

# Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington

Edward G. Schreiner, Kirsten A. Krueger, Patricia J. Happe, and Douglas B. Houston

**Abstract:** The relationship between native ungulates (mainly Roosevelt elk, *Cervus elaphus* L.) and the occurrence of three patch types in an old-growth (220- to 260-year-old) Sitka spruce (*Picea sitchensis* (Bong.) Carrière) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) temperate coniferous rain forest was investigated on the South Fork Hoh River in Olympic National Park. The distribution, frequency, and size of two understory patches (grass, moss) and patches where shrubs had escaped herbivory (refugia) were sampled along transects. Vegetation standing crop, percent cover, species richness, and equitability along transects were compared with conditions in two 8-year-old 0.5-ha ungulate exclosures. Ungulate herbivory profoundly affected the distribution and abundance of understory patch types. Grass-dominated patches disappeared following 8 years of protection from ungulate herbivory. Ungulates maintained a reduced standing crop, increased forb species richness, and determined the distribution, morphology, and reproductive performance of several shrub species. There is clearly a dynamic relationship between patch type, tree fall, and ungulate herbivory in these old-growth forests. Our results show that ungulate herbivory is a driving force shaping vegetation patterns in coastal coniferous forests.

**Résumé :** Nous avons étudié la relation entre les ongulés indigènes, principalement le Wapiti de Roosevelt, *Cervus elaphus* L., et la présence de trois types de groupements végétaux dans une forêt coniférienne pluviale tempérée de 220 à 260 ans. Cette forêt de la rivière South Fork Hoh, dans le parc national Olympic, est dominée par l'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière) et la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.). La distribution, la fréquence et la taille de deux groupements végétaux de sous-étage, les herbacées et les mousses, et de groupements où les arbustes ont échappé aux herbivores (refuges) ont été échantillonnées à l'aide de transects. La biomasse végétale, le pourcentage de recouvrement, la richesse spécifique et l'équitabilité le long des transects ont été comparés aux conditions prévalant à l'intérieur de deux exclos de 0,5 ha, vieux de 8 ans. L'alimentation des herbivores a profondément affecté la distribution et l'abondance des types de groupements. Les groupements dominés par les herbacées ont disparu après 8 ans de protection contre les ongulés herbivores. Les ongulés ont maintenu la biomasse végétale à un niveau bas, augmenté la richesse en espèces dicotylédones et déterminé la distribution, la morphologie et la performance reproductive de plusieurs espèces arbustives. Dans ces forêts anciennes, il existe clairement une relation dynamique entre le groupement végétal, la chute d'arbres et l'alimentation des ongulés herbivores. Nos résultats démontrent que l'alimentation des ongulés herbivores est un élément moteur régissant les patrons végétaux en forêt coniférienne côtière.

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## Introduction

Investigations of interactions between ungulates and vegetation in structurally elaborate ecosystems such as old-growth coniferous forests are limited. Ungulates are known to modify forest vegetation when colonizing new areas (Bradner et al. 1990; McInnes et al. 1992; Pastor et al. 1993) or influence seedling regeneration in midseral forests (Anderson and Loucks 1979). Substantial changes in vegetation occur as the ungulate populations reach an accommodation with their food supply (e.g., Caughley 1970). In contrast, the sustained interactions between long-established native ungulate populations and old-growth coniferous forests are poorly understood. This has certainly been the case for elk (*Cervus elaphus* L.) and black-tail deer (*Odocoileus hemionus columbianus* Raf.) inhabiting coniferous forests of the Olympic Peninsula, Washington, where these ungulates have lived for at least 3000 years

(Croes and Hackenberger 1988). Until recently, the only information on ungulate–vegetation relationships for this area consisted of periodic vegetation surveys and early accounts of locally heavy grazing (e.g., the “overgrazing” in Skinner 1936 and Schwartz and Mitchell 1945).

A study of ungulate herbivory at the “patch” level (*sensu* Forman and Godron 1986) held considerable interest because we observed three understory patch types that were evidently affected by ungulates (mainly elk) in the South Fork Hoh River (SFH) floodplain of Olympic National Park. Patch types included (1) those dominated by grasses with some forbs and ferns (G patches), (2) those with a combination of forbs, ferns, and shrubs in a matrix of dense moss cover (M patches), and (3) those where shrubs had escaped ungulate herbivory (refugia). Several previous studies have demonstrated that herbivores caused patches to form in vegetation of grasslands (Belsky 1986; Coffin and Lauenroth 1988; Day and Detling 1990; Hobbs and Mooney 1991), but similar dynamics have not been reported in coniferous forests.

