

## Ungulate-Forest Relationships in Olympic National Park: Retrospective Exclosure Studies

### Abstract

Twenty-five ungulate exclosures were established in Olympic National Park (23) and Olympic National Forest (2) in the 1930's and 1950's. We gleaned information from the early studies and, where possible resampled vegetation within and adjoining exclosures from 1987-1990 to describe effects of ungulates on forest vegetation. Exclosures were established on low elevation (< 350 m) ungulate ranges; 21 were located on river valley floors in the Sitka Spruce or Western Hemlock Forest Zones, 2 were on valley walls or other upland sites in the Western Hemlock and Silver Fir Zones, 2 were in clearcuts. We provide examples where ungulate herbivory influenced the composition, morphology, and standing crop of forest vegetation at all structural layers (i.e., herbaceous understory, shrubs, lower tree canopy, and overstory canopy). In communities initially dominated by grasses or grasslike plants on valley floors, exclusion of ungulates resulted in decreased cover of grasses and forbs (usually), decreased species richness of forbs, and sometimes increased height and abundance of ferns. Shrub size and density increased following exclusion, particularly salmonberry and huckleberry. Ungulates influenced the recruitment and morphology of vine maple. Ungulate effects on establishment of overstory species were variable; browsing appeared to affect recruitment of Pacific silver fir and western red cedar following clearcut logging, but effects on other species were unclear. The importance of ungulate herbivory in determining forest composition is discussed in relation to the scale of other processes.

### Introduction

The importance of herbivores to ecosystem dynamics has been documented in studies of natural grazing systems (e.g., Crawley 1983, Naiman 1988, McNaughton *et al.* 1989, Frank and McNaughton 1992). In long-established ungulate systems such as the Serengeti, herbivores not only determine substantially the genetic and species composition of grassland vegetation, but herbivory may actually increase plant productivity by accelerating nutrient fluxes through the ecosystem (McNaughton 1985). Forest systems are less well understood, but moose (*Alces alces*) browsing is known to change the species composition, structure, nutrient availability, and long-term dynamics of boreal forests (Pastor *et al.* 1988, McInnes *et al.* 1992). These and other studies show that mammalian herbivores interact strongly with vegetation and are not just passive components of ecological systems. Early attempts to evaluate ungulate-forest relationships on the Olympic Peninsula began over 50 years ago when ungulate exclosures were constructed and periodically maintained. Only preliminary findings from these studies have been published (Schwartz and Mitchell 1945). We examine information assembled from 25 ungulate exclosures established in the 1930's and 1950's in Olympic National Park and Olympic National For-

est. Our goal was increased understanding of the long-term effects of native ungulates in forests in the Pacific Northwest. This work is part of a larger effort to understand the influence of ungulate herbivory on forest dynamics (Happe *et al.* 1990, Schreiner *et al.* submitted, Happe 1993, Woodward *et al.* 1993).

Although exclosures have been widely used to evaluate effects of wild and domestic ungulates and other mammals on plant communities, data derived from them may be difficult to interpret. Potential problems include small size and numbers, subjective placement of exclosures and associated sample plots, and modification of soil moisture and temperature regimes by the fences (Daubenmire 1940, Heady 1968, Houston 1982). Ungulates may be attracted to the fences, thus intensifying grazing or trail formation immediately outside. The intensity of herbivory may therefore be exaggerated when grazed plots are located too near the fence (Heady 1968). Moreover, it is risky to apply interpretations from a few exclosures to entire ungulate ranges because exclosures are small relative to ecological forces, such as fire, that drive vegetation dynamics over time (e.g. Mueggler and Bartos 1977).

We acknowledge these difficulties and others, such as the lack of statistical design, in the early studies on the Olympic Peninsula. Nevertheless, these exclosure studies span 55 years and provide an opportunity to evaluate long-term effects of

