmonberry enclosed and actual production when leaves and twigs were combined, indicating exact compensation in salmonberry production (Table 11j). S did not differ between years, and did not differ from zero ($P > 0.05$). Herbivory also affected the proportion of leafy tissue in current years growth. The proportion of leafy tissue in maximum standing crop biomass was reduced ($P = 0.0001$) however, the proportion of actual production that went to leaves as compared to twigs was increased ($P = 0.0001$) (Table 11k). Thus herbivory did not change the amount of biomass produced, but production of leaves increased at the expense of twigs.

There was no correlation between actual production, utilization, S, or enclosed production of salmonberry with canopy closure ($P > 0.05$). Salmonberry biomass, actual production, and utilization were positively correlated with BSD; actual production and utilization increased exponentially with increasing stem diameter, however salmonberry enclosed production did not increase with increases in BSD for stems larger than 8mm BSD (Fig. 32). Salmonberry percent biomass consumed was correlated curvilinearly with salmonberry BSD; percent biomass consumed was greatest in the smallest and largest of the shrubs sampled (100% of enclosed production) and moderate in medium-sized shrubs (50% enclosed production) (Fig. 32e).

Salmonberry actual production was positively correlated with enclosed production ($P < 0.05$). The relationship was linear with twigs and curvilinear with leaves (Fig. 33). At high levels of leaf enclosed production, leaf actual production remained constant (Fig. 33a). There was no correlation between leaf or twig utilization and enclosed production ($P > 0.05$); cervids did not eat more from plants that had more available biomass (Fig. 33d). Actual production of salmonberry leaves and twigs was positively correlated with

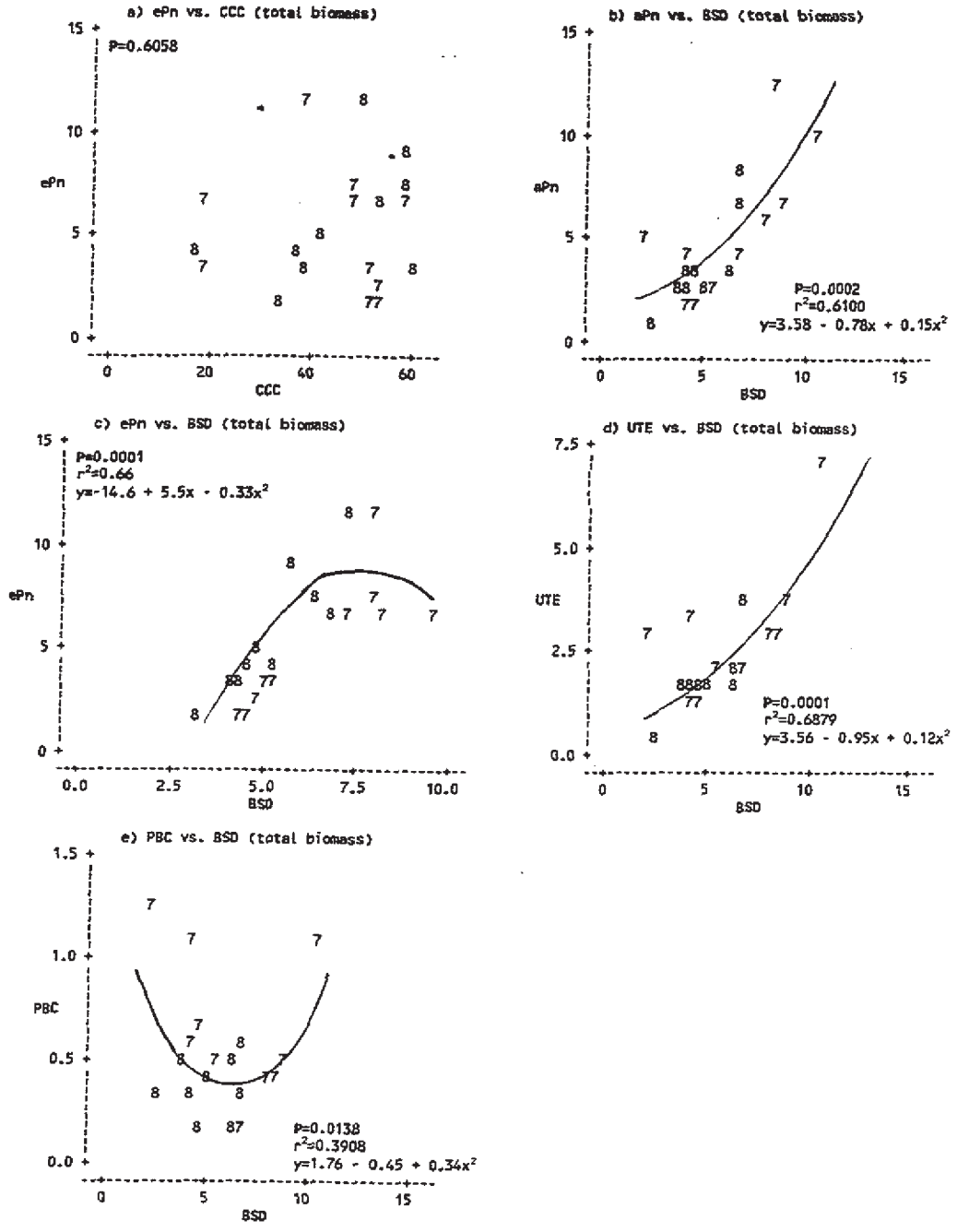


Figure 32. The relationship, during summer, between salmonberry a) total (leaf and stem) ungrazed production (ePn) (g/plant) and percent coniferous canopy closure (CCC), b) total production under herbivory (aPn) (g/stem) and stem basal stem diameter (BSD) (mm), c) ePn and BSD, d) total utilization (UTE) (g/stem) and BSD, and e) total percent biomass consumed (PBC) and BSD. Data value indicates sample year (7=1987, 8=1988).

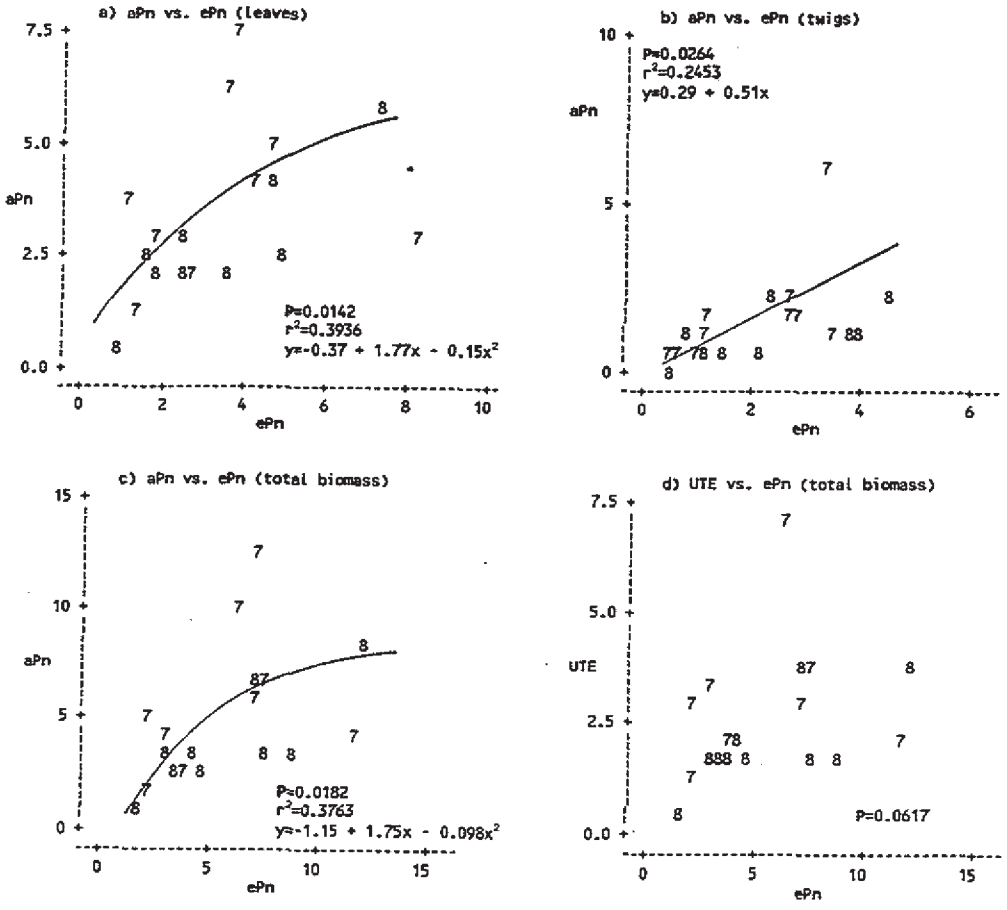


Figure 33. Relationship between salmonberry production under herbivory (aPn,g/stem) and ungrazed production (ePn, g/stem) during summer for a) leaves, b) twigs, and c) total biomass, and d) relationship between total utilization (UTE, g/stem) and ePn. Data value indicates sample year (7=1987, 8=1988).

utilization ($P < 0.05$), but the relationship differed between components. Leaf actual production increased throughout the range of observed utilization levels, although the rate of increase declined at higher levels of utilization (Fig. 34a). Twig actual production increased with utilization until 0.6 g/plant, and then decreased with increasing utilization (Fig. 34b). There was no correlation between utilization and S (Fig. 34 d,e,f), and no significant relationship between percent biomass consumed and actual production ($P > 0.05$) (Fig. 35 a,b,c). However, leaf and twig S were correlated with percent biomass consumed ($P < 0.05$). Both relationships were curvilinear; leaf production was maximized at 150% biomass consumed, and overall actual production was maximized at 100% biomass consumed. Twig production was never stimulated by herbivory, however the depressive effects of herbivory on twig production decreased as utilization increased, and there was exact compensation at 50% biomass consumed (Fig. 35 d,e,f). Although actual production increased with increasing percent biomass consumed, low to moderate levels of herbivory (20-60% biomass consumed) decreased actual production (Fig. 35f).

Red Huckleberry

Because red and blue huckleberry were found primarily in FS, and only sporadically in GS, grazing effects on huckleberry were investigated in FS only. I monitored utilization on 41 and 80 red huckleberry stems during 1987 and 1988 respectively. Red huckleberry occurred in all 10 FS sites each year. Use of red huckleberry by cervids peaked early in the growing season immediately following bud burst during both years. In 1987 use dropped sharply in June, and was non-existent in August (Fig. 36). During 1988 use of red huckleberry continued into August, but at lower levels than in May. Forty six percent of tagged red huckleberry stems were browsed in 1987, and 67% in 1988. There was no difference in mean utilization or percent production consumed per plant between years ($P > 0.05$). Use averaged 0.27 and 0.13 g of leaves and twigs per plant, respectively, or 16.0 and 10.9% production consumed (13.8% total percent production consumed).

Herbivory had less effect on red huckleberry than salmonberry. Red huckleberry maximum standing crop biomass was reduced by herbivory ($P < 0.05$), however the effect was greater with leaves than twigs (Table 12a). Crude protein content of red huckleberry twigs

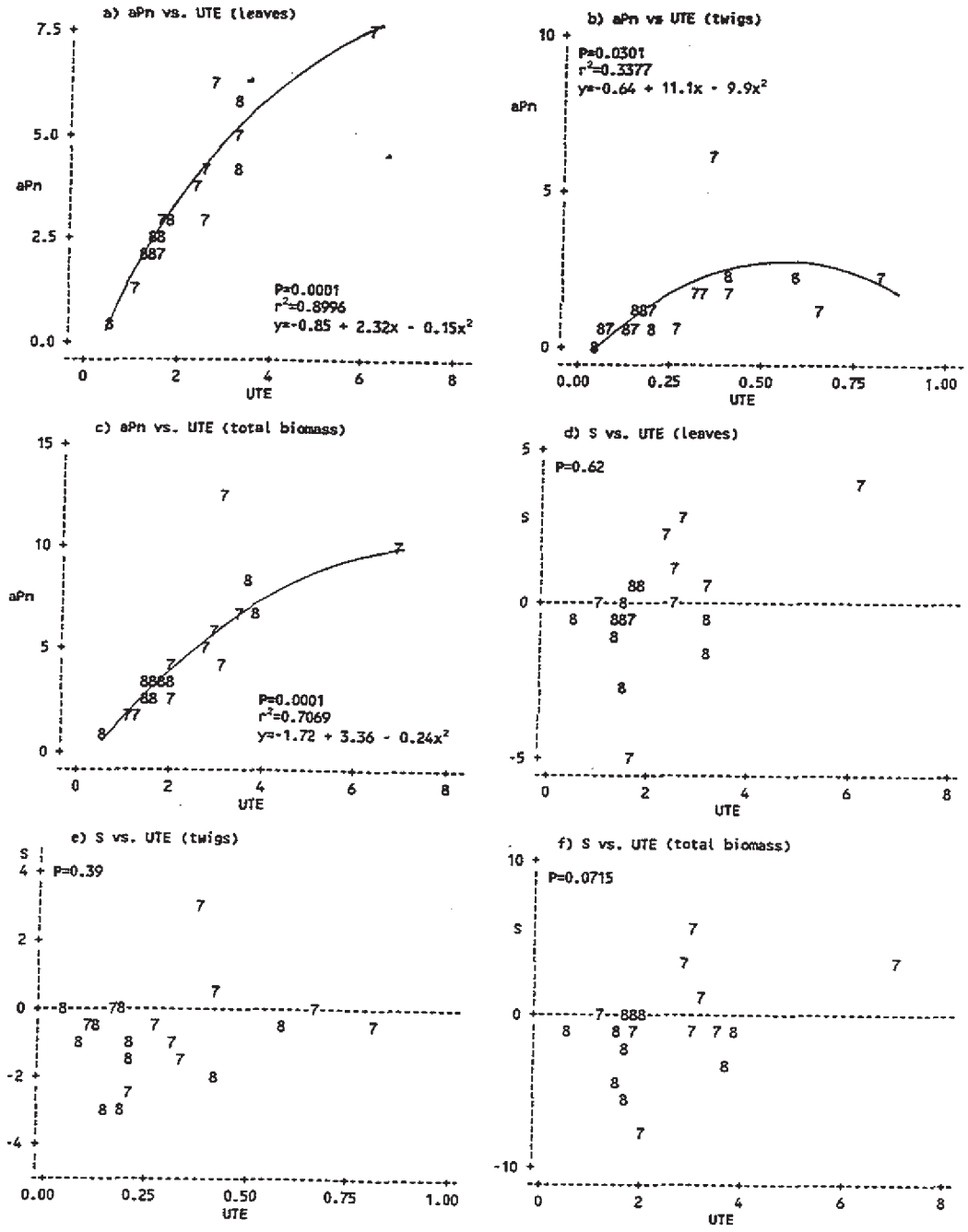


Figure 34. Relationships between salmonberry production under herbivory (aPn, g/stem) and utilization (UTE, g/stem) during summer for a) leaves, b) twigs, and c) total biomass, and relationships between the effect of herbivory on production (S, grazed - ungrazed production) (g/stem) and UTE for d) leaves, e) twigs, and f) total biomass. Data value indicates sample year (7=1987, 8=1988).