Our curiosity about grass and moss patches was aroused because it seemed that patches, often only a few square metres, previously dominated by grasses became dominated by ferns and shrubs when protected from herbivory. Conversely, M patches maintained their basic structure and species composition, except that plants became larger. These observations were coupled with increased awareness that elk diets are heavily weighted to grasses and forbs during periods of parturition, lactation, and body growth (Leslie et al. 1984; Happe 1993; Houston et al. 1994). It seemed possible for elk population dynamics to be influenced disproportionately by the frequency of comparatively small patches of graminoid vegetation occurring in the understory.

We became interested in shrub refugia because we noted that patches outside exclosures were also protected from ungulate herbivory. These “refugia” (*sensu* Harper 1977) on the roots of fallen trees and behind log barriers contained several species of shrubs that successfully produced flowers and fruit, unlike the majority of their heavily browsed neighbors on the valley floor. Hence, refugial shrub patches may provide a crucial source of seeds for recolonization of the valley floor by species that might otherwise be absent from the floodplain.

The present study is part of a broad effort to understand the role of native ungulates in the dynamics of old-growth forests in Olympic National Park. Based on their studies of elk and deer in the Hoh River valley of Olympic National Park Jenkins (1981) and Leslie and Starkey (1982) suggested that the park’s resident unmanipulated ungulate populations existed in dynamic equilibrium with their food supply. In fact, locally heavy use of the food supply is evidently the “natural” condition (Leslie and Starkey 1982). Previous studies have examined the relationship between establishment of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and historic low densities of elk (Harmon and Franklin 1983), forage quality of shrubs in old-growth forests and nearby clearcuts (Happe et al. 1990), and vegetation inside and outside of 25 small exclosures established in the 1930s and 1950s (Woodward et al. 1994). Here, we examine the structure and patch dynamics of understory vegetation in the same area.

In the following study we (1) examined a watershed floodplain to determine the distribution, size, and frequency of G and M patch types, (2) quantified the frequency and species composition of shrub “refugia,” and (3) compared standing crop and structure of G and M patches in and out of two 0.5-ha ungulate exclosures established in 1980.

## Study area

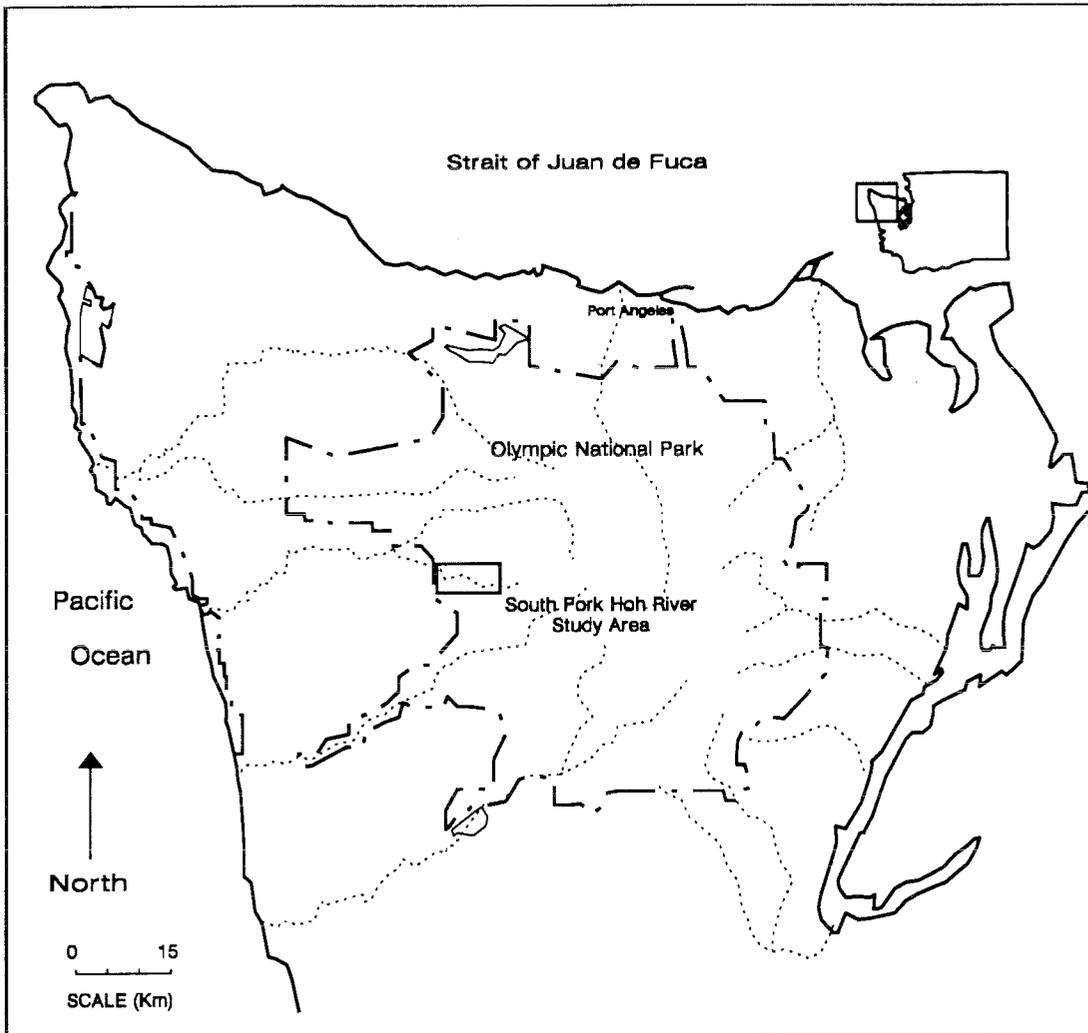
Fieldwork was conducted along 8 km of the SFH, Olympic National Park, Washington, U.S.A. (Fig. 1), from June through August 1987. This glacially carved, U-shaped drainage (Tabor 1987) is located on the west side of the park at about 47°47'N, 123°56'W, and 215 m elevation. Over 80% of annual precipitation (320 cm/year) falls as rain from October through April. Mount Olympus, at the headwaters of the SFH, receives an estimated 610 cm/year and represents the highest known precipitation for the lower 48 states (Phillips and Donaldson 1972). Mean annual temperature averages 10°C (Harmon and Franklin 1989), with January minimum and August maximum temperatures averaging, respectively, −4.6°C and 33.3°C from 1985 to 1988 (U.S. National Park Service 1991). Even at these low elevations, the frost-free season only extends from June through September.