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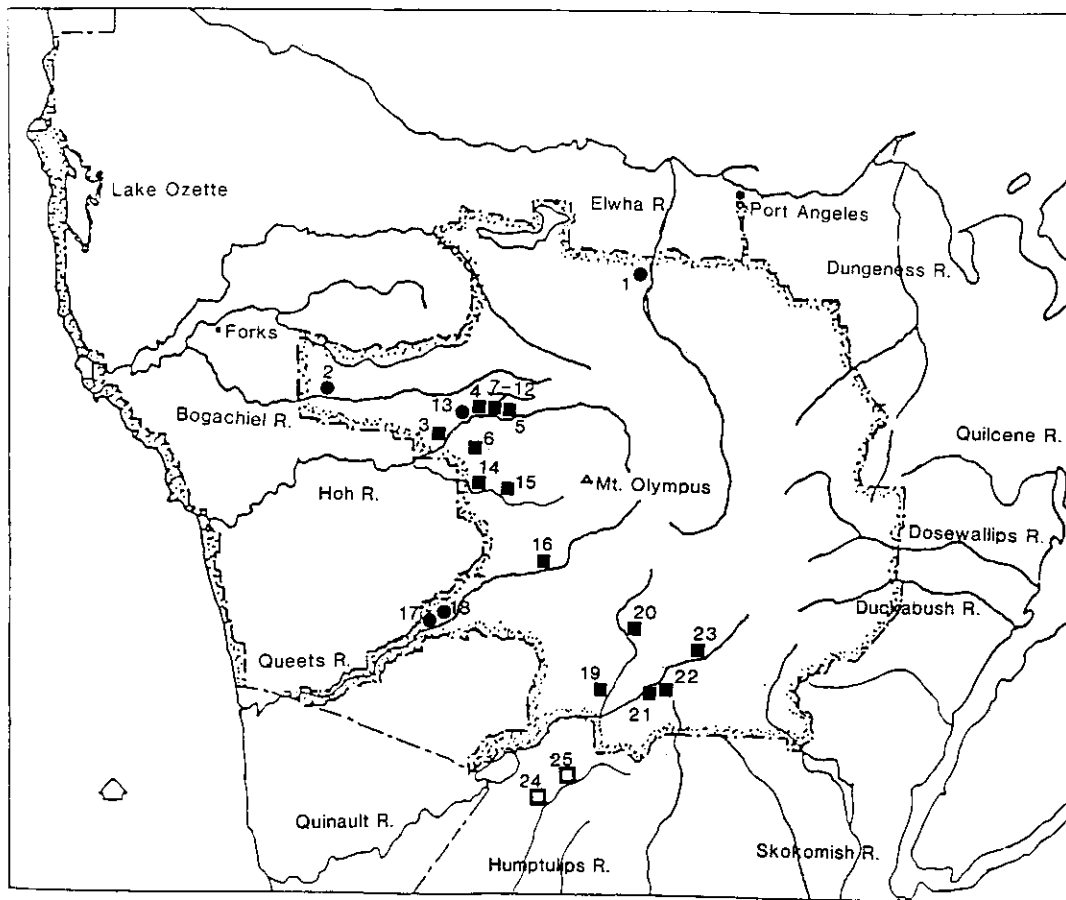


Figure 1. Approximate locations of 25 ungulate exclosures, Olympic Peninsula, Washington (Schwartz ■, Newman ●, and USFS □).

ungulates on the coniferous "rain" forest ecosystem unique to the Olympic Peninsula (Franklin and Dyrness 1988). Exclosures can provide insight into ecological processes if the information is interpreted carefully (e.g., Pastor *et al.* 1988, McInnes *et al.* 1992).

### Study Area

Exclosures were established on low elevation (<350 m) ungulate ranges on the western half of Olympic National Park, Washington (Figure 1). The area has a maritime climate with relatively dry summers and wet winters. Annual precipitation ranges from 150 to 400 cm (NOAA 1978) with winter precipitation falling mostly as rain. Mean annual temperature at Forks is 10°C, with January as the coldest month (4°C) and July-August the warmest (16°C) (Phillips and Donaldson 1972).

Twenty-one exclosures were located on river valley floors in the Sitka spruce (*Picea sitchensis*) or Western Hemlock (*Tsuga heterophylla*) Zones (*sensu* Franklin and Dyrness 1988) where plant communities occur on river terraces of successively greater age (Fonda 1974). Valley floor forests have been described as a serc from pioneer red alder (*Alnus rubra*) on active floodplains, through black cottonwood (*Populus trichocarpa*)/Sitka spruce on younger terraces, to stands of western hemlock and Sitka spruce on older terraces (Fonda 1974). However, these successional patterns vary among river valleys depending on disturbance history (McKee *et al.* 1982). Three exclosures were located on valley walls in the western hemlock or Pacific silver fir (*Abies amabilis*) zones; one was in an old field.

Elk show two life history patterns in the study area: (1) year-round residence and (2) seasonal

migrations to high elevation summer ranges (Jenkins and Starkey 1982, Schroer 1987, Schroer *et al.* 1993). Elk densities on winter ranges in the park are approximately 6-7 elk/km<sup>2</sup> (Houston *et al.* 1987, 1988). Elk utilize certain vegetation types and landforms disproportionately. This produces a marked gradient in herbivory: use is concentrated on younger river terraces and floodplains, it is lower on older terraces, and least on the valley walls (Jenkins and Starkey 1982, 1984). Black-tailed deer (*Odocoileus hemionus*) occur throughout the area, but generally at lower densities. The elk:deer biomass ratio is estimated to be about 100:7 on west side river drainages (Leslie 1983). Ungulate predators include cougar (*Felis concolor*) and black bear (*Ursus americanus*).