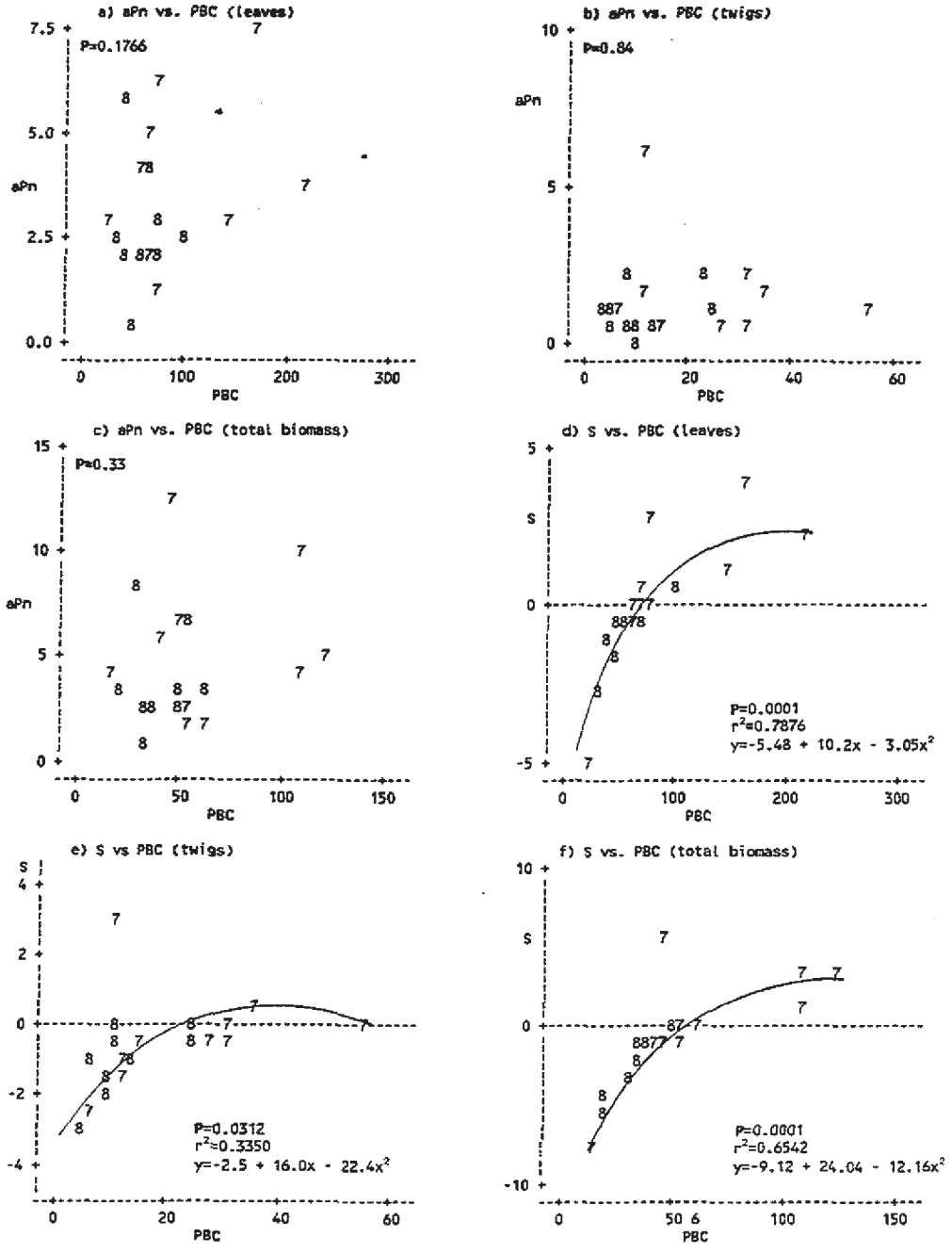


Figure 35. Relationships between salmonberry production under herbivory (aPn, g/stem) and percent biomass consumed (PBC) during summer for a) leaves, b) twigs, and c) total biomass, and relationships between the effect of herbivory on production (S, grazed - ungrazed production) (g/stem) and PBC for d) leaves, e) twigs, and f) total biomass. Data value indicates sample year (7=1987, 8=1988).

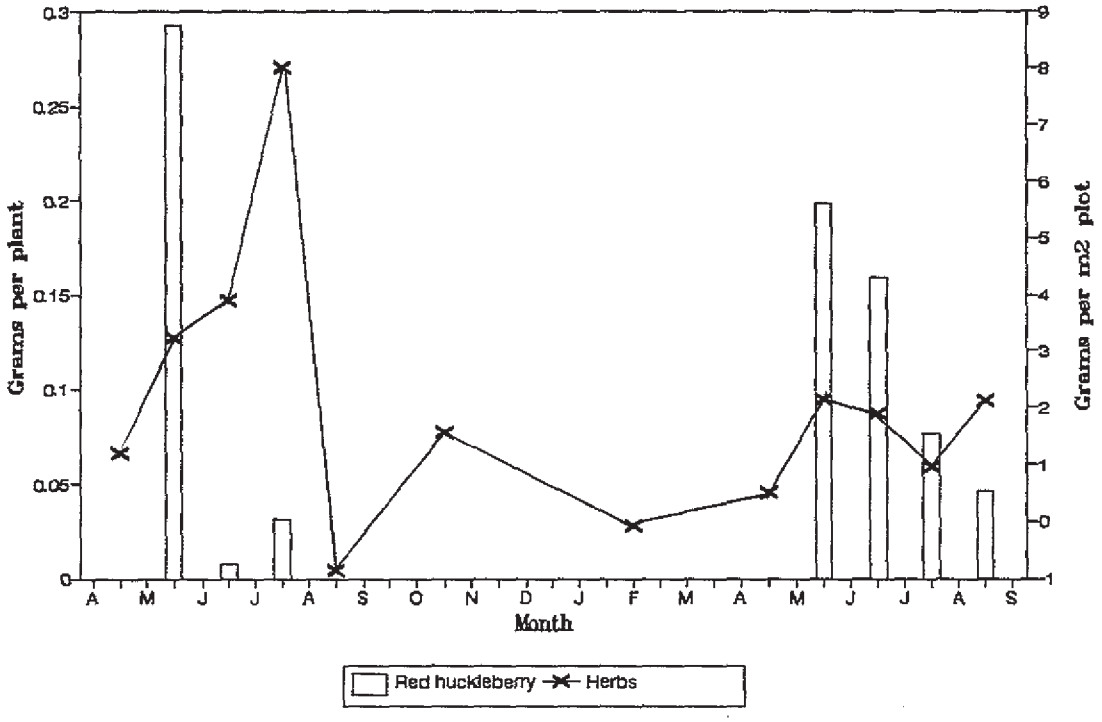


Figure 36. Year-round utilization of herbaceous biomass (g/m^2) and summer utilization of red huckleberry (g/plant) in forb-dominated strata in the South Fork Hoh, April 1987 - September 1988.

Table 12. Means and P values from two-way ANOVAs on the effect of cervid herbivory and year on current years growth of *red huckleberry* leaves, twigs, and total combined biomass in old-growth forests in the South Fork Hoh, Olympic National Park, during summer 1987 and 1988.

	E[a]	A[b]	G[c]	Stderr	Year	Tmt	Y*Tmt	COVAR[d]
a) Maximum Standing Crop biomass of current years growth (g/plant)								
Leaves[e]	2.06[a]	1.63[b]	1.46[b]	0.147	0.7572	0.0202	0.8174	0.0325
Twigs	1.92	1.29	1.51	0.181	0.7397	0.0594	0.5093	
Total	4.02[a]	2.93[b]	2.90[b]	0.314	0.7445	0.0230	0.7392	0.0978
b) Percent Crude Protein[f]								
Leaves	13.45		14.58	0.343		0.0512		
Twigs	5.57[a]		6.62[b]	0.201		0.0079		
c) Percent In Vitro Digestible Dry Matter								
Leaves	50.21		50.09	0.570		0.9042		0.1705
Twigs	28.25		30.70	0.830		0.0749		
d) Plant Height (cm)								
Total	82.47[a]	74.86[b]	76.26[b]	1.343		0.0028		0.0001
e) Height Growth (cm) during year (1988 only)								
Total	12.73[a]	4.51[b]	5.90[b]	1.321		0.0010		
f) Volume (g/m^3/plant)								
Total	0.0905	0.0846	0.0787	0.0106	0.2584	0.7497	0.3735	0.0397
g) Biomass Concentration (g/m^3/plant)								
Leaves	30.86	30.84	24.07	3.967	0.4937	0.3903	0.8365	
Twigs	28.33	25.58	23.47	3.176	0.8510	0.5616	0.7065	
Total	59.18	56.41	47.53	7.029	0.6653	0.4809	0.7934	
h) Crude Protein Concentration (g/m^3/plant) (1988 only)								
Leaves	364.2		302.7	37.00		0.2782		
Twigs	145.4		157.4	21.14		0.6695		
Total	509.6		460.2	52.50		0.5266		
i) In Vitro Digestible Dry Matter Concentration (g/m^3/plant) (1988 only)								
Leaves	1369.6		1053.1	139.45		0.1525		
Twigs	750.3		762.2	106.38		0.9393		
Total	2120.0		1815.2	226.53		0.3732		
j) Production (g/plant)[g]								
Leaves	2.08[a]	2.05[a]	1.43[b]	0.151	0.7843	0.0099	0.7880	0.0135
Twigs	1.92	1.48	1.51	0.181	0.7407	0.1837	0.5121	
Total	4.05[a]	3.55[ab]	2.87[b]	0.315	0.7587	0.0470	0.7746	0.0490
k) Leaf/twig ratio								
Biomass	1.1	1.27	1.12	0.054	0.5307	0.0749	0.2825	
Production	1.1[a]	1.39[b]	1.12[a]	0.057	0.5701	0.0018	0.3259	
l) Number of berries per plant								
1988	1.836	3.311	3.001	1.205		0.6659		
m) Weight of berries per plant								
1988	0.4059	0.9947	0.3757	0.384		0.4451		

[a]E: enclosed, or ungrazed control, treatment. Plants were protected by an enclosure from March through August each year.
[b]A: manipulated treatment; plant was enclosed with the control treatment, but herbivory was simulated monthly matching use on paired plant in G treatment.
[c]G: grazed treatment. Plant was exposed to cervid herbivory.
[d]Covar: covariant use in ANOVA. Was basal stem diameter in all analyses except for height, where last years' height was used
[e]values with same letter superscript were not different ($P < 0.05$)
[f]forage quality measurements were made during 1988 only, and for only the C and G treatments
[g]production for E treatment was weight of current years growth (CYG) at maximum standing crop biomass, for A (actual production under herbivory) was biomass plus sum of weight removed by simulated utilization, for G (apparent production under herbivory) was weight of CYG at maximum standing crop biomass.

increased with herbivory ($P = 0.0079$), but CP of leaves did not ($P = 0.0512$) (Table 12b). Herbivory had no effect on red huckleberry IVD ($P > 0.05$) (Table 12c). Herbivory decreased red huckleberry incremental height increase ($P = 0.0010$) (Table 12e), but that reduction in plant stature was not sufficient to decrease plant volume (Table 12f). Consequently, there was no difference in red huckleberry biomass or nutrient concentration between treatments ($P > 0.05$) (Table 12g,h,i).

Cervid herbivory affected red huckleberry production, but the effect varied between components. Actual and enclosed production of leaves did not differ, indicating exact compensation (Table 12j). Herbivory had no effect on twig production (i.e., actual production = enclosed production = grazed production); and when leaves and twigs were combined, enclosed production did not differ from actual production, but it was greater than grazed production. S did not differ between years and did not differ from zero ($P > 0.05$). Leaf/twig ratio did not differ between treatments at maximum standing crop biomass ($P = 0.0749$), however a greater proportion of leaves was produced by grazed than by ungrazed red huckleberry ($P = 0.0018$) (Table 12k). Herbivory did not affect the number or weight of berries produced in 1988 ($P > 0.05$), but the variation within treatments was very high (Table 12 l,m).

As with salmonberry, there was no correlation between production or utilization of red huckleberry and canopy closure ($P > 0.05$). Also, actual production, enclosed production, and utilization were positively correlated with BSD ($P < 0.05$) (Fig. 37). Red huckleberry utilization was approximately constant in medium to large-sized plants (BSD > 8 mm). There was no relationship between percent biomass consumed and plant size ($P = 0.34$). Also, similar to salmonberry, red huckleberry leaf and twig actual production were positively correlated with enclosed production ($P < 0.01$), and there was no relationship between utilization and enclosed production ($P > 0.05$) (Fig. 38). Unlike salmonberry, there was no correlation between red huckleberry actual production and utilization or percent biomass consumed, nor was there any relationship between S and utilization ($P > 0.05$) (Fig. 39).

Thus it appeared that observed levels of cervid herbivory in the SFH had little effect on red huckleberry, with the exception of decreased leaf standing crop biomass, and increased leaf production at the expense of twig production. The net result of cervid herbivory in red huckleberry was to decrease biomass available per shrub, but there

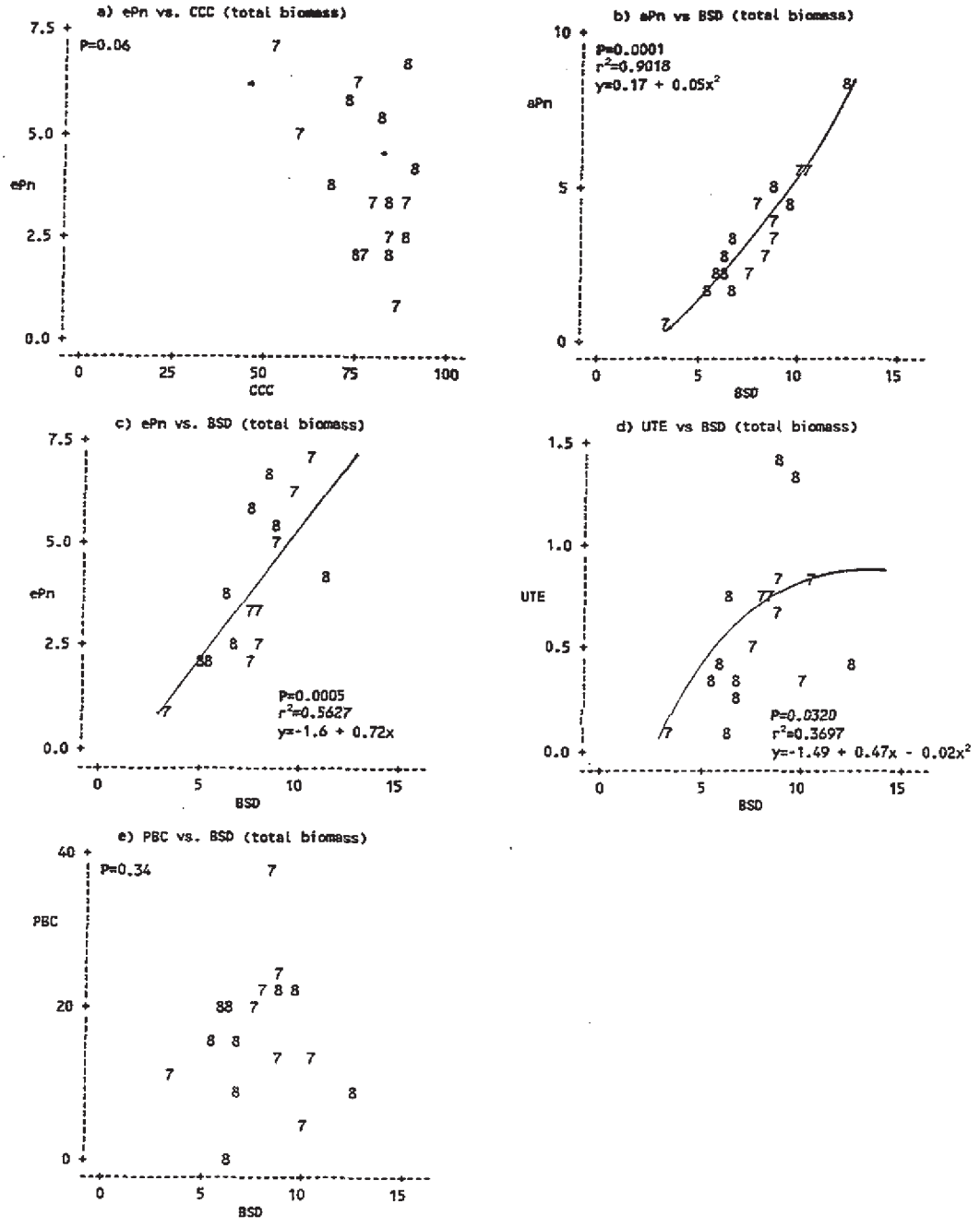


Figure 37. The relationship during summer between red huckleberry a) total (leaf and twig) ungrazed production (ePn) (g/plant) and percent coniferous canopy closure (CCC), b) total production under herbivory (aPn) (g/stem) and stem basal stem diameter (BSD) (mm), c) ePn and BSD, d) total utilization (UTE) (g/stem) and BSD, and e) total percent biomass consumed (PBC) and BSD. Data value indicates sample year (7=1987, 8=1988).