Fauna include relatively conspicuous elk, black-tailed deer, and banana slugs (*Ariolimax columbianus* G.), as well as snowshoe hare (*Lepus americanus* Erxleben), mountain beaver (*Aplodontia rufa* Raf.), coyote (*Canis latrans* Say), black bear (*Ursus americanus* Pallas), cougar (*Felis concolor* L.), and bobcat (*Lynx rufus* Schreber). Density estimates are available only for wintering elk, and these averaged 6.8 elk/km<sup>2</sup> from 1985 to 1988 (Houston et al. 1987, 1988). The elk:deer biomass ratio was estimated to be near 100:7 in the adjacent Hoh River Valley (Leslie and Starkey 1982). Our field observations suggested similar relationships in the SFH, where elk are clearly the dominant ungulate. Elk activity is concentrated year round on the valley floor (Jenkins and Starkey 1982, 1984), which determined the focus of our study.

Fluvial processes determine distribution of forests on the valley floor (Fonda 1974; Franklin et al. 1982; Swanson and Lienkaemper 1982; McKee et al. 1982; Smith and Henderson 1986). Coniferous forests in the SFH include extensive 220- to 260-year-old Sitka spruce and western hemlock stands on upper river terraces. The upper canopy (mainly Sitka spruce) is 75–80 m in height. Stem diameter of the Sitka spruce averaged 100 cm at breast height; total aboveground biomass of trees was estimated at 556–669 Mg/ha (McKee et al. 1982). Lower terraces are dominated by Sitka spruce with vine maple (*Acer circinatum* Pursh) or black cottonwood (*Populus balsamifera* L. ssp. *trichocarpa* (Torr. & Gray) Brayshaw), while riparian vegetation and the lowest terraces are dominated by red alder (*Alnus rubra* Bong.).

Understory vegetation also varies to some extent with geomorphology. On older “upper” terraces, huckleberry (Alaska huckleberry, *Vaccinium alaskense* T.J. Howell), mosses (mainly feather moss, *Hylocomium splendens* (Hidw.) B.S.G.), ferns (sword fern, *Polystichum munitum* (Kaulfuss) Presl; deer fern, *Blechnum spicant* (L.) Sm.; bracken, *Pteridium aquilinum* (L.) Kuhn), and forbs (Oregon oxalis, *Oxalis oregana* Nutt. ex Torr. & Gray; false lily-of-the-valley, *Maianthemum dilatatum* (Wood) A. Nels. & J.F. Macbr.) are important components. Vine maple and grasses (redtop, *Agrostis stolonifera* L.; roughstalk bluegrass, *Poa trivialis* L.) with ferns (lady fern, *Athyrium filix-femina* (L.) Roth) and forbs (trailing buttercup, *Ranunculus repens* L.; Oregon oxalis; enchanter’s nightshade, *Circaea alpina* L.) tend to dominate younger surfaces (Fonda 1974; McKee et al. 1982).

Fig. 1. Location of the study area in relation to Olympic National Park and Washington State.



## Methods

### Data collection