## Methods

Twenty-three exclosures were established in Olympic National Park during two periods when there was concern about elk-vegetation relationships: 1934-1936 (18 exclosures) and 1952-1958 (5). J. E. Schwartz constructed 12 permanently closed exclosures and two series of three "take-down" exclosures which could be left open for predetermined amounts of time. These exclosures were actually established on Olympic National Forest lands that became Olympic National Park in 1938. The second pulse of exclosure construction was by C. C. Newman, who also repaired and measured some of the Schwartz exclosures. In addition, two exclosures were established in 1957 in Olympic National Forest. Although our work focused on the park, exclosures in the national forest provided an opportunity to compare the effects of ungulate herbivory in managed forests. From 1987 to 1990 we gleaned information from the early studies and, wherever possible, resampled vegetation within and adjoining exclosures. The names and numbers used to identify exclosures changed over time which resulted in considerable confusion. Exclosures are numbered from north to south for our presentation (Table 1, Figure 1).

### Schwartz Permanent Exclosures (Nos. 3-6, 14-16, 19-23)

J. E. Schwartz constructed 12 permanent exclosures from 1934 to 1936 in the Hoh, South Fork Hoh, Queets and Quinault river valleys. Two have never been relocated or sampled (Nos. 6, 20). The remaining 10 were either 0.09 ha (n=6) or

0.19 ha (n=4) and were constructed of split rails and barbed wire (n=8) or woven wire (n=2). Schwartz was concerned about the level of browsing on three species he considered "key browse species," salmonberry (*Rubus spectabilis*), vine maple (*Acer circinatum*), and huckleberry (*Vaccinium parvifolium*, and *V. alaskense*) (Schwartz 1939, Schwartz and Mitchell 1945, Schwartz pers. comm. 1990).

Schwartz described vegetation by estimating "density of ground cover" on a scale of 1-10 in one (sometimes two) 9.3 m<sup>2</sup> plots inside exclosures. Estimates included only herbaceous species and omitted mosses. On different 9.3 m<sup>2</sup> plots he charted aerial cover of shrubs and also estimated percent cover of "grass" (including sedges), and "weeds" (i.e., forbs including ferns). Unfortunately only preliminary data from seven exclosures remain (Schwartz and Mitchell 1945).

### Schwartz Takedown Exclosures (Nos. 7-12)

Schwartz constructed six "takedown" exclosures in 1936 in addition to the permanent exclosures. These were designed to measure the effects of regulated browsing on vine maple (Nos. 7-9) and huckleberry (Nos. 10-12). The three exclosures forming each series were less than 50 meters from one another. The original objective was to allow wintering elk to browse shrubs to predetermined levels (25, 50, 75% utilization of annual production), close the exclosures and monitor shrub response (Schwartz 1939). All exclosures were opened in spring 1937 and closed permanently by 1938 (Schwartz 1990 pers. comm.). All data have been lost.

C. C. Newman (1953) repaired six of the Schwartz exclosures and sampled vegetation inside and outside four in 1952 and 1955. Percent cover was estimated as <1% or as midpoints in 10 subsequent classes at 10% increments. Shrub stems were counted on 2.3 m<sup>2</sup> circular plots.

### Newman Exclosures (Nos. 1, 2, 13, 17, 18)

Newman constructed five variously sized exclosures of woven wire from 1953 to 1958 (Table 1). Three were in Sitka spruce stands in different river valleys (Bogachiel, No. 2; Hoh, No. 13; Queets, No. 18), one in a red alder stand (Elwha, No. 1) and one along an old-field/vine maple ecotone (Queets, No. 17). Three exclosures were established at particularly heavily grazed sites (Nos. 1, 13, 17).



TABLE 1. Continued.

Area/ID	Date Est.	Orig. (Mo.)	Area (ha)	Veg. Type	YEARS SAMPLED AND METHODS USED <sup>1</sup>											Comments	
					35	40	45	50	55	60	65	70	75	80	85		90
22 Quat. No. 4 (Graves Cr.)	1935 (?)	S	0.09	BLM/VM.SB (F,L)	A	A	P			P							D
23 Quin. No. 5 (Fire Cr.)	1936 (?)	S	0.09	SILP/HB (W)						P							D

<sup>1</sup> N- C. Newman; S- J. Schwartz; F- U.S. Forest Service.

<sup>2</sup> Major overstory tree/shrub (ALD- red alder, BLM- bigleaf maple, HEM- western hemlock, SILP- Pacific silver fir, SPR- Sitka spruce, HB- huckleberry, SB- salmonberry, VM- vine maple) and location (W- valley wall, F- valley floor, Upper (U) and Lower (L) terraces).

<sup>3</sup> Measurements include:

A- Cover in 9.3 m<sup>2</sup> plots, B- Cover & stem count in 2.3 m<sup>2</sup> plots, C- tree mortality and growth, D- Examination and/or measurements, this study, P- photo.

Photos taken the same year as measurements are not indicated. X- Known to be no longer functional.

<sup>4</sup> Also cover and sociability, Sharpe 1956.

Apparently, No. 17 was to evaluate the ability of vine maple to recolonize an abandoned hayfield in the absence of browsing. No. 13 was built mainly to determine if vine maple and bigleaf maple require mineral soil to reproduce from seed; one half of the enclosure and a corresponding outside plot were spaded in 1953.