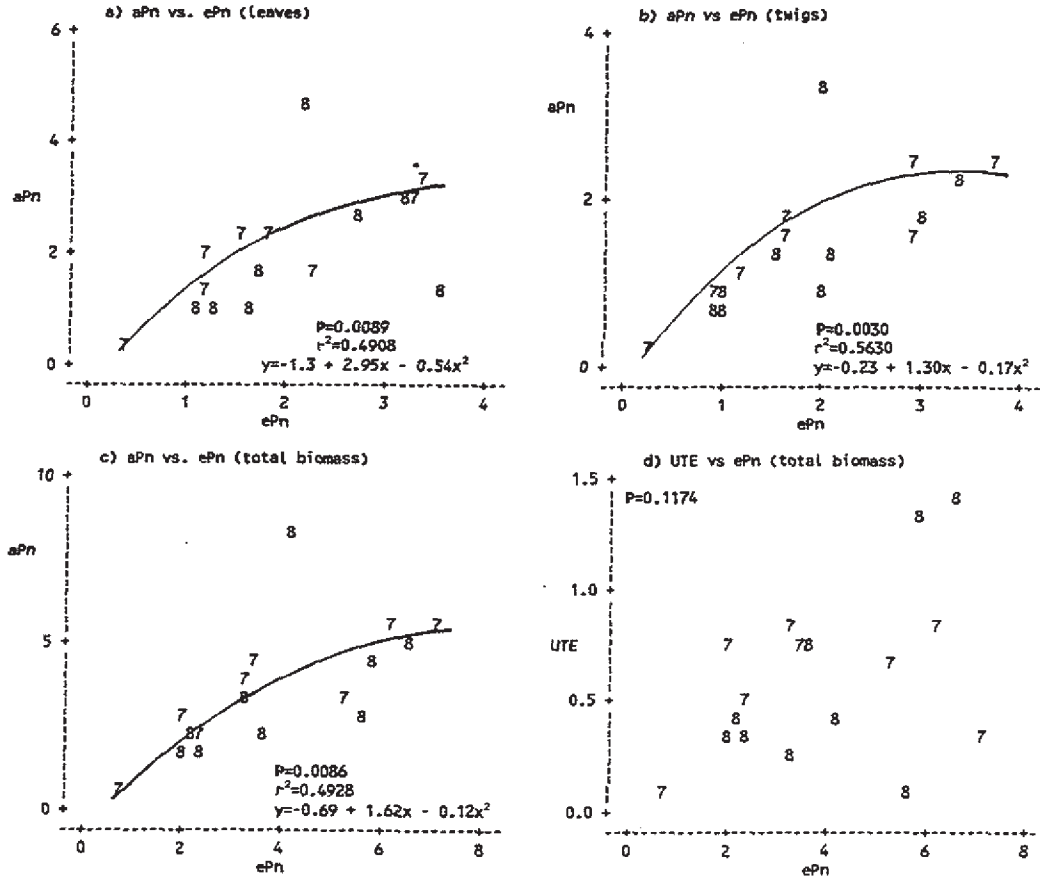


Figure 38. Relationship between red huckleberry production under herbivory (aPn,g/stem) and ungrazed production (ePn, g/stem) during summer for a) leaves, b) twigs, and c) total biomass, and d) relationship between total utilization (UTE, g/stem) and ePn. Data value indicates sample year (7=1987, 8=1988).

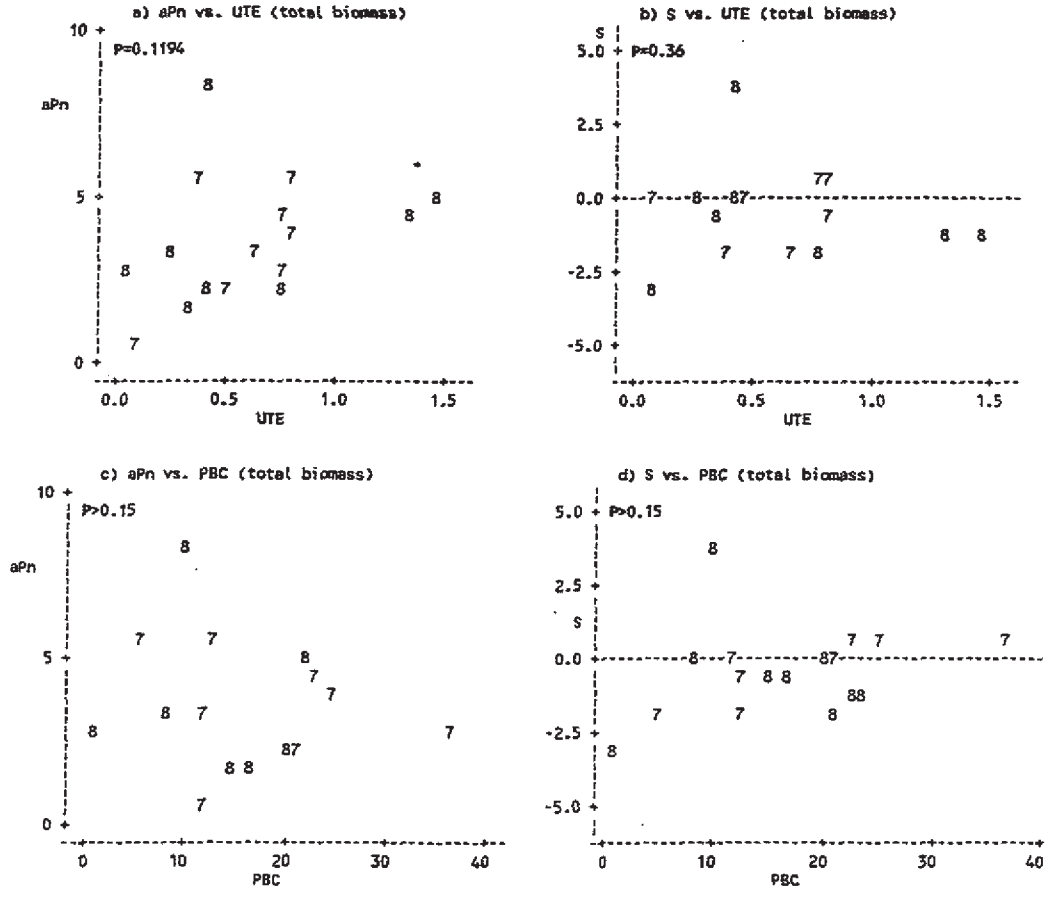


Figure 39. Relationships between production and utilization of red huckleberry total biomass during summer; a) production under herbivory (aPn, g/stem) and utilization (UTE, g/stem), b) the effect of herbivory on production (S, grazed - ungrazed production) (g/stem) and UTE, c) aPn and percent biomass consumed (PBC), and d) S and PBC. Data value indicates sample year (7=1987, 8=1988).

was no difference on a biomass concentration basis between grazed and ungrazed plants.

Blue Huckleberry

Thirty-two blue huckleberry stems were monitored in 1987, and 62 in 1988. Blue huckleberry occurred in 8 out of 10 FS plots each year. Yearly and monthly patterns of blue huckleberry use were very similar to that of red huckleberry; i.e., blue huckleberry use was greatest in May of each year, immediately following bud burst (Fig. 40). Forty-seven and 63% of blue huckleberry plants were browsed in 1987 and 1988, respectively. Blue huckleberry utilization did not differ between years ($P > 0.05$), and appeared slightly greater than red huckleberry utilization. Leaf and twig use averaged 0.27 and .089 g, or 23.3 and 15.3 percent production consumed respectively (mean total plant percent production consumed= 20.8).

Cervid utilization affected biomass and production of blue huckleberry. Standing crop biomass of twigs and total phytomass were greater on control than on grazed plants ($P < 0.05$), but there was no difference between treatments in leaf standing crop biomass ($P = 0.0675$) (Table 13a). Although herbivory reduced biomass, it had no effect on blue huckleberry CP or IVD ($P > 0.05$) (Table 13b,c). Herbivory reduced blue huckleberry growth from 9.7 cm in control plants to 3.8 cm in grazed plants ($P >0.01$) (Table 13d,e). Unlike red huckleberry, blue huckleberry volume was reduced by herbivory ($P =0.0248$), however the decrease in volume was offset by decreased biomass, and resulted in no difference in biomass or nutrient concentration between treatments ($P > 0.05$) (Table 13g,h,i).

Cervid herbivory influenced blue huckleberry production ($P < 0.05$) (Table 13j). There was no difference between enclosed and actual production of leaves, indicating exact compensation, but twig enclosed production was greater than twig actual production, indicating undercompensation (Table 13j). When leaves and twigs were combined, the net result was exact compensation. S differed between years; S of leaves was positive in 1987, and twig S was negative in 1988. As with red huckleberry, there was no difference in the relative proportions of leaf and twig tissue between grazed and ungrazed blue huckleberry standing crop biomass ($P = 0.47$). However, the proportion of leaf production was significantly greater in grazed than ungrazed blue huckleberry ($P = 0.0058$) (Table 13k).

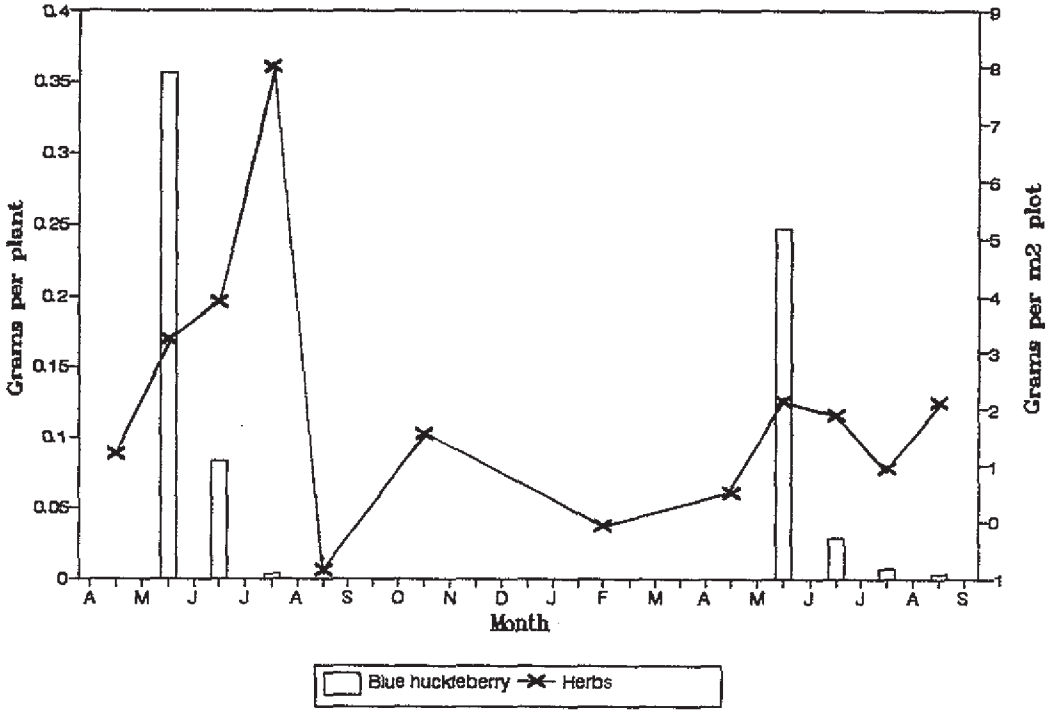


Figure 40. Year-round utilization of herbaceous biomass (g/m^2) and summer utilization of blue huckleberry (g/plant) in forb-dominated strata in the South Fork Hoh, April 1987 - September 1988.

Table 13. Means and P values from two-way ANOVAs on the effect of cervid herbivory and year on current years growth of blue huckleberry leaves, twigs, and total combined biomass in old-growth forests in the South Fork Hoh, Olympic National Park, during summer 1987 and 1988.

	E[a]	A[b]	G[c]	Stderr	Year	Tmt	Y*Tmt	COVAR[d]
a) Maximum Standing Crop biomass of current years growth (g/plant)								
Leaves[e]	1.04	0.78	0.79	0.084	0.0717	0.0675	0.5420	
Twigs	0.71[a]	0.43[b]	0.46[b]	0.060	0.1089	0.0057	0.4541	0.1257
Total	1.75[a]	1.24[b]	1.25[b]	0.123	0.0835	0.0116	0.4240	
b) Percent Crude Protein[f]								
Leaves	14.18		13.34	0.320		0.1127		
Twigs	5.85		6.35	0.172		0.0888		
c) Percent In Vitro Digestible Dry Matter								
Leaves	43.69		41.99	0.6548		0.1161		
Twigs	23.13		23.00	0.8000		0.9142		
d) Plant Height (cm) (1988 only)								
Total	42.69[a]	34.79[b]	37.15[b]	1.400		0.0057		0.0006
e) Height Growth (cm) during year (1988 only)								
Total	9.70[a]	1.61[b]	3.84[b]	1.209		0.0012		
f) Volume (g/m^3/plant)								
Total	0.0168[a]	0.0118[b]	0.0114[b]	0.00015	0.7340	0.0248	0.3618	0.0125
g) Biomass Concentration (g/m^3/plant)								
Leaves	64.37	72.44	74.52	7.370	0.1278	0.5734	0.4143	0.0982
Twigs	41.02	39.28	44.28	5.818	0.0783	0.8282	0.7465	
Total	105.65	108.03	118.76	12.332	0.0902	0.7291	0.8738	
h) Crude Protein Concentration (g/m^3/plant) (1988 only)								
Leaves	788.2		918.7	99.8		0.3907		
Twigs	214.5		220.4	24.20		0.8689		
Total	1002.7		1139.1	118.09		0.4452		
i) In Vitro Digestible Dry Matter Concentration (g/m^3/plant) (1988 only)								
Leaves	2473.1		2886.1	323.18		0.4011		
Twigs	852.4		804.4	122.89		0.7915		
Total	3325.5		3690.4	422.18		0.5635		
j) Production (g/plant)[g]								
Leaves	1.01[a]	1.21[a]	0.79[b]	0.095	0.0859	0.0180	0.1622	
Twigs	0.71[a]	0.55[b]	0.46[b]	0.054	0.1247	0.0090	0.2211	0.0200
Total	1.72[a]	1.73[a]	1.25[b]	0.121	0.0962	0.0126	0.1029	0.0531
k) Leaf/Twig ratio								
Biomass	1.69	1.93	1.9	0.150	0.6728	0.4745	0.3250	
Production	1.67[a]	2.38[b]	1.9[a]	0.141	0.6879	0.0058	0.2389	0.0692

[a]E: enclosed, or ungrazed control, treatment. Plants were protected by an enclosure from March through August each year.
[b]A: manipulated treatment; plant was enclosed with the control treatment, but herbivory was simulated monthly matching use on paired plant in G treatment.
[c]G: grazed treatment. Plant was exposed to cervid herbivory.
[d]Covar: covariant use in ANOVA. Was basal stem diameter in all analyses except for height, where last years' height was used
[e]values with same letter superscript were not different ($P < 0.05$)
[f]forage quality measurements were made during 1988 only, and for only the C and G treatments
[g]production for E treatment was weight of current years growth (CYG) at maximum standing crop biomass, for A (actual production under herbivory) was biomass plus sum of weight removed by simulated utilization, for G (apparent production under herbivory) was weight of CYG at maximum standing crop biomass.

As with salmonberry and red huckleberry, blue huckleberry actual production, enclosed production and utilization were positively correlated with BSD ($P < 0.05$), and as with red huckleberry, utilization of blue huckleberry stabilized in larger shrubs (Fig. 41). Once again, there was no correlation between percent biomass consumed and BSD ($P = 0.15$) (Fig. 41); indicating that the cervids consumed the same percentage of biomass in small and large shrubs. As with red huckleberry, blue huckleberry actual and enclosed production were positively correlated. However, unlike red huckleberry, blue huckleberry utilization was also correlated with enclosed production ($P < 0.05$); the cervids ate more from plants with more available biomass (Fig. 42). Unlike red huckleberry, blue huckleberry actual production was positively correlated with utilization and percent biomass consumed ($P < 0.05$), however the relationship was stronger for leaves than twigs; leaf actual production continued to increase throughout the observed range of utilization. Leaf S was also positively correlated with utilization and percent biomass consumed ($P < 0.05$), but twig S was not ($P > 0.05$) (Fig.s 43,44).