Percent cover by species was estimated on eight (four inside, four outside) 2.3 m<sup>2</sup> circular plots. Plots were established systematically, one in each quarter of the enclosure with a similar pattern (usually) outside. Data were collected by park personnel regularly through 1965 and again in 1982, although methods and seasons varied.

#### Olympic National Forest Enclosures (Nos. 24,25)

Two 0.8 ha enclosures made of woven wire were established in 1957 on clearcut western hemlock/Pacific silver fir stands logged in 1955; both were essentially intact in 1990. Logging slash was left unburned at No. 24 and burned at No. 25. One-half of each enclosure was planted with 2-year old Douglas-fir (*Pseudotsuga menziesii*) seedlings and the other half was allowed to regenerate naturally. Mortality and growth rates were measured from 1957 to 1962 on 100 planted Douglas-fir seedlings inside and outside each enclosure (Harrison 1963). Species composition and cover of shrubs, grasses and forbs were measured inside No. 24 during 1957 (Brent 1957).

#### Recent Samples

*Schwartz Permanent Enclosures.* We examined eight enclosures from 1986-1990; none was intact. Tree composition was sampled in six ex-

closures (Nos. 3, 14, 19, 21, 22, 23) using one or two 100-400 m<sup>2</sup> plots inside and outside (the two remaining sites had been altered by extensive treefall and were not sampled). Cover of large organic debris (LOD) was estimated and tree age was obtained for all individuals in each plot, either from increment cores taken close to the ground or basal sections of saplings 1-4 cm in diameter. Overstory cover was estimated overall and for each species to the nearest 10 percent. Inside and outside plots were comparable with respect to overstory composition and cover of LOD. Plots inside enclosures were placed a minimum of 2 m from fence lines, while outside plots were at least 10 m and usually much further from fence lines. Quinault River enclosures (Nos. 19-23) were sampled by Pfister and Pfister (1989) under our direction. Sampling focused on vine maple age and morphology in No. 4 (see takedown enclosures).

*Schwartz Takedown Enclosures.* We relocated the six takedown enclosures in 1990. While examining the vine maple series, we noticed that apically dominant stems originated either directly from the ground or from branches of older stems, and stem orientation varied from vertical to horizontal. Therefore, we measured age, stem length (rather than height above ground), number, diameter, and morphology (originating from branch or ground rooted) of stems > 1 cm. Samples were taken inside Nos. 7 and 9; we also included No. 4 (permanent) because vine maple density was comparable. Takedown No. 8 was not sampled because vine maple was sparse. Plot sizes ranged from 9.5 x 14.3 m to 20 x 20 m for a total area of 675 m<sup>2</sup> inside and 850 m<sup>2</sup> outside. Because enclosures were placed specifically around clumps of vine maple, we deliberately established outside

plots in stands having comparable composition and stem density.

We measured dimensions of huckleberry clumps (stems arising from a common root crown) in 8.5 x 14 m plots inside and outside Nos. 11 and 12. Exclosure 10 was omitted because huckleberry was uncommon. Outside plots were chosen which had huckleberry-dominated shrub layers, and overstory types, slopes, aspects and geomorphic surfaces similar to the exclosures. We counted the number of stems and measured height of the tallest stem, length and width of each clump. Canopy area was computed as an ellipse from the length and width. Several of the largest stems at each site were cut for determining age.

**Newman Exclosures.** We examined all five Newman sites from 1987-1990; two exclosures were intact (Nos. 1 and 2). We measured cover of shrubs (1 x 4 m plots) and herbaceous species (1 x 1 m plots) in classes of <1, 1-5, 6-25, 26-50, 51-75, 76-95, and 96-100%. Fourteen subplots were placed in a single 8 x 20 m macro plot inside exclosures and distributed seven each in two 8 x 20 m macro plots outside. As with the Schwartz exclosures, cover of LOD was measured, and ages of all trees > 1 cm in diameter at the base were determined from cores or basal disks.

**Olympic National Forest Exclosures.** We sampled species composition, age and growth (i.e., dbh and height) of trees on two (burned, No. 25) or three (unburned, No. 24) 225 m<sup>2</sup> plots inside and out of each exclosure. We sampled the unplanted site at No. 25 and the planted site at No. 24. We avoided sampling other sites because vegetation heterogeneity prevented us from locating paired plots in and out of exclosures.

**Photographs.** In addition to sampling vegetation, we examined historic photographs. We located 48 photos of Schwartz exclosures from construction through 1980, 349 photos or slides of Newman exclosures, and 2 photos of the Forest Service exclosures.

Analysis, interpretation, and presentation of data from all four groups of exclosures posed certain difficulties. Although the total number of exclosures is large, only four vegetation types were replicated (see Table 1). Within these groups, some exclosures were not found, or appeared to be atypical for reasons other than herbivory, or included too few individuals (particularly trees) to provide meaningful conclusions. Therefore, our presenta-

tion is mostly narrative and focuses on replicated comparisons; statistical treatments are limited to robust tests with the fewest underlying assumptions. Percentage data was transformed by the arcsine of the square root before analysis. Interpretations from measurements were also compared to the photos.