Swordfern Utilization, Production, Biomass, and Forage Quality

Swordfern occurred in 47% of FS and 55% of GS annual exclosures. Swordfern utilization was greater in GS than in FS ($P <0.05$). Mean swordfern utilization in FS was 0.85 g/plant, or 6.2% actual production; swordfern was grazed in only 33% of plots, or 32% of plants in FS. Utilization of swordfern in GS averaged 6.21 g/plant or 25.3% actual production, and swordfern was grazed in 100% of the plots and 83% of the plants. On swordfern plants that were browsed, an average of 51 and 57% of the fronds were browsed in GS and FS respectively. In both strata, swordfern use during summer peaked in May in 1987 and during June in 1988 (Fig. 45).

Because swordfern distribution and plant size was variable, it was not always possible to obtain paired plants across 3 treatments. The number of previous years fronds differed between ungrazed, manipulated, and grazed treatments ($P = 0.0310$) (Table 14a). Since swordfern biomass and production are correlated with number of fronds, and number of current years' fronds was correlated with number of previous years' fronds, plants were apparently poorly paired across treatments. Control plants were smaller than manipulated or grazed plants. Low sample size and high variability may have obscured grazing and production relationships in swordfern.

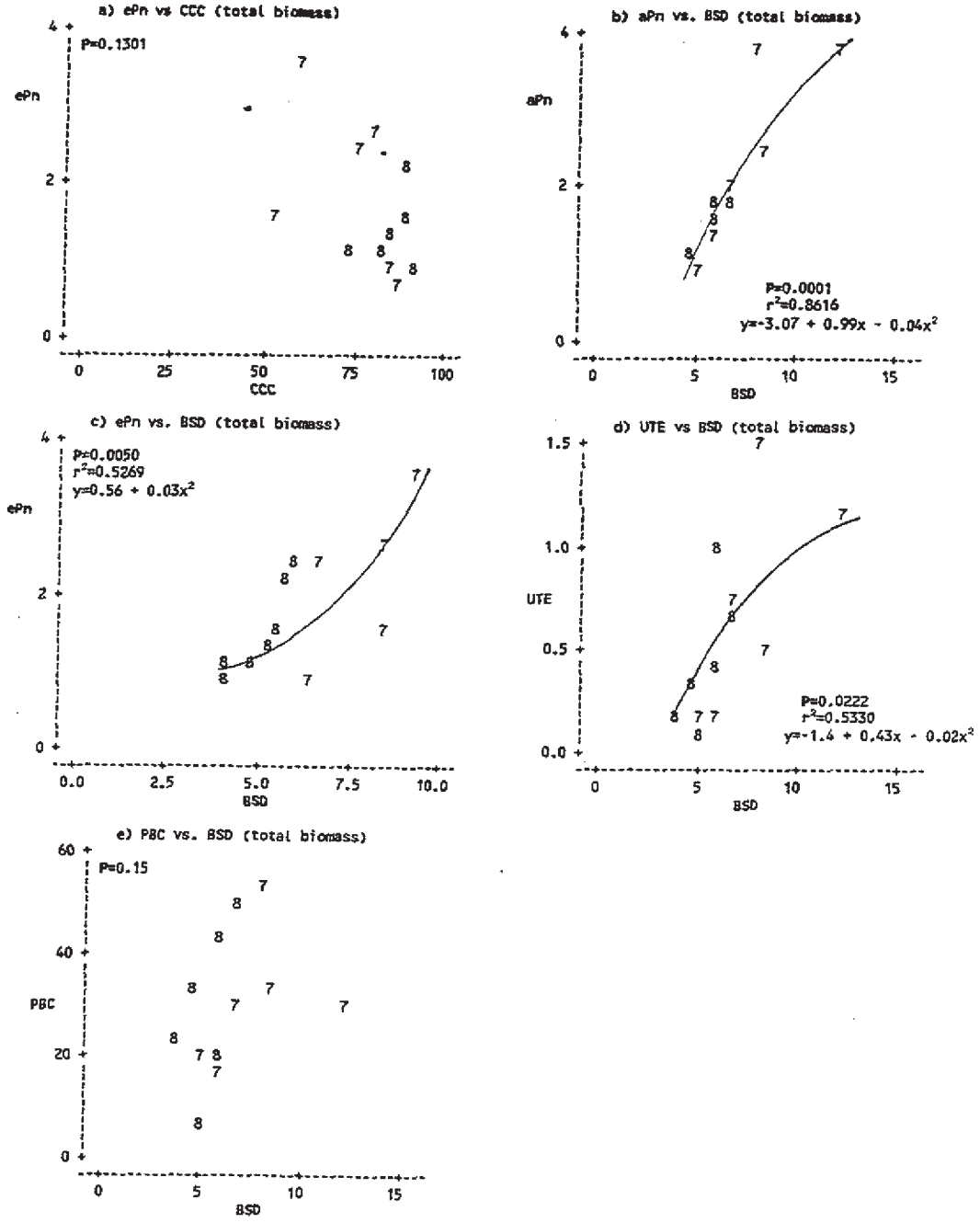


Figure 41. The relationship during summer between blue huckleberry a) total (leaf and twig) ungrazed production (ePn) (g/plant) and percent coniferous canopy closure (CCC), b) total production under herbivory (aPn) (g/stem) and basal stem diameter (BSD) (mm), c) ePn and BSD, d) total utilization (UTE) (g/stem) and BSD, and e) total percent biomass consumed (PBC) and BSD. Data value indicates sample year (7=1987, 8=1988).

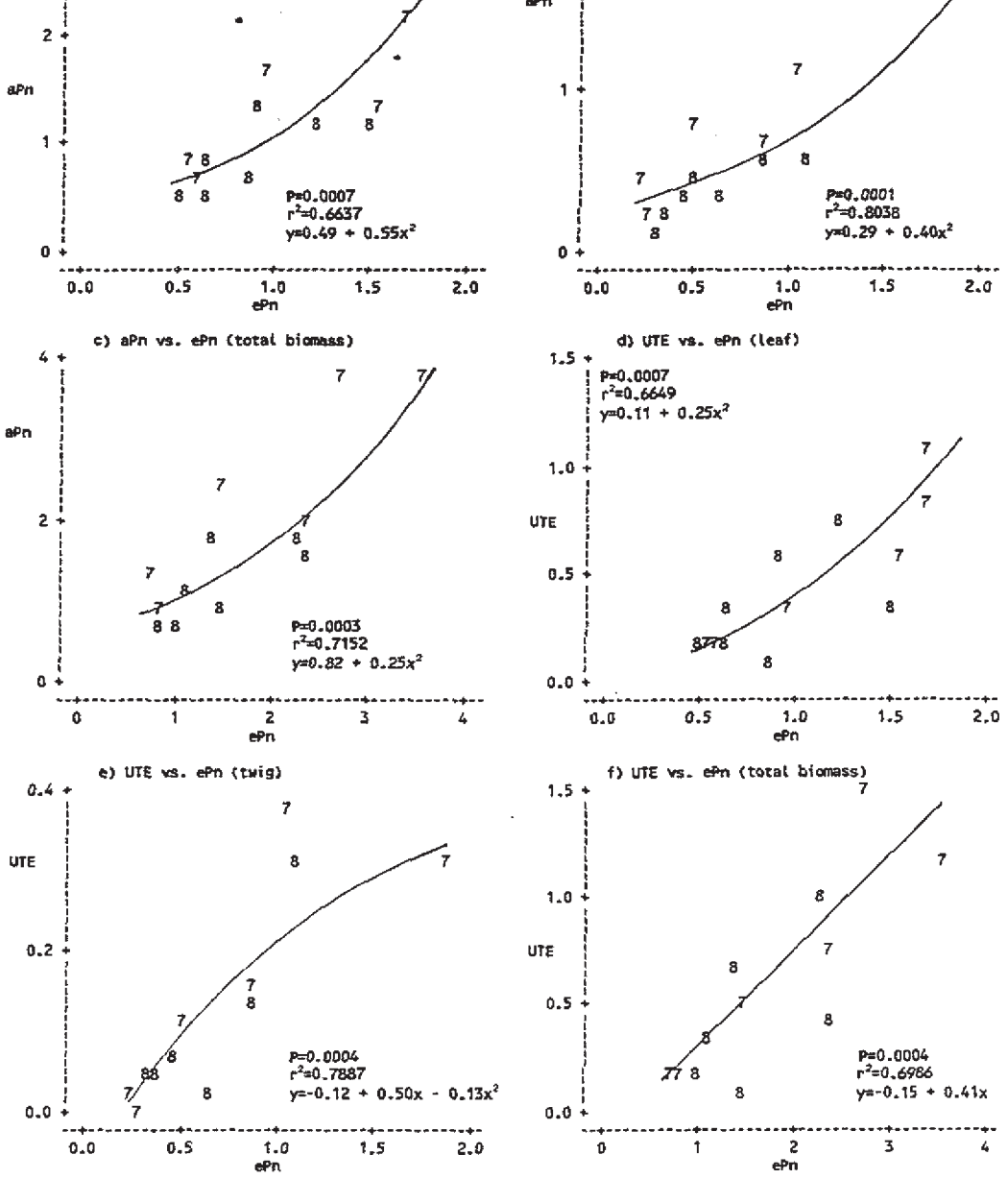


Figure 42. Relationship between blue huckleberry production under herbivory during summer (aPn, g/stem) and ungrazed production (ePn, g/stem) for a) leaves, b) twigs, and c) total biomass, and relationship between total utilization (UTE, g/stem) and ePn for d) leaves, e) twigs, and f) total biomass. Data value indicates sample year (7=1987, 8=1988).

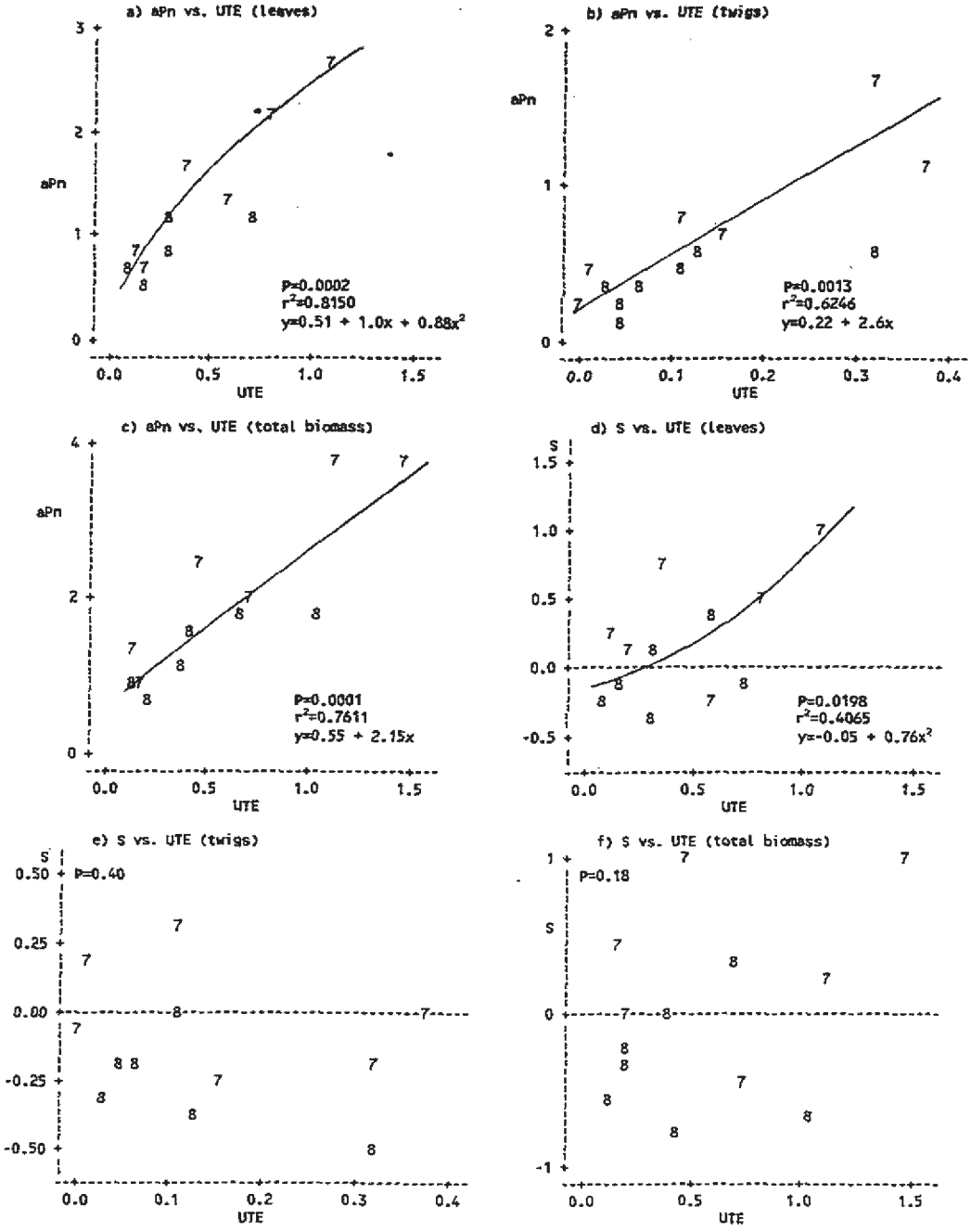


Figure 43. Relationships between blue huckleberry production under herbivory (aPn, g/stem) and utilization (UTE, g/stem) during summer for a) leaves, b) twigs, and c) total biomass, and relationships between the effect of herbivory on production (S, grazed - ungrazed production) (g/stem) and UTE for d) leaves, e) twigs, and f) total biomass. Data value indicates sample year (7=1987, 8=1988).

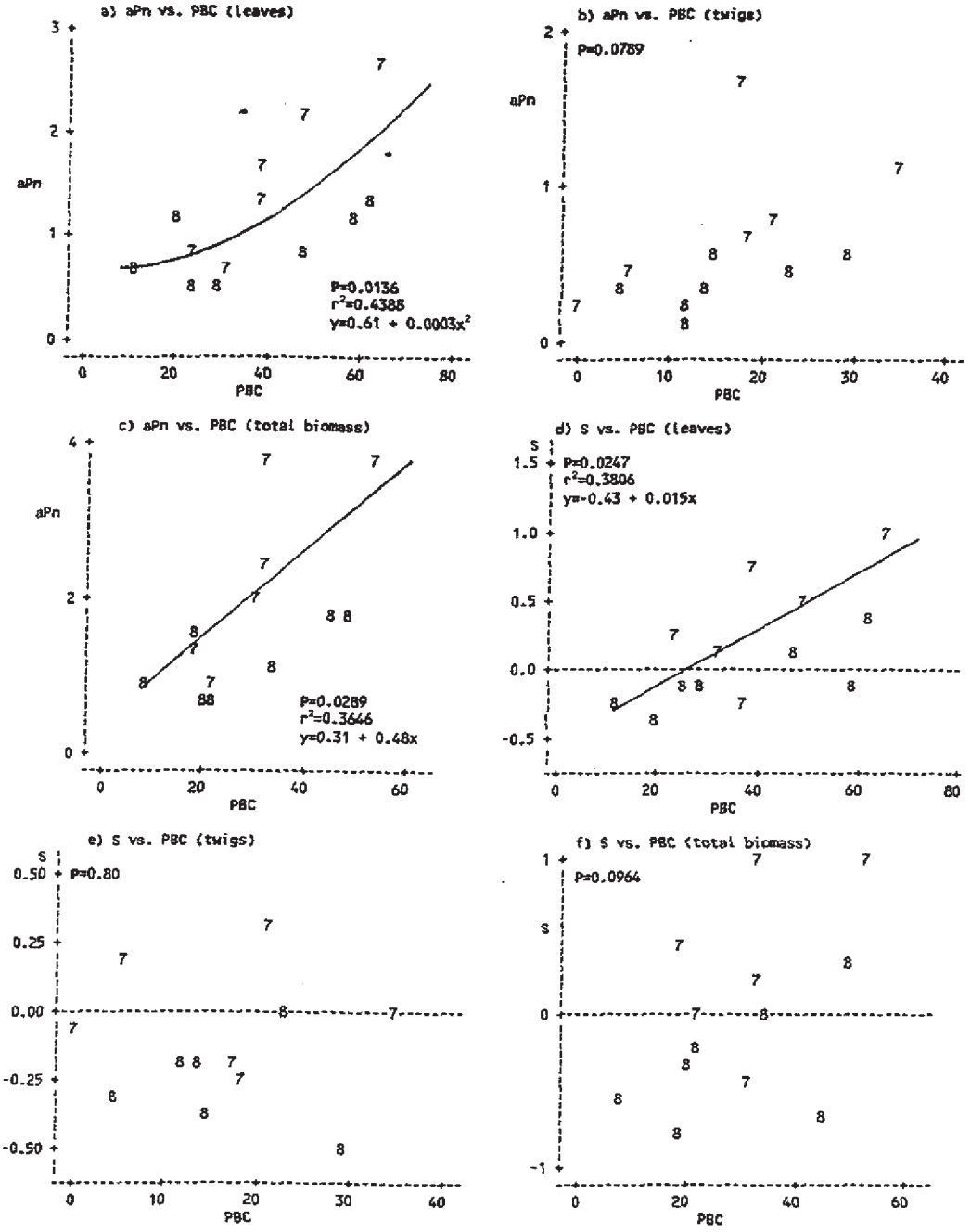


Figure 44. Relationships between blue huckleberry production under herbivory (aPn, g/stem) and percent biomass consumed (PBC) during summer for a) leaves, b) twigs, and c) total biomass, and relationships between the effect of herbivory on production (S, grazed - ungrazed production) (g/stem) and PBC for d) leaves, e) twigs, and f) total biomass. Data value indicates sample year (7=1987, 8=1988).