## Results

We believe that all exclosures were initially effective in excluding elk and deer. Fences were generally at least 2.5 m high with construction which appeared to preclude ungulates, but not smaller herbivores such as snowshoe hares (*Lepus americanus*) and rodents. We do not know how long some exclosures were effective (Table 1). Several of the Schwartz exclosures were in disrepair by the early 1950's (Newman 1953), but some were enough intact that Newman considered repairs worthwhile.

### Herbaceous Understory

Results from the Schwartz exclosures showed that understory vegetation responded quickly, and changes persisted for at least 21 years (Table 2). Specifically, grass cover decreased and ferns tended to increase. Similarly, grass cover decreased with time inside four of five Newman exclosures while forbs and ferns generally showed parallel changes in and out (Table 3).

Data from Newman exclosures were recorded by species, providing information about changes in species richness of forbs. During the first three years of measurements at No. 1 on the Elwha, five to eight species were encountered inside and five to seven outside. After 31 years, youth-on-age (*Tolmiea menziesii*) completely dominated the herbaceous layer inside, while eight species of forbs occurred in outside plots. At the other four sites, data collected until 1965 showed that cover of clover (*Trifolium* spp.) (Nos. 2, 13, 17), liverworts (No. 2), buttercup (*Ranunculus repens*) (Nos. 2, 17) and dandelion (*Taraxacum officinale* and/or perhaps *Hypochaeris radicata*) (No. 17) declined inside exclosures but persisted outside. Oregon oxalis (*Oxalis oregana*) (No. 13), dock (*Rumex* spp.) (No. 13), and chickweed (*Stellaria* spp.) (No. 1) had similar cover in and out of exclosures. Thus, species richness of forbs outside exclosures was greater than or equal to richness inside and total cover of forbs tended to be greater outside exclosures by 1987.

TABLE 2. Summary of vegetation cover changes for Schwartz and Newman exclosures at several post-establishment time intervals. Symbols indicate change in vegetation category. Comparisons are between vegetation inside exclosures and inside at an earlier date (Schwartz, 3 year interval), or with outside (all others). Data are from Schwartz and Mitchell (1939), Newman (1953, 1955), and Sharpe (1956).

Exclosure	Intervals (years)	Change in Vegetation Cover <sup>1</sup>			
		Grasses	Forbs	Ferns	Shrubs
Coniferous Forest (Schwartz <sup>2</sup> )					
No. 3	3, 17, 20	-	0	?	+
No. 4	3, 17, 20, 21	-	0	+	+
No. 5	3	-	+	?	+
No. 9	17, 20	0	0	0	+
No. 14	17, 20	0	0	+	+
No. 18	2-4	?	0	0	0
No. 19	3	-	-	?	+
No. 20	3	?	-	?	+
No. 21	3	-	-	?	+
Coniferous Forest (Newman)					
No. 2	2-7, 9, 10, 12	-	0	0	+
No. 13	3-5, 7-9, 12	-	?	+	+
Alder Flat (Newman)					
No. 1	1-3, 5, 6, 8, 9	-	0	?	?
Bigleaf Maple (Newman)					
No. 22	3, 17	-	-	0	+
Old Field (Newman)					
No. 17	2-4, 5, 7-9	-	0	?	?

<sup>1</sup>Key: (-) = less inside at every interval, (+) = more inside at every interval, (0) = no difference or contradictory changes with interval, (?) = category was not reported.

<sup>2</sup>Decrease in grass cover and increase in shrub cover inside exclosures was significant over 3-year interval for Schwartz exclosures ( $p < 0.05$ , sign tests); grass cover was significantly less and shrub cover was significantly greater inside versus outside at 17-year interval ( $p < 0.05$ , sign tests).

TABLE 3. Dimensions of huckleberry clumps in Schwartz take-down exclosures Nos. 11 and 12 and control plots.

		Distribution			Clump Dimensions		
		Clump Density (no./m <sup>2</sup> )	Stem Density (no./m <sup>2</sup> )	Canopy Area (area/m <sup>2</sup> )	Height (cm)	Canopy Area (m <sup>2</sup> /m <sup>2</sup> )	Stems (no.)
In	No. 11	0.51	6.2	0.24	56.1	0.41	10.6
	No. 12	<u>0.58</u>	<u>5.4</u>	<u>0.50</u>	<u>94.1</u>	<u>0.86</u>	<u>9.3</u>
	Mean	0.54	5.8	0.37	75.1	0.64	10.0
Out	No. 11	0.47	2.0	0.14	62.8	0.31	4.0
	No. 12	<u>0.54</u>	<u>3.0</u>	<u>0.22</u>	<u>69.6</u>	<u>0.41</u>	<u>6.0</u>
	Mean	0.50	2.5	0.18	66.2	0.36	5.0

Photographs generally corroborated measurements. The most striking changes in vegetation occurred following ungulate exclusion from plant communities where understories were dominated initially by grasses or grass-like plants, as opposed to moss and swordfern dominated sites (compare Figures 2 and 3). These relationships held in both conifer forests and alder stands, represented in both Schwartz and Newman exclosures.

### Shrubs

Shrub species, particularly salmonberry and huckleberry, increased inside both the Schwartz and Newman exclosures (Tables 2 and 3). This occurred in all forest types and was supported by the photographs.

Our measurements focused on huckleberry at Nos. 11 and 12. Huckleberries produce multiple stems from a single root mass, and each clump seemed to represent an individual plant. Fifty-four years post-establishment, clump density was similar inside and out, however canopy dimensions and numbers of individual stems were greater inside (Table 4). Canopy area inside was greater by a factor of nearly two. Effects persisted even after the exclosures had collapsed because ungulates rarely consumed thick, woody stems. The largest stem we found had 4 cm basal diameter and was 32 years old.

### Lower Tree Canopy

Nearly all vine maple individuals established both in and out of exclosures since construction in 1936 (Figure 4). However, mode of establishment and morphology was affected by ungulates. Ground-rooted individuals (established from seed or lateral root buds) predominated inside exclosures, while branches that achieved apical dominance after the main trunk had fallen were the source of new individuals outside (Figure 4).

Age and stem length of cohorts were compared inside and out of exclosures (Figure 5). The majority of young stems outside tended to be shorter than 2 m, while many stems inside were longer than 2 m (Figure 5a). Stem length of 15 to 29-year-old trees showed similar bell-shaped distributions both inside and out (Figure 5b). Finally, cohorts older than 29 years outside fell predominantly into two stem classes and were rarely longer than 8 m (Figure 5c).

### Overstory

We saw relatively few consistent effects of herbivory on overstory composition in Schwartz and Newman exclosures. They were simply too small to contain enough individuals to give conclusive results. The only replicated results came from Nos. 3 and 18 with hemlock overstories and significant LOD inside (22%, 38%) and out (16%, 38%). More western hemlock established inside Nos. 3 (22 stems) and 18 (19 stems) compared with outside (No. 3, 14 stems; No. 18, 4 stems) following exclosure construction. In contrast, more Sitka spruce established outside (No. 3, 15 stems; No. 18, 5 stems) than in (No. 3, 2 stems; No. 18, 0 stems).

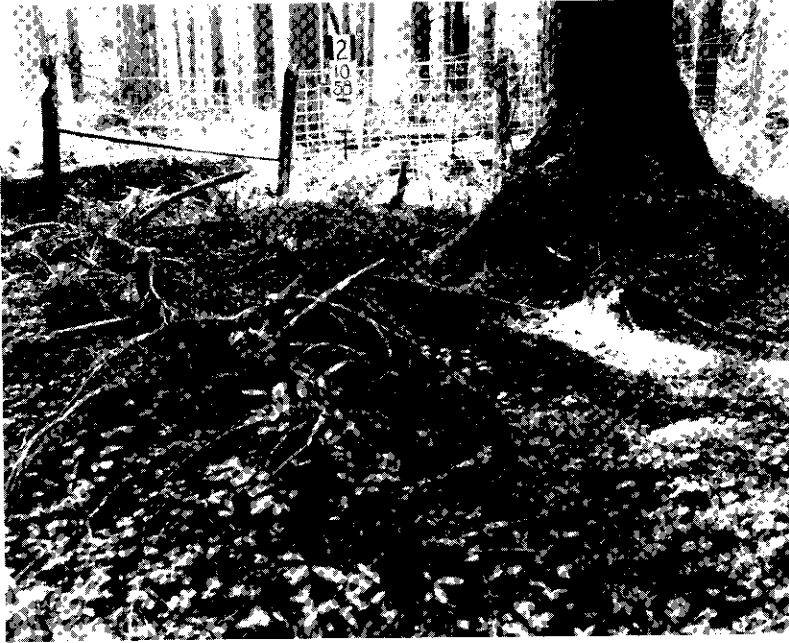
Results from the Olympic National Forest exclosures showed that total density (living and dead) and density of stems living after 33 years were greater inside exclosures for Pacific silver fir and western red cedar (Table 5). Density of living Douglas-fir did not differ in and out of No. 24, but there were more dead stems outside. We did not sample the planted portion of No. 25.

## Discussion

### Utility of Exclosure Studies

Although these early exclosures provide insight into the effects of herbivory, subsequent ungulate biologists would likely consider them to be too small (e.g., Heady 1968), because fences of small exclosures may alter microclimate and grazing intensity. We do not know the proximity of fences to most plots used to sample vegetation in the original studies. However, several surviving sample points outside Nos. 1, 3, and 22 were within a few meters of the fence, possibly exaggerating levels of herbivory sampled by Schwartz and Newman. The rugged construction of exclosures may have interfered with normal air currents and provided additional shade; they may have harbored a larger than normal snowshoe hare population (Sharpe 1956). Taller plants seen along fencelines today may be explained by greater light interception and/or by reduced competition from grazed plants outside fencelines. Also, vegetation contrasts may have been exaggerated in the Schwartz exclosures because they were located on heavily grazed sites.