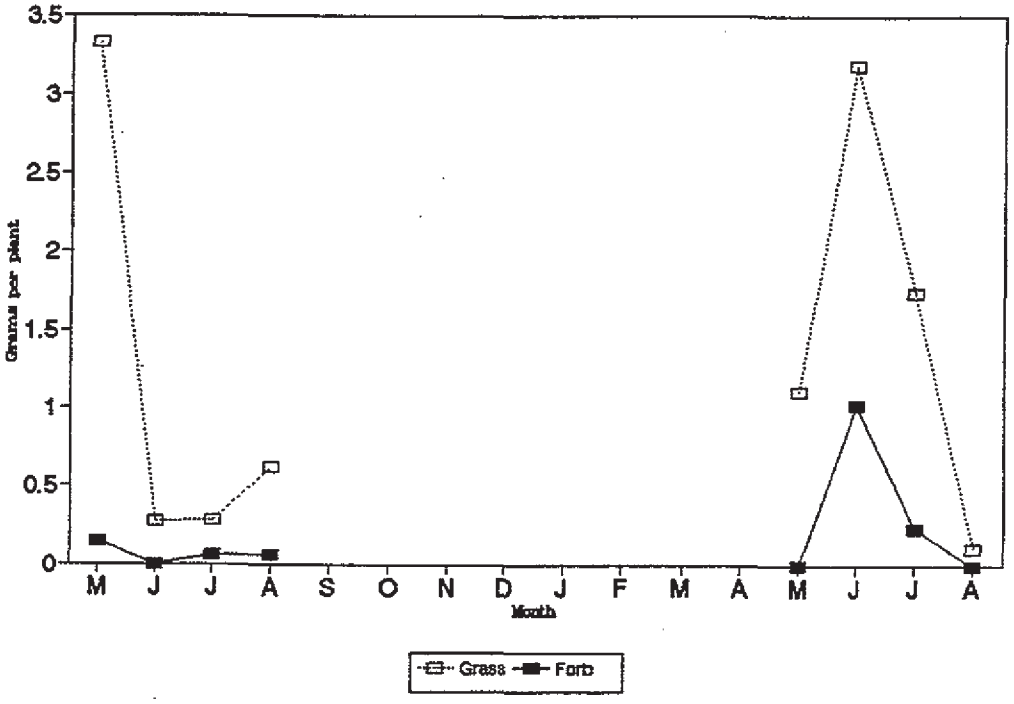


Figure 45. Monthly swordfern utilization (g/plant) during summer in grass and forb dominated strata in the South Fork Hoh, May 1987-August 1988.

Table 14. Means and P values from three and two-way ANOVAs on the effects of cervid herbivory, year, and strata on current years growth of swordfern in old-growth forests in the South Fork Hoh, Olympic National Park, during summer 1987 and 1988.

	E[a]	A[b]	G[c]	Stderr	n	Year	Str	Y*S	Tmt	T*Y	T*S	T*Y*S	covar[d].
a) Number of last years fronds						0.1270	0.2382	0.6227	0.0310	0.5449	0.7833	0.9686	
GS[e]	15.26	22.84	34.41	5.796	7	0.1804			0.1104	0.8163			
FS[f]	7.00	15.33	15.50	4.345	3	0.1693			0.4443	0.8692			
b) Maximum Standing Crop biomass of current years growth (g/plant)						0.4926	0.0091	0.4797	0.0728	0.6271	0.5076	0.9922	0.0058
GS	35.78[a]	19.02[b]	22.99[b]	4.750	7	0.4249			0.0449	0.7232			0.0126
FS	12.68	11.78	9.78	1.801	3	0.1725			0.5953	0.6939			
c) Production						0.4474	0.0952	0.5288	0.1388	0.6469	0.7258	0.9701	0.0045
GS	36.26	25.02	22.79	4.788	7	0.4165			0.1341	0.7474			0.0099
FS	12.68	14.21	9.78	1.785	3	0.2743			0.3859	0.5340			
d) Mean frond weight						0.3505	0.7347	0.8096	0.0035	0.5645	0.5068	0.9721	
GS	2.01[a]	1.07[b]	1.05[b]	0.023	9	0.3713			0.0143	0.5519			
FS	1.69	1.31	0.71	0.260	3	0.5423			0.2144	0.8648			
e) Mean unbrowsed frond weight						0.5206	0.4408	0.8439	0.0746	0.7309	0.3625	0.8595	
GS	2.00		1.39	0.305	9	0.5014			0.2038	0.4063			
FS	1.69		0.83	0.211	3	0.6508			0.2128	0.5879			
f) Total number current years fronds						0.3914	0.1035	0.5741	0.9058	0.7038	0.8577	0.9791	0.0038
GS	20.20	21.81	23.77	3.661	7	0.3892			0.7937	0.7550			0.0105
FS	7.42	10.67	11.58	3.219	3	0.9614			0.6837	0.8134			
g) Difference in number last years - current years fronds.						0.0760	0.6774	0.7553	0.9058	0.7038	0.8577	0.9791	0.0070
GS	-8.58	-6.97	-5.01	3.661	7	0.1377			0.7937	0.7550			0.0150
FS	-1.96	-4.32	-3.51	2.951	3	0.0604			0.8437	0.7007			
h) Percent current years fronds browsed						0.5836	0.6816	0.2666	0.0001	0.6986	0.7337	0.1887	
GS	0.50[a]	51.19[b]	54.59[b]	4.816	9	0.9178			0.0001	0.6378			
FS	0.00[a]	57.30[b]	51.20[b]	5.270	3	0.2826			0.0273	0.1900			
i) Percent last years fronds browsed						0.6478	0.8256	0.2551	0.6772	0.3387	0.9837	0.2295	
GS	55.23	67.45	73.45	8.269	7	0.3388			0.3247	0.6215			
FS	61.77	59.93	42.54	10.827	3	0.4551			0.5101	0.4147			
j) Unbrowsed frond mean percent Crude Protein							0.8789		0.7367	0.2778			
GS	7.52		8.37	0.372	5				0.1810				
FS	8.82		7.27	2.365	2				0.7230				
k) Unbrowsed frond mean percent in vitro digestible dry matter							0.1245		0.3949		0.8811		
GS	17.29		15.60	1.476	5				0.4652				
FS	19.58		17.21	3.478	2				0.7142				
l) Weight crude protein per plant (g)							0.1313		0.6052		0.4170		
GS	2.45		2.64	0.453	5				0.7868				
FS	1.11		0.31	0.396	2				0.3897				
m) Weight in vitro digestible dry matter per plant (g)							0.1833		0.3136		0.8004		
GS	5.80		4.70	1.068	5				0.5066				
FS	2.44		0.65	0.689	2				0.3175				

[a]E: Enclosed control, or ungrazed, treatment. Plants were protected by an enclosure from March through August each year.
[b]A: manipulated treatment; plant was enclosed with the control treatment, but herbivory was simulated monthly matching use on paired plant in G treatment.
[c]G: grazed treatment. Plant was exposed to cervid herbivory.
[d]Covar: covarient use in ANOVA. Was last year number of fronds (NFLY) in all analyses
[e]GS: grass dominated strata
[f]FS: forb dominated strata

Table 14. Continued.

[a]values with same letter superscript were not different ($P < 0.05$)
[b]production for C treatment was weight of current years growth (CYG) at maximum standing crop biomass, for A (actual production under herbivory) was biomass plus sum of weight removed by simulated utilization, for G (apparent production under herbivory) was weight of CYG at maximum standing crop biomass.
[f]forage quality measurements were made during 1988 only, and for only the C and G treatments

Herbivory had no apparent effect on swordfern in FS, but did affect swordfern in GS. Cervid herbivory reduced biomass in GS ($P < 0.0156$), but not in FS ($P > 0.7564$) (Table 14b). Herbivory caused no detectible difference in production ($P = 0.1388$), thus there was exact compensation (Table 14c). Herbivory reduced mean frond weight in GS ($P = 0.0110$), but this was due to the presence of browsed fronds. There was no difference between treatments in unbrowsed frond weight ($P = 0.0746$), nor was there any difference between treatments in frond number ($P = 0.9058$); thus herbivory did not stimulate plants to produce more fronds. Herbivory also did affect swordfern CP or IVD, in either FS or GS (Table 14j,k,l,m).

There was no relationship between canopy closure and swordfern enclosed production, actual production, or utilization ($P > 0.05$). Maximum standing crop biomass of ungrazed swordfern was positively correlated with number of previous years fronds ($P = 0.0133$), but there was no relationship between actual production, utilization, percent biomass consumed, or percent production consumed and number of previous years fronds ($P > 0.05$) (i.e., cervids did not eat more from larger plants, and influence of herbivory on production influenced the relationship between previous and current years production) (Fig. 46). Swordfern actual production was positively correlated with utilization ($P = 0.0001$), but S was not ($P = 0.40$) (Fig. 47 a,b). There was a positive relationship between S and percent biomass consumed ($P = 0.0139$) (Fig. 47 d). Thus the cervids ate more from more productive plants, but the percent of biomass consumed was not correlated with production. Actual production was stimulated by herbivory; as a greater percent of biomass was consumed, actual production increased. Low levels of utilization had a negative effect on actual production (Fig. 47d).

Although there was no difference between strata in swordfern biomass, production, or forage quality, utilization was greater on swordfern growing in GS. The lack of effect in FS was probably a consequence of the low levels of herbivory. Herbivory reduced swordfern biomass in GS, but had no effect on production, forage quality, frond number, or frond weight. Several treatment effects approached significance, and lack of treatment effects may be due to high sample and experimental error, and inadequate power in the statistical tests. However, percent biomass consumed was positively related to S.

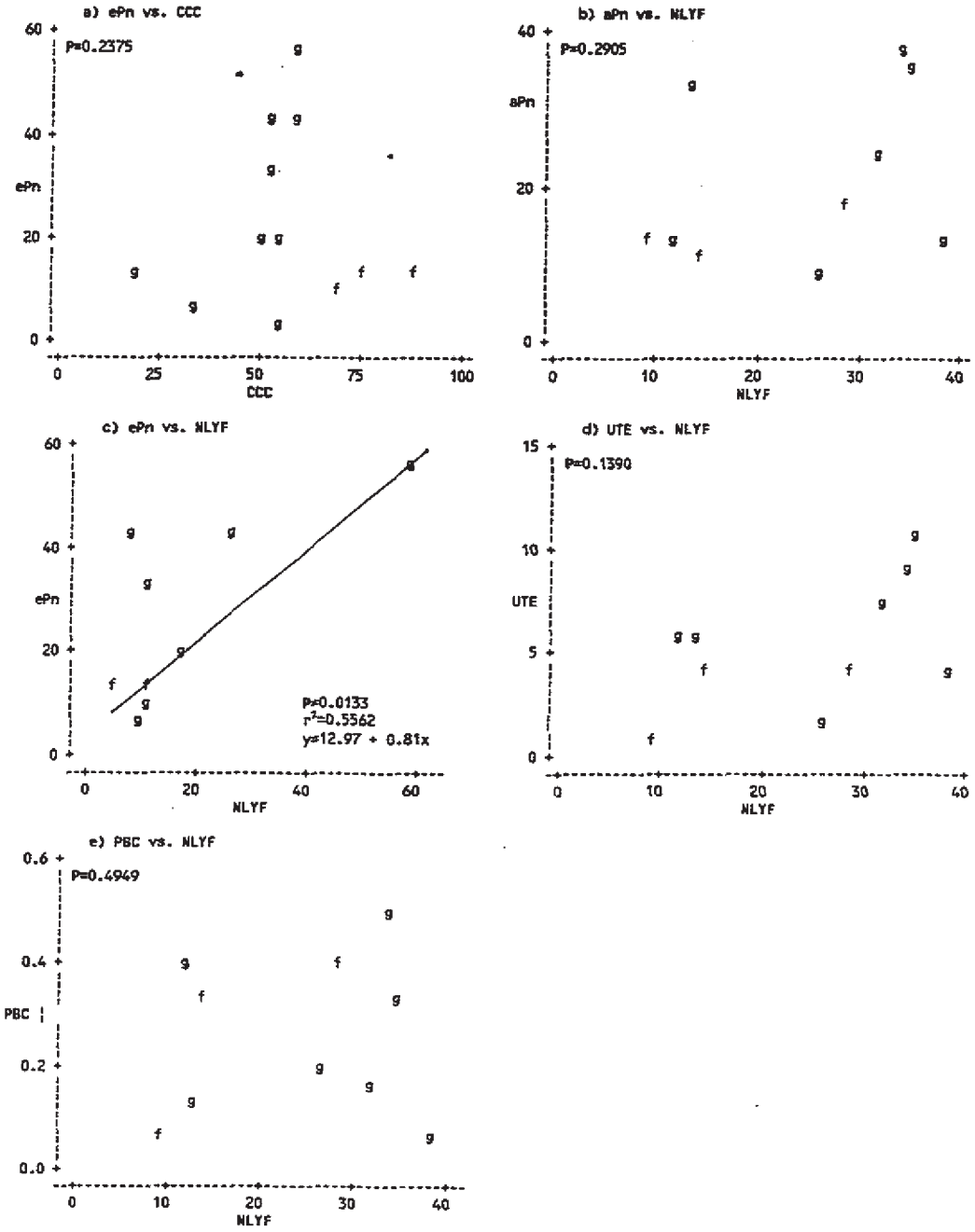


Figure 46. Relationships during summer between swordfern a) ungrazed production (ePn, g/plant) and percent coniferous canopy closure (CCC), b) production under herbivory (aPn, g/plant) and number of last years fronds (NLYF), c) ePn and NLYF, d) utilization (UTE, g/plant) and NLYF, and e) percent biomass consumed (PBC) and NLYF. Value for observation indicates strata (g=grass strata, f=forb strata).

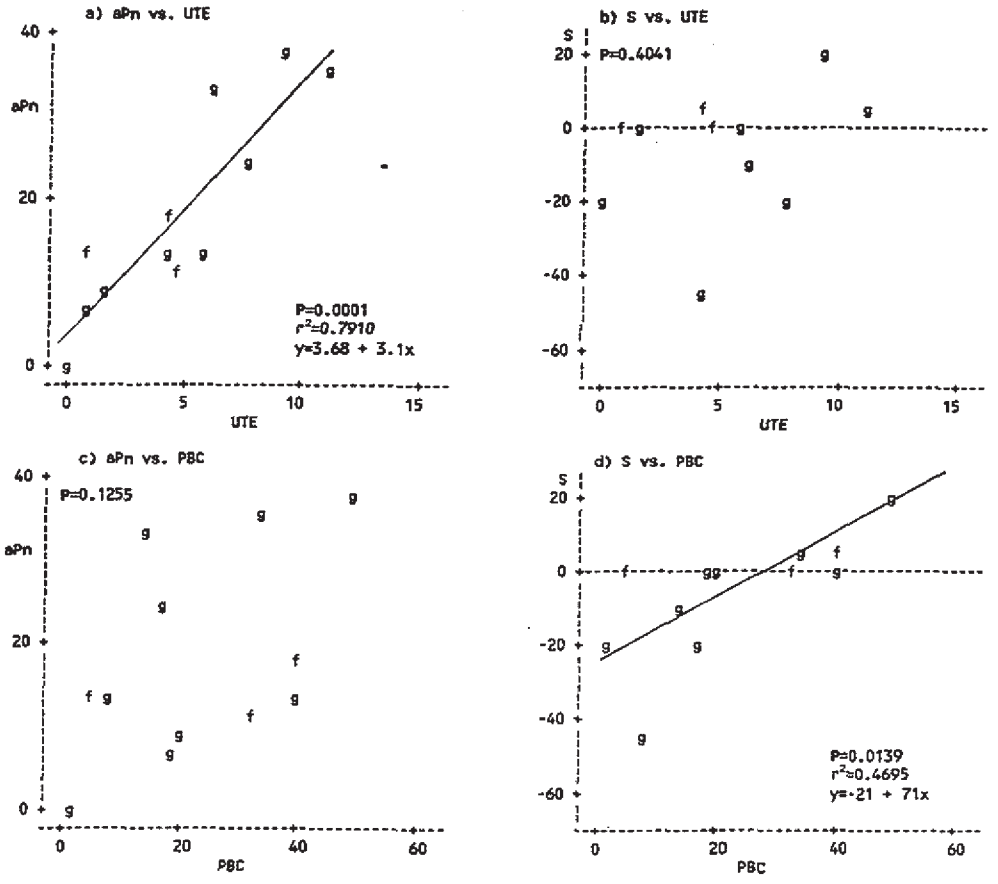


Figure 47. Relationships between swordfern production and utilization during summer; a) production in grazed plants (aPn, g/plant) and utilization (UTE, g/plant), b) the effect of herbivory on production (S:ungrazed - grazed production) and UTE, c) aPn and percent biomass consumed (PBC), and c) S and PBC. Value for observation indicates sample strata (g=grass strata, f=forb strata).

Discussion

Cervid Diets

Old-growth stands supplied an important component to the cervid forage base in the SFH throughout the year. The majority of key dietary genera occurred in old-growth stands, and were consumed there. There were many discrepancies between cervid diet and forage utilization data; diets included several species that were not found in old-growth stands, and the seasonal use patterns of several forages, such as grasses, did not correspond with seasonal occurrence in diets. Those discrepancies arose because cervids foraged in other communities within the SFH drainage, including alder flats and gravel bars, which contain additional forage species (Jenkins and Starkey 1984, Leslie et al. 1984). Additionally, several herbaceous and shrub genera were ubiquitous throughout the valley (Smith and Henderson 1986).

Forbs were important components of diets of both deer and elk. Forbs provided high quality forage throughout the year, but forb availability was limited in fall and winter. Conifers, particularly hemlock and cedar, were important forages during winter when the availability of other forages decreased. Although nutrient quality of hemlock was low relative to other forages (Study 1, Leslie et al. 1984) foraging efficiency on hemlock (rate of intake) was high (Spalanger et al. 1988). Coniferous browse was available primarily in old-growth stands. Although hemlock was available as seedlings, saplings, and browse at the lower edges of the canopy of mid-story trees, hemlock and cedar were also available through blowdown of branches and windthrow of large trees. During winter 1988 3 hemlock blew down in the vicinity of the annual exclosures. Although I did not measure biomass removed, utilization was heavy. New trails led to the trees, biomass was removed below the terminus of CAG, and there were abundant fecal deposits. Newman (1958) and Leslie (1982) also observed that blowdown provided important winter forage, but its availability was sporadic, and dependent upon occurrence of storms with sufficient winds.

In both the SFH and MFH (Leslie et al. 1984), the degree of dietary overlap between deer and elk was great. In the SFH both deer and elk consumed more graminoids and forbs, and less ferns and conifers than they did in the MFH (Leslie et al.1984). These differences were probably a function of greater valley floor

development and more availability of grassy openings within spruce-hemlock forest in the SFH than in the MFH (Franklin 1982). Elk and deer diets in the SFH fell within the range of elk and deer diets observed elsewhere in the region (Brown 1961, Hanley 1980, Rochelle 1980, Anderson 1985, Jenkins and Starkey 1991). However elk use of forbs in the SFH appeared to be greater and shrub use lower than commonly observed for the subspecies (Jenkins and Starkey 1991). Similarly, deer use of forbs was greater than observed in most other diets (Brown 1961, Hanley 1980, Anderson 1985, but see Rochelle 1980).

Herbaceous Standing Crop Biomass, Production, and Utilization

Peak standing crop herbaceous biomass in GS in the SFH was greater than biomass measured for seral forests in the MFH (Leslie 1982), but was similar to biomass measured in big-leaf maple and old-growth forest clearings. Biomass in FS in the SFH was less than what was observed in the MFH (Leslie 1982). As in the SFH, Leslie (1982) observed that the difference in standing crop between habitats diminished during winter, when availability was low throughout the system. Herbaceous standing crop biomass in the SFH was less than observed in other grazing systems such as the Serengeti (mean 501 g/m^2), and less than Hanley (1980) observed in seral (342 - 380 g/m^2) but greater than he observed in climax (81 g/m^2) habitats in the western Cascades in Washington. My estimates of herbaceous biomass are an underestimate of forage availability, for I have no estimate of browse or coniferous biomass.

Similarly, herbaceous actual production in the SFH (GS:133.7 g/m^2, FS:20.59 g/m^2) was less than observed in other grazing systems (664 g/m^2 Serengeti, McNaughton 1985; 278 g/m^2 Yellowstone, Frank and McNaughton 1992). However, unlike those other systems, production in old-growth spruce-hemlock stands in the SFH occurred year-round, with flushes of production during spring and early summer, but continuing in significant amounts into fall.

At first glance, it appeared that I may have measured maximum standing crop biomass before the actual maximum; biomass in GS peaked in early September, (Fig. 2) but I measured biomass in August. However, the rate of production decreased in September, and several species were visibly senescing. Much of GS biomass in September was cured grass. Consequently, forage quality, and the availability and concentration of nutrients was less in September than in August.

During March minimum standing crop biomass was measured accurately in FS, but I was too late to measure minimum biomass accurately in GS. Green-up occurred earlier under the more open canopies in GS. During March, violets (*Viola*) and spring beauties (*Montia*) had already begun to emerge in GS, however FS forbs, such as false lily-of-the-valley (*Maianthemum dilatatum*) and wood sorrel didn't appear in some FS sites until May.

Effects of Cervid Herbivory on the Herbaceous Layer

The effect of cervid herbivory on herbaceous production and biomass differed between years, strata, and forage category. These differences can be attributed to differences between years in weather and the timing of production and herbivory. Spring temperatures were warmer during 1987 than 1988 (Fig. 2), and spring green-up in GS occurred earlier during 1987 than 1988. Actual production in GS was 25 g/m^2 and 5 g/m^2 during April 1987 and 1988, respectively. During 1987 percent production consumed was less than 50% until June, and peaked during July at 80%. The heavy herbivory during July 1987 resulted in decreased actual production and standing crop biomass, but regrowth occurred during August as percent production consumed decreased (Fig. 3). During April 1988, percent grass production consumed was greater than 100%, although utilization was similar between years (Fig. 4). During April, grasses may have been more vulnerable to heavy herbivory than in mid-summer due to depleted root reserves (Menke and Trlica 1981), and thus cervid herbivory retarded the rate of actual production into May. Consequently, although grass enclosed production and utilization didn't differ between years, due to the difference in the timing of production and utilization, I observed overcompensation in grasses in 1987, and undercompensation in 1988.

The late spring in 1988 also retarded onset of GS forb and ladyfern production, but had less effect on total annual actual production. I observed exact compensation in GS ferns and forbs during both years. Ladyfern and forb production was minimal during April 1988, and their production didn't increase until after cervid herbivory in GS eased during May. Thus GS forbs and ladyferns were not grazed intensively at as critical a time as grasses were (forb and ladyfern percent production consumed did not exceed 100% during spring 1988).

Because FS actual production did not peak until May each year, actual production in FS was not delayed in 1988. Percent production consumed during July was greater than 100% during both years, and resulted in a drop in standing crop biomass in FS during August 1987 and 1988. Utilization decreased during August 1987, and FS plots regrew into September 1987. However, percent production consumed was greater than 100 % during August 1988, and FS biomass decreased into September 1988. Consequently, I observed overcompensation in FS herbs in 1987, and exact compensation during 1988.

The level of herbivory as related to actual production (percent production consumed) in the SFH (GS:35%, FS:40%) was less than levels observed in the Serengeti (range 17-95%, mean 60%, McNaughton 1985) but similar to levels observed in Yellowstone (range:22-58%, mean: 46%, Frank and McNaughton 1992). Unlike those systems, most herbivores were non-migratory in the SFH, and utilized forages year-round. Unlike in the Serengeti, I rarely observed S rising to an asymptote of percent biomass consumed; the level of grazing pressure at any site was usually not sufficient to depress the rate of production stimulation, let alone decrease production. This is most likely because the ecological carrying capacity of the range is set by forage availability during winter, and that level is below what the range could support during summer.

Intake and foraging efficiency of ungulates are a function of bite size (g/bite), bite rate (bite/time), prehension and processing time, and travel time between foraging patches (Trudell and White 1981, Wickstrom et al 1984). Rates of intake increase as the height and biomass concentration of the herb layer increases (Burlison et al. 1991, Ataja et al. 1992, Illius et al 1992, Laca et al. 1992). Intake also increases with standing crop, but only up to a point, or asymptote, above which no increase in intake occurs as standing crop increases (Wickstrom et al 1984, Hudson and Watkins 1985, Spalanger et al. 1988). Intake also increases with forage quality and increased leaf area in shrubs (Spalinger et al 1988, Anderson and Saether 1992). Within a given foraging environment, foraging efficiency also varies among herbivore species, depending upon digestive constraints, nutritional requirements, and bite size (Hanley 1982). Intake asymptotes for mule deer and Rocky Mountain elk were 5-10 and 150 g/m^2, respectively, in grass pastures. The amount of biomass at the asymptote decreased when forbs and shrubs were added to the forage base (Wickstrom et al 1984, Hudson and Watkins 1985). Similarly, Spalanger et al. (1988) reported intake was constant over biomass

(i.e. no asymptote) for Sitka black-tailed deer, except when leaf size was small, and even then it was at 0.2 g/m^2.

Cervid herbivory decreased both maximum and minimum herbaceous standing crop biomass, in both FS and GS. Except in FS during winter, the percent reduction was not great (12% GS during both seasons, FS:16% summer, 34% winter). The effect of herbivory on herbaceous biomass reduction was greatest on ferns and forbs, and was not significant with grasses. However, due to reduction in plant height, particularly in GS, herbivory increased the concentration of biomass in GS.

In GS during summer, cervid herbivory increased herbaceous CP content, and the increase in IVD approached significance ($P = 0.0934$). Herbaceous forage quality was also slightly improved during winter in GS, but the changes were not significant. Those CP and IVD results support the results of the first study; the effects of herbivory on forage quality were greatest with CP, occurred primarily during summer, and were not carried over into winter. However, when the effect of herbivory on biomass concentration was added to changes in forage quality, the result was greater concentration of both CP and IVD in grazed GS herbs, during both summer and winter. Increased forage quality and biomass and nutrient concentration in the herb layer was primarily influenced by the grass component. Herbivory increased grass nutrient concentration during both seasons, but significantly increased forb CP concentration only during summer, and only in GS, and had no significant effect on fern nutrient concentration, during either season.

In GS within old-growth spruce-hemlock forests, elk and deer herbivory decreased height and biomass of herbs, but the reduction in plant height was not large as compared to cervid mouth size, and forage standing crop biomass was not below the intake asymptote for either species. However herbivory also increased biomass and nutrient concentration, resulting in the creation of a better foraging environment, on an annual basis, in GS patches, i.e., a form of grazing lawn was produced (McNaughton 19884, Hobbs and Swift 1988).

In FS, although percent biomass and percent production consumed were similar to GS, and I found over or exact compensation in herb production, herbivory did not improve biomass concentration, forage quality, or nutrient concentration. This is probably a reflection of the different response to herbivory between forbs and grasses, and the lower proportion of grasses in the FS biomass. Because biomass did not fall below the intake asymptote for deer, even during winter,

herbivory either improved or had no effect on the foraging environment for deer. The implications for elk are unclear; biomass in FS was below the elk asymptote in all seasons. However nutrient concentration did not differ between grazed and ungrazed FS plots, and production was enhanced in one year.

In summary, cervid herbivory created and maintained a 'grazing lawn' in GS for both deer and elk at times of both maximum and minimum biomass. In FS herbivory had either a slightly positive or no effect on the foraging environment for deer during either season, but may have decreased foraging efficiency for elk during winter.

Effects of Cervid Herbivory on Shrubs and Swordfern

I did not assess cervid use of shrubs and swordfern during winter, so the amount and impacts of herbivory may have been underestimated. However, cervid use of shrubs was greatest during the growing season (Table 5, Newman 1958).

For shrubs, utilization was greatest on salmonberry, which corroborates results from the fecal analysis of this study and observations of earlier observers (Riley 1919, Murie 1935, Skinner 1936, Schwartz 1943). Moderate to high levels of cervid herbivory (30 to 100 % biomass consumed) stimulated salmonberry, blue huckleberry, and swordfern production in the SFH, however low levels of herbivory often decreased production. The negative effects of low levels of utilization may be a result of experimental error. At low levels of herbivory utilization was a small percent of biomass, and poor pairing between treatments would have a greater effect on plants with low levels of utilization than plants with high levels. Also, as the percent utilization increased, shrubs put more of their resources into leaf production at the expense of twigs. The increase in investment in photosynthetic tissue may have enabled the grazed plants to increase their rate of production.

Herbivory of shrubs, especially salmonberry, had several beneficial effects for cervids. First, by reducing plant height growth, herbivory kept browse within reach of cervids (salmonberry and red huckleberry grew above elk reach in the 0.5 ha exclosures). Secondly, compact growth form promoted by browsing increased biomass and nutrient concentration. Lastly, the greater production of leafy tissue, which is easier to prehend and digest than twigs, may have improved cervid foraging efficiency. The failure of browse leaves to respond to herbivory with increased tannins further supports this

effect. Thus, on an annual basis the cervids also created a "grazing lawn" with salmonberry and to some extent with blue huckleberry. Red huckleberry utilization was too light to have any effect on plant structure or nutrient content, and the sampling effort on swordfern was insufficient to support firm conclusions.

As in Study 1, herbivory had a greater effect on shrub CP than IVD, affected salmonberry forage quality more than any other shrub, and affected stem nutrients more than leaf nutrients. *In vitro* digestibility of salmonberry leaves and swordfern were less in this study than in Study 1 (Tables 2,11,14). Those differences are related to differences in sample processing between experiments, and the consequent effect on tannin activity. In the first study forages were oven dried, whereas in the second they were frozen and lyophilized. Unlike oven drying, freeze drying preserves tannins, enabling them to interfere with and reduce *in vitro* digestion. This interpretation is supported by the lack of difference between studies in IVD of forages with no or low tannins (red huckleberry, wood sorrel).

CONCLUSIONS AND ECOLOGICAL IMPLICATIONS

Cervid herbivory is a natural phenomenon in the SFH ecosystem, shaping old-growth spruce-hemlock communities over several spatial and temporal scales. For the most part, cervid herbivory created more favorable foraging environments, including the creation and maintenance of a "grazing lawn". In the short term, and on a small scale, herbivory increased biomass and nutrient concentration of herbaceous and salmonberry biomass within GS patches. Additionally, except for salmonberry stems, cervid herbivory did not lead to increased tannin astringency. The effects of herbivory were most prevalent during summer, when the ungulates faced their greatest nutrient and energy demands (i.e., growth, lactation, fat deposition), but some effects carried over into the winter months.