These caveats granted, we believe the primary influence on vegetation change was the exclusion of ungulates. Our results may reflect ungulate



1958



1962

Figure 2. Inside No. 18 along the Queets River several months and four years post-establishment. Note that comparatively little change in composition or standing crop has occurred in the moss (*Hylecomium splendens*) and oxalis dominated plant community on this upper terrace.



1955

Figure 3. Number 13 on the Hoh River at 2 years, 6 years, and 12 years post-establishment. Note increased standing crop of grasses initially, which were displaced by salmonberry. A grass-dominated community with scattered ferns persists outside. Note the decomposition of the log at left background and the growth rate of the spruce.



1959



1965

TABLE 4. Comparison of establishment and survival of Pacific silver fir, western red cedar and western hemlock in and out of two exclosures established in clearcuts. Slash was burned in one clearcut (No. 25) and left in the other (No. 24). Douglas-fir was sampled only at No. 24. Results are the mean of two plots (No. 25) or three plots (No. 24) in and out of exclosures.

		Stems/ha					
		Living		Dead		Total	
		In	Out	In	Out	In	Out
P. Silver Fir	No. 24	104	15	0	59	104	74
	No. 25	156	44	155	22	311	66
W. Red Cedar	No. 24	104	0	15	0	119	0
	No. 25	289	44	266	67	555	111
W. Hemlock	No. 24	888	889	341	1081	1229	1970
	No. 25	1778	1311	2178	644	3956	1955
Douglas-fir	No. 24	326	340	15	104	341	444

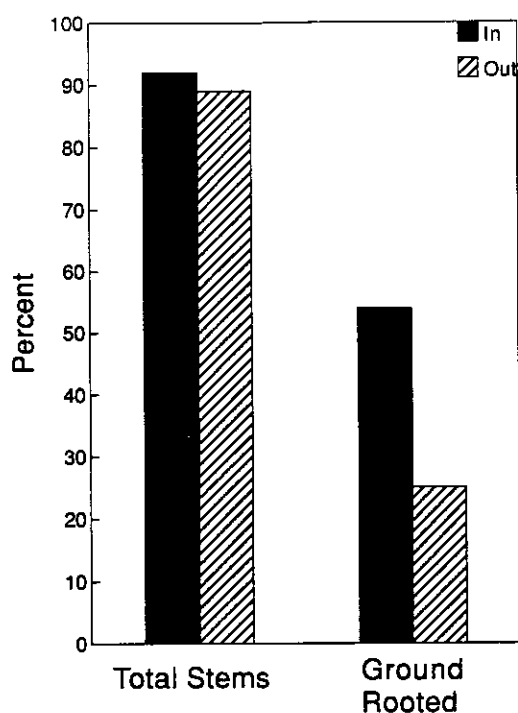


Figure 4. Establishment of vine maple since exclosure construction in 1936. Nearly all stems in and out of exclosures have established since 1936 (left), while a higher percentage (at  $p = 0.060$ ) of stems inside exclosures are ground-rooted (right).

herbivory at the high end of the grazing intensity gradient described earlier, because a high level of grazing was prerequisite for siting many exclosures (Schwartz 1990 pers. com.). Of 22 exclosures

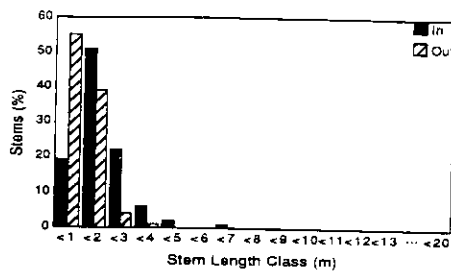
examined by us in the park, only one was on a valley wall, seven were on "upper terraces," ten were on "lower" terraces and four were on valley floor sites where terrace level could not be determined.

#### Effects of Ungulates on Vegetation

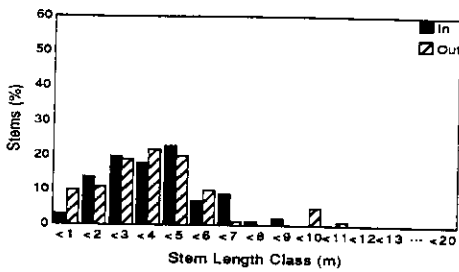
*Understory.* The greatest changes in herbaceous understory vegetation resulting from exclusion of ungulates occurred in communities initially dominated by grasses or grass-like plants. Specifically, grass cover decreased, abundance and height of ferns usually increased, species richness of forbs decreased, and forb cover usually decreased. Because the decrease in grass cover was not necessarily linked to an increase in forb cover, ungulates apparently did not mediate a direct competitive relationship between grasses and forbs. Forb species that declined in the absence of ungulates included clover, buttercup, and dandelion—a response possibly explained by trampling tolerance and greater light requirements. In contrast, youth-on-age thrived in the absence of grazing at No. 1, perhaps reflecting shade tolerance. Moreover, because clover, buttercup, and dandelion are introduced species, our results support the hypothesis that most introduced plants may become less abundant in the absence of disturbance (Harper 1977).