Even though all sites were under a forest canopy, cervid herbivory was a major factor influencing production in both strata. For the herbaceous layer, the correlation between actual production and herbivory was stronger than the correlations between actual and enclosed production or canopy closure. The lack of correlation between actual and enclosed production is unlike other systems (McNaughton 1985). McNaughton (1985) also reported correlations between enclosed production and utilization, but in most cases I did not. In such a structurally diverse system, herbivory may be influenced by factors besides enclosed production, including species composition, forage patch size, nearness to travel routes, and proximity to other preferred foraging areas. For shrubs, actual and enclosed production were correlated, however utilization was also correlated with production, and altered the relationship between production and plant size (stem BSD).

Concerns over reductions in preferred shrub species, such as elderberry and salmonberry, caused many earlier researchers to conclude that cervids were overutilizing the forage. The cervid-induced reduction in salmonberry and height and volume did preclude it from dominating the GS understory, and appeared to totally inhibit sexual reproduction. However, because it was rhizomatous, salmonberry was poised to take advantage of release from herbivory. Such release occurred naturally in the SFH, in the form of refugia created by windthrow of large trees. Refugia frequency in the SFH was 20.6/km (Schreiner et al. in prep). In several long term exclosure experiments in ONP, salmonberry rapidly increased in stature and

cover, and dominated a site in as little as 3 years (Schwartz and Mitchell 1945, Newman 1958, Harmon 1987).

Although ladyfern comprised a small percent of elk or deer diets, and was a small percent of grazed plot biomass, the heavy utilization that it received was highly significant ecologically. Upon release from herbivory, ladyfern overtopped, shaded out, and outcompeted almost all other herbaceous forage in sites where salmonberry is not present (Schwartz 1943, Newman 1958, Harmon 1987). In conjunction with the increase in salmonberry and ladyfern dominance, a total disappearance of grasses and decrease in some forbs was recorded in GS patches in exclosures (Schwartz 1943, Newman 1958, Harmon 1987, Schreiner et al. in prep, Woodward et al. 1993).

Thus, in the long term cervid herbivory increased species diversity on a small spatial scale, within GS patches. On an even longer temporal scale, the distinction between GS and FS patches diminishes with long term exclusion (Schreiner et al. in prep). Thus cervid herbivory also leads to diversity of plant associations within the old-growth forest matrix. The loss of GS patches with long-term cervid exclusion would result in the loss of the most productive understory sites, decrease in the cervid forage base, and ultimately cervid carrying capacity, particularly for elk. Although GS comprised only 25% of old-growth terraces, production and utilization were 6.5 and 5.7 times greater in GS than FS respectively, and GS provided 69 and 66% of herbaceous production and utilization respectively in old-growth stands. The loss in herbaceous production would be partially offset by increased shrub availability, but herbs provide better quality forage throughout longer periods of the year than shrubs.

McNaughton (1986a) postulated that the grazing lawn theory is most applicable to co-evolved systems. Many of the herbaceous species in the GS were exotic, which is problematical when discussing how "natural" the grazing system is, or determining if the herbivore-vegetation system is co-evolved. Because the exotics were so ubiquitous, it was impossible to determine how the system functioned prior to the introduction of these species. However, with the current species mix, the grazing lawn hypothesis appears to be valid.

The consequences of cervid-induced habitat alteration seemed to benefit both deer and elk. The maintenance of GS clearly benefitted elk, for GS provided grasses which they are adapted to consume. Furthermore, GS contained large patches containing abundant concentrated biomass, which are more suitable to foraging by large herds (Hanley 1980). However, herbivory also increased forage quality

and maintained shrubs at low stature, which should benefit deer which are more limited by forage quality and are smaller than elk (Hanley 1982).

Old-growth sitka spruce-western hemlock stands do not supply all elk and deer forage needs, but they supply a relatively stable, year-round forage base, and are an important component of the system for cervids in the SFH. In periodic severe winters the canopy provides crucial snow interception, and forage in the form of browse and windthrow.

Prior concerns about excessive use and overpopulation (Riley 1918, Sumner 1938, Schwartz 1943) have recently given way to the view that elk populations in western drainages in ONP are stable, and at ecological carrying capacity (Newman 1958, Jenkins 1981). This more recent hypothesis is supported by the observations that the elk population has stable social groups, a high proportion of old-age individuals, and low recruitment (Jenkins 1980, Jenkins and Starkey 1982, Leslie and Jenkins unpublished data). The existing level of herbivory, although greatly influencing the structure and composition of the forest understory, may actually produce greater and more stable forage for herbivores. In the SFH, as in other areas where herbivores are a natural component, the removal of herbivory would cause noticeable changes to the system.

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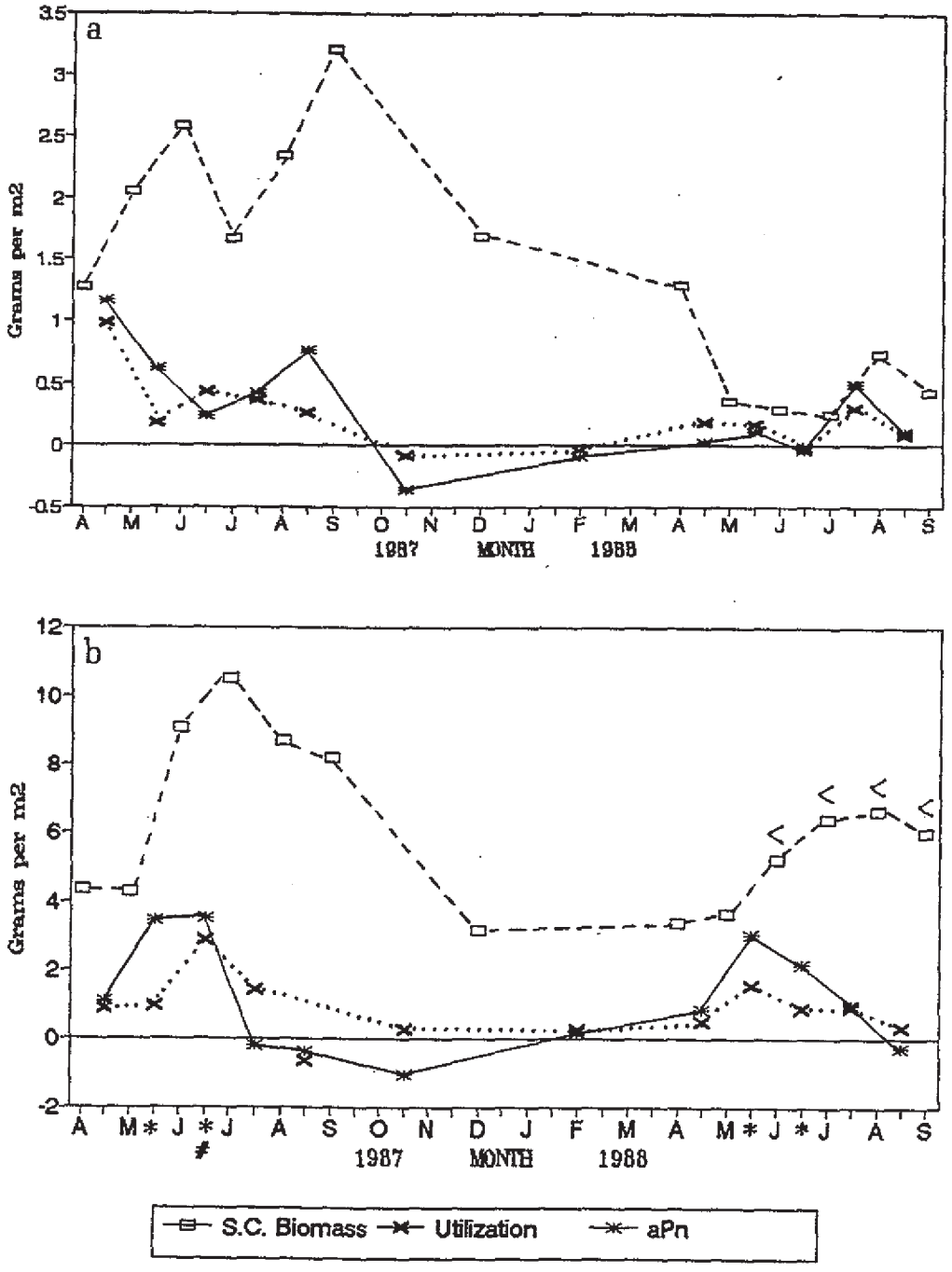
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APPENDICES

Appendix 1



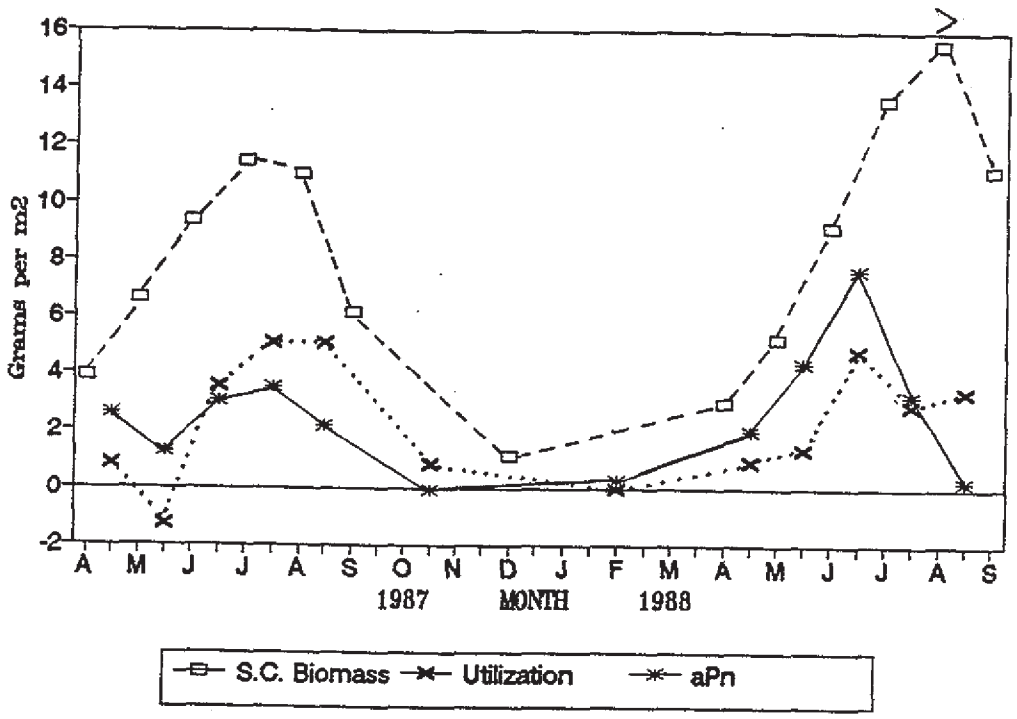
Mean monthly standing crop biomass, utilization, and production (g/m^2) of foamflower in a) grass and b) forb dominated strata in the South Fork Hoh, April 1987-September 1988. < indicates value was less ($P< 0.05$) in 1988 than during same month in 1987. * indicates production was greater than 0 ($P< 0.05$) during sample period. # indicates utilization was greater than 0 ($P < 0.05$) during sample period.

Appendix 1 (continued). Means and P values from 3-way ANOVAs on the effects of strata, year, and cervid exclusion, by season, on foamflower in old-growth forests in the South Fork Hoh, Olympic National Park, 1987-1989.

	GS[a]				FS[b]									
SEASON YEAR	E[c]	G[d]	Stder	n	E	G	Stderr	n	Year	Strata	Y*S	Tmt	Y*T	S*T	Y*S*T
a) Biomass (g/m^2)															
SUMMER[e]									0.0979	0.5907	0.7360	0.1163	0.0087	0.1120	0.3719
1987	3.18	3.38	0.962	7	3.90	5.02	0.805	8		E>G 1988 only					
1988	8.36	3.76	0.962	7	7.04	5.60	0.805	10							
WINTER[f]									0.7578	0.6433	0.2257	0.0467	0.2440	0.7082	0.6481
1987	3.06	2.61	0.722	8	2.39	2.04	0.681	9							
1988	2.66	1.54	0.681	9	4.26	2.35	0.646	10							
b) Plant Height (cm)															
SUMMER									0.0997	0.9681		0.0028	0.4166	0.2732	
1987					8.71	7.73	0.505	10							
1988	10.63	8.17	0.603	7	10.04	8.83	0.505	10							
WINTER									0.1024	0.4764	0.1372	0.0034	0.0436	0.5597	0.8551
1987	7.80	4.90	0.802	5	7.19	4.69	0.634	8	E>G 1988 only						
1988	5.20	4.08	0.802	5	5.85	5.50	0.567	10							
c) Biomass Concentration (g/m^3)															
SUMMER									0.6433	0.7649		0.5955	0.0517	0.1690	
1987					46.84	63.68	9.180	10							
1988	76.79	43.25	10.97	7	69.77	64.55	9.182	10							
WINTER									0.4764	0.4661	0.7029	0.9895	0.0051	0.3300	0.4661
1987	38.34	90.35	15.64	5	34.77	52.30	12.36	8	E<G 1987 only						
1988	80.29	57.05	15.64	5	76.32	47.56	11.06	10							
d) Percent Crude Protein															
SUMMER									0.6125	0.5317	0.4469	0.2939	0.9246	0.0321	0.4731
1987	9.18	11.48	0.857	2	9.54	9.22	0.495	6	E<G GS only						
1988	9.30	10.54	0.495	6	9.92	9.78	0.404	9							
WINTER									0.8749	0.0276	0.2362	0.6867	0.4650	0.6410	0.1230
1987	12.81	11.23	0.864	1	8.66	9.50	0.496	3							
1988	10.47	10.42	0.499	3	9.53	9.02	0.386	5							
e) Percent In Vitro Digestible Dry Matter															
SUMMER									0.5898	0.0084	0.0507	0.4063	0.5551	0.5854	0.8616
1987	25.15	24.75	2.725	2	25.65	23.25	1.573	6							
1988	21.01	21.19	1.573	6	28.89	28.00	1.285	9							
WINTER									0.1541	0.0111	0.9567	0.9488	0.8609	0.3702	0.9282
1987	31.28	33.23		1	38.32	37.09	0.327	3							
1988	29.29	30.99	2.666	3	36.25	35.36	1.504	5							
f) Crude Protein Concentration (g/m^3)															
SUMMER									0.6107	0.7721		0.7587	0.1110	0.1681	
1987					4.67	5.98	0.822	8							
1988	7.17	4.54	0.983	7	6.54	6.45	0.822	10							
WINTER									0.6362	0.2036	0.5059	0.9360	0.0041	0.3438	0.3806
1987	4.91	10.15	1.478	5	3.14	4.87	1.168	8	E<G 1987 only						
1988	8.14	5.73	1.478	5	7.08	4.48	1.044	10							
g) In Vitro Digestible Dry Matter Concentration (g/m^3)															
SUMMER									0.4920	0.3431		0.3758	0.1825	0.3078	
1987					11.81	13.56	2.289	10							
1988	16.13	9.19	2.561	7	19.33	17.65	2.289	10							
WINTER									0.6104	0.7724	0.6063	0.8370	0.0100	0.2161	0.5664
1987	11.99	30.02	5.362	5	13.41	18.88	4.239	8	E<G 1987 only						
1988	22.34	17.83	5.362	5	25.94	16.67	3.791	10							

[a]GS: grass dominated strata
[b]FS: forb dominated strata
[c]E enclosed control, or ungrazed, treatment
[d]G: grazed treatment
[e]SUMMER: samples collected July-August
[f]WINTER: samples collected in early March

Appendix 2



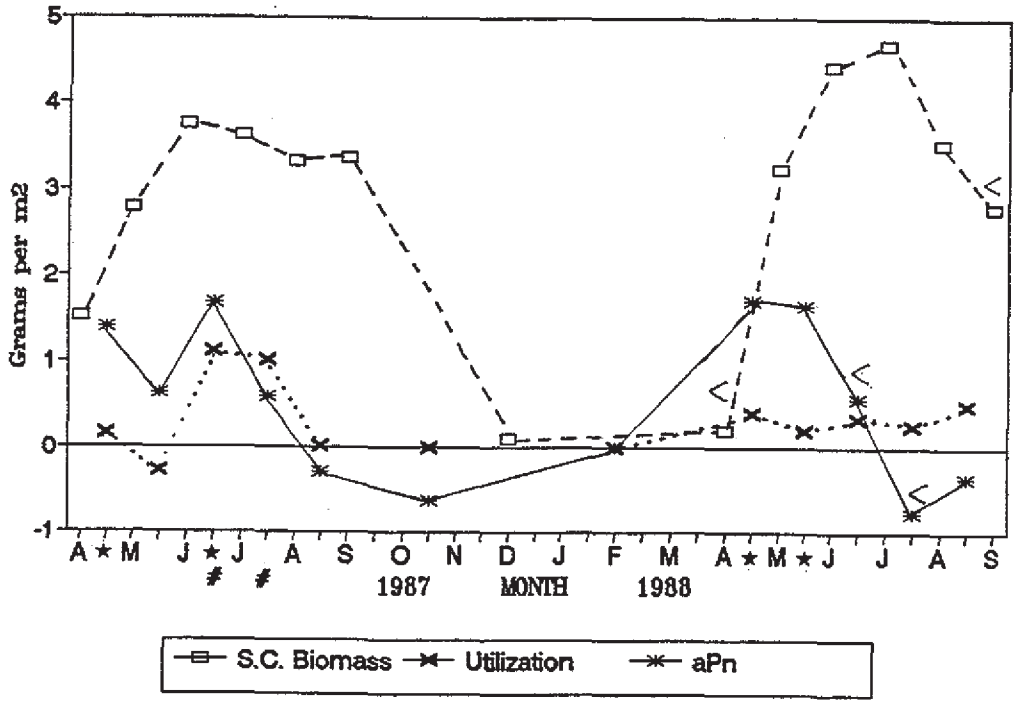
Mean monthly standing crop biomass, utilization, and production (g/m^2) of buttercup in grass-dominated strata in the South Fork Hoh, April 1987-September 1988. < indicates value was less ($P < 0.05$) in 1988 than during same month in 1987. > indicates value was greater ($P < 0.05$) in 1988 than during same month in 1987.

Appendix 2 (continued). Means and P values from 2-way ANOVAs on the effects of year and cervid exclusion, by season, on buttercup in grass dominated strata in old-growth forests in the South Fork Hoh, Olympic National Park, 1987-1989.

SEASON YEAR	E[a]	G[b]	Stder	n	Year	Tmt	Y*T
a) Biomass (g/m^2)							
SUMMER[c]					0.9522	0.0506	0.0547
1987	35.84	11.13	5.734	5			
1988	24.01	21.51	4.533	8			
WINTER[d]					0.3828	0.1987	0.2402
1987	10.20	2.91	2.803	4			
1988	3.67	2.63	2.119	7			
b) Plant Height (cm)							
SUMMER					0.7301	0.0001	0.0670
1987	26.08	12.98	1.494	5			
1988	22.61	14.99	1.181	8			
WINTER					0.0017	0.0312	0.2290
1987	8.17	4.50	1.029	3			
1988	4.81	3.41	0.674	7			
c) Biomass Concentration (g/m^3)							
SUMMER					0.8387	0.4366	0.1802
1987	127.41	100.80	30.258	5			
1988	103.20	154.65	23.921	8			
WINTER					0.4032	0.7896	0.5594
1987	142.70	110.87	34.059	3			
1988	73.51	76.75	22.297	7			
d) Percent Crude Protein							
SUMMER					0.4561	0.0013	0.1406
1987	11.21	15.10	0.728	3			
1988	11.25	13.19	0.446	8			
WINTER					0.1872	0.7756	0.1803
1987	19.25	17.67	0.970	2			
1988	20.34	21.49	0.686	4			
e) Percent In Vitro Digestible Dry Matter							
SUMMER					0.8555	0.0444	0.8974
1987	76.38	74.14	1.431	3			
1988	76.16	73.60	0.877	8			
WINTER					0.1262	0.0090	0.8614
1987	75.64	71.00	1.132	2			
1988	78.17	73.90	0.801	4			
f) Crude Protein Concentration (g/m^3)							
SUMMER					0.8899	0.1469	0.3696
1987	14.27	15.93	5.023	5			
1988	11.45	21.58	3.971	8			
WINTER					0.5056	0.7181	0.3738
1987	30.11	19.59	7.493	3			
1988	15.25	16.66	4.906	7			
g) In Vitro Digestible Dry Matter Concentration (g/m^3)							
SUMMER					0.8651	0.5277	0.1752
1987	97.43	75.29	21.382	5			
1988	78.36	112.08	16.905	8			
WINTER					0.4201	0.6615	0.5120
1987	108.61	78.72	25.674	3			
1988	56.64	56.53	16.808	7			

[a]E: enclosed control, or ungrazed, treatment
[b]G: grazed treatment
[c]SUMMER: samples collected in August
[d]WINTER; samples collected in early March

Appendix 3



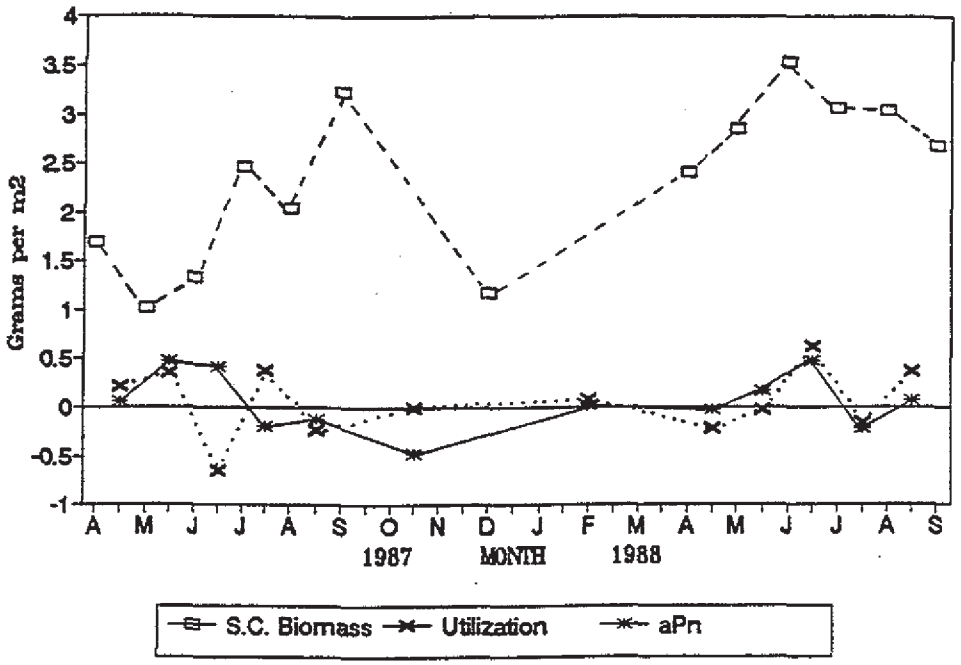
Mean monthly standing crop biomass, utilization, and production (g/m^2) of wood sorrel in forb dominated strata in the South Fork Hoh, April 1987-September 1988. < indicates value was less ($P< 0.05$) in 1988 than during same month in 1987. > indicates value was greater ($P< 0.05$) in 1988 than during same month in 1987. * indicates production was greater than 0 ($P< 0.05$) during sample period. # indicates utilization was greater than 0 ($P < 0.05$) during sample period.

Appendix 3 (continued). Means and P values from 2-way ANOVAs on the effects of year and cervid exclusion on wood sorrel in forb dominated strata in old-growth forests in the South Fork Hoh, Olympic National Park, 1987-1989.

	E[a]	G[b]	(stdr)	n	Year	Tmt	Y*Tmt
a) Biomass (g/m^2)					0.0466	0.1613	0.0874
1987	2.66	2.85	0.549	10			
1988	5.93	4.10	0.549	10			
b) Plant Height (cm)					0.3266	0.0461	0.9642
1987	10.38	9.12	0.613	9			
1988	11.34	10.03	0.582	10			
c) Biomass Concentration (g/m^3)					0.1425	0.5510	0.2024
1987	29.09	33.26	5.439	9			
1988	49.97	40.10	5.150	10			
d) Percent Crude Protein					0.5170	0.7661	0.7014
1987	12.65	12.33	0.622	5			
1988	12.18	12.18	0.260	8			
e) Percent In Vitro Digestible Dry Matter					0.0043	0.2923	0.2117
1987	60.09	59.32	0.771	5			
1988	51.74	54.65	1.456	8			
f) Crude Protein Concentration (g/m^3)					0.1704	0.5060	0.1883
1987	3.63	4.13	0.667	9			
1988	6.18	4.89	0.633	10			
g) In Vitro Digestible Dry Matter Concentration (g/m^3)					0.2970	0.7914	0.3012
1987	17.22	19.89	3.215	9			
1988	25.71	21.70	3.051	10			

[a]E: enclosed control, or ungrazed treatment
[b]G: grazed treatment

Appendix 4



Mean monthly standing crop biomass, utilization, and production (g/m^2) of strawberry-leaf raspberry in forb dominated strata in the South Fork Hoh, April 1987-September 1988.

Appendix 4 (continued). Means and P values from 2-way ANOVAs on the effects of year and cervid exclusion, by season, on strawberry-leaf raspberry in forb dominated strata in old-growth forests in the South Fork Hoh, Olympic National Park, 1987-1989.

SEASON YEAR	E[a]	G[b]	Stder	n	Year	Tmt	Y*T
a) Biomass (g/m^2)							
SUMMER[c]					0.6269	0.1925	0.8215
1987	2.48	1.63	0.723	10			
1988	3.18	1.99	0.762	9			
WINTER[d]					0.3252	0.0483	0.5503
1987	2.89	1.32	0.571	9			
1988	1.85	0.97	0.571	9			
b) Plant Height (cm)							
SUMMER					0.8614	0.1559	0.5470
1987	6.20	5.98	0.276	8			
1988	6.46	5.90	0.260	9			
WINTER					0.1704	0.0219	0.0250
1987	8.13	5.31	0.553	6	E>G 1987 only		
1988	5.49	5.45	0.553	8			
c) Biomass Concentration (g/m^3)							
SUMMER					0.7766	0.2448	0.8211
1987	44.19	31.10	13.962	8			
1988	53.49	34.15	13.164	9			
WINTER					0.8935	0.1903	0.5648
1987	36.40	29.57	8.681	8			
1988	39.82	22.76	8.681	8			
d) Percent Crude Protein							
SUMMER					0.9994	0.0482	0.5376
1987	11.33	11.69	0.187	5			
1988	11.21	11.82	0.209	4			
WINTER					0.5594	0.1860	0.0014
1987	10.87	9.83	0.130	3	E>G 1987 only		
1988	9.88	10.22	0.110	5			
e) Percent In Vitro Digestible Dry Matter							
SUMMER					0.2033	0.2388	0.9975
1987	39.99	41.65	1.228	5			
1988	43.36	45.03	1.373	4			
WINTER					0.6206	0.2776	0.6663
1987	47.34	50.40	5.804	3			
1988	41.95	49.72	4.496	5			
f) Crude Protein Concentration (g/m^3)							
SUMMER					0.7699	0.2914	0.8121
1987	5.02	3.73	1.587	8			
1988	6.10	4.07	1.496	9			
WINTER					0.8289	0.1565	0.7061
1987	3.99	2.95	0.938	8			
1988	4.06	2.29	1.032	8			
g) In Vitro Digestible Dry Matter Concentration (g/m^3)							
SUMMER					0.6884	0.3096	0.8706
1987	17.52	12.93	5.394	8			
1988	21.61	15.29	5.086	9			
WINTER					0.5804	0.2792	0.6152
1987	17.93	15.53	3.916	8			
1988	16.78	10.36	3.916	8			

[a]E: enclosed control, or ungrazed treatment
[b]G: grazed treatment
[c]SUMMER: samples collected July-August
[d]WINTER: samples collected in early March

Appendix 5

Means and P values from 2-way ANOVAs on the effects of year and cervid exclusion on false lilly-of-the-valley in forb dominated strata in old-growth forests in the South Fork Hoh, Olympic National Park, 1987-1989.

Year	E[a]	G[b]	stdr)	n	Year	Tmt	Y*T
a) Biomass (g/m^2)							
1987	0.47	0.25	0.312	7	0.0127	0.0242	0.0884
1988	2.00	0.61	0.312	7			
b) Percent Crude Protein							
1987	11.86	11.15	0.163	2	0.5466	0.6193	0.208
1988	10.00	11.37	0.785	2			
c) Percent In Vitro Digestible Dry Matter							
1987	76.41	78.20	2.192	2	0.0163	0.5044	0.7769
1988	89.80	90.57	0.456	2			
d) Plant Height (cm)							
1987	9.56	10.60	0.924	5	0.919	0.7118	0.3379
1988	10.57	9.73	0.437	3			
e) Biomass Concentration (g/m^3)							
1987	2.78	3.07	0.232	5	0.0326	0.1543	0.0803
1988	29.27	7.28	10.099	3			
f) Crude Protein Concentration (g/m^3)							
1987	0.34	0.36	0.032	5	0.0294	0.1799	0.1046
1988	2.92	0.86	1.030	3			
g) In Vitro Digestible Dry Matter Concentration (g/m^3)							
1987	2.09	2.41	0.119	5	0.0308	0.1634	0.0833
1988	26.42	6.57	9.294	3			

[a]E: enclosed control, or ungrazed, treatment
[b]G: grazed treatment

Appendix 6

Means and P values from 2-way ANOVAs on the effects of year and cervid exclusion, by season, on *Oenanthe sarmentosa* in grass dominated strata in old-growth forests in the South Fork Hoh, Olympic National Park, 1987-1989.

SEASON YEAR	E[a]	G[b]	Stder	n	Year	Tmt	Y*T
a) Biomass (g/m^2)							
SUMMER[c]					0.7765	0.2732	0.611
1987	4.69	1.85	1.666	5			
1988	4.47	3.40	1.666	5			
WINTER[d]					0.3328	0.7281	0.804
1987	1.53	1.35	0.177	3			
1988	1.28	0.68	0.169	5			
b) Percent Crude Protein							
SUMMER					0.8670	0.1382	0.6871
1987	10.83	12.91	0.911	3			
1988	11.32	12.61	0.911	3			
c) Percent In Vitro Digestible Dry Matter							
SUMMER					0.0115	0.3869	0.5795
1987	69.20	65.77	2.180	3			
1988	74.47	73.66	2.180	3			
d) Plant Height (cm)							
SUMMER					0.1237	0.1247	0.8729
1987	20.50	15.35	7.177	2			
1988	14.28	10.04	0.258	5			
WINTER					0.0295	0.1021	0.9943
1987	5.00	4.17	0.656	3			
1988	3.74	2.90	0.312	5			
e) Biomass Concentration (g/m^3)							
SUMMER					0.2406	0.8768	0.8578
1987	15.06	13.33	13.843	2			
1988	30.34	33.94	11.093	5			
WINTER					0.9696	0.5274	0.3472
1987	32.52	28.54	7.775	3			
1988	29.39	30.11	2.718	5			
f) Crude Protein Concentration (g/m^3)							
SUMMER					0.2282	0.6364	0.7272
1987	1.64	1.53	1.467	2			
1988	3.29	4.27	1.157	5			
WINTER					0.9512	0.5021	0.3422
1987	7.39	6.49	1.767	3			
1988	7.11	7.36	0.745	5			
g) In Vitro Digestible Dry Matter Concentration (g/m^3)							
SUMMER					0.2307	0.9233	0.8978
1987	10.50	9.44	10.029	2			
1988	22.76	24.52	8.213	5			
WINTER					0.8903	0.4285	0.3157
1987	22.04	19.34	5.269	3			
1988	22.10	23.59	2.672	5			

[a]E: enclosed control, or ungrazed treatment
[b]G: grazed treatment
[c]SUMMER: samples collected July-August
[d]WINTER: samples collected in early March