*Shrubs.* In the absence of ungulates, shrub size and stem density increased, particularly salmonberry and huckleberry, with possible effects on other layers. The consequent increase in shade is an additional environmental modification due to

a) 5-14 Years



b) 15-29 Years



c) 30-54 Years

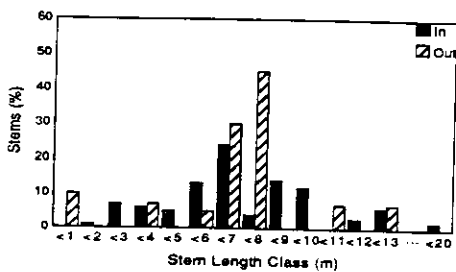


Figure 5. Distribution of stem length classes for three age cohorts of vine maple at Nos. 4, 7, and 9 (combined), measured 54 years post-establishment. Comparison is made between stems growing inside and outside exclosures.

herbivory experienced by the herbaceous layer. Competition with shrubs has been used by others to explain reduced Douglas-fir regeneration inside exclosures compared with out (Hanley and Taber 1980).

*Lower Tree Canopy.* Vine maple is consumed by both elk and deer (Leslie *et al.* 1984). In spite of its ability to grow beyond the reach of ungulates, its life history does not allow it to avoid herbivory. Commonly, the flexible trunks bend to the ground (Anderson 1969), which makes foliage and twigs available to ungulates. In addition, basal sprouts are browsed. Their persistence in the presence of

ungulates may be at the expense of stem length growth. Stems were longer and distributed in more stem length classes in the absence of ungulates. In addition, we suspect that ungulates limited establishment of vine maple from seeds or by lateral root buds, thus encouraging a clumped distribution.

*Overstory.* The ability of ungulates to influence the eventual composition of the overstory (by differentially affecting species recruitment) could not be determined. Ungulates seemed to influence recruitment under certain circumstances. In valley floor sites where large organic debris (LOD) was present and western hemlock dominated the overstory, elk may have impaired establishment of hemlock in favor of Sitka spruce. Ungulates inhibited establishment of western redcedar and Pacific silver fir in Olympic National Forest clearcuts surrounded by mature forests during the 1950's. Our results showing greater mortality of planted Douglas-fir outside No. 24 contrasts with those of Hanley and Taber (1980) showing greater mortality of planted Douglas-fir inside exclosures.

The effect of ungulate herbivory in these forests is complex and the intensity of herbivory varies considerably in time and space. Our varied results, particularly with reference to western hemlock establishment, illustrate these points. Additionally, results from sampling tree age distributions (Harmon and Franklin 1983) did not support the hypothesis that western hemlock saplings on the South Fork Hoh River became established when elk densities were low (due to over hunting at the turn of the century). However, more recent observations of two intact 0.5-ha exclosures established in 1980 on the South Fork Hoh River show that elk do hinder hemlock establishment (Harmon pers. comm., Schreiner, pers. obs.). These contrasting results suggest that ungulate effects on tree establishment vary temporally and spatially.

These exclosures generally represent examples of fairly intense herbivory. Elk subpopulations may have just passed through an eruptive overshoot (Jenkins 1981) when the first exclosures were established in the 1930's (Woodward *et al.* 1993). Thus, levels of herbivory measured initially may have been more intense than subsequent levels. By the late 1950's, Newman (1958) considered that elk and vegetation had reached acceptable equilibria in the park, the current view as well (Jenkins 1981, Schreiner *et al.* submitted). We believe these exclosures illustrate the general nature

of ungulate herbivory in western Olympic Peninsula forests, although the intensity of effects change with ungulate density.

### Ungulates and Forest Dynamics

Forest processes operate at a variety of scales, some which can be influenced by ungulate herbivory and some which cannot. Formation of canopy openings (i.e., gaps; see Platt and Strong 1989) is an important process influencing forest composition at various time intervals and at both fine- and coarse-grained spatial scales. Fine-grained gaps are created by insect, root pathogen, and wind induced mortality of one to a few trees (Spies and Franklin 1989). These small gaps are produced so frequently that differential establishment of various tree species in them may change the composition of the canopy over time. The enclosure studies reflect the effects of herbivory at these fine-grained, relatively short duration scales. At such scales, ungulates seem capable of influencing the direction and rate of plant succession.

However, chronic disturbances operating at small spatial scales over short time frames are overridden by larger, landscape-scale disturbances.

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- The longer term dynamics of unmanaged forests on the western Olympic Peninsula appear to be driven by infrequent large-scale disturbances, such as fires (Agee 1993), floods (Fonda 1974), or catastrophic windthrow (Henderson *et al.* 1989). While ungulate herbivory may indeed affect forest regeneration at the scale of individual tree gaps, their influence following large, catastrophic disturbances seems inconsequential by comparison. Our results support the general conclusion that the extent to which herbivores can cause changes in forest ecosystem processes may depend on the scales of other disturbances (Pastor *et al.* 1988).

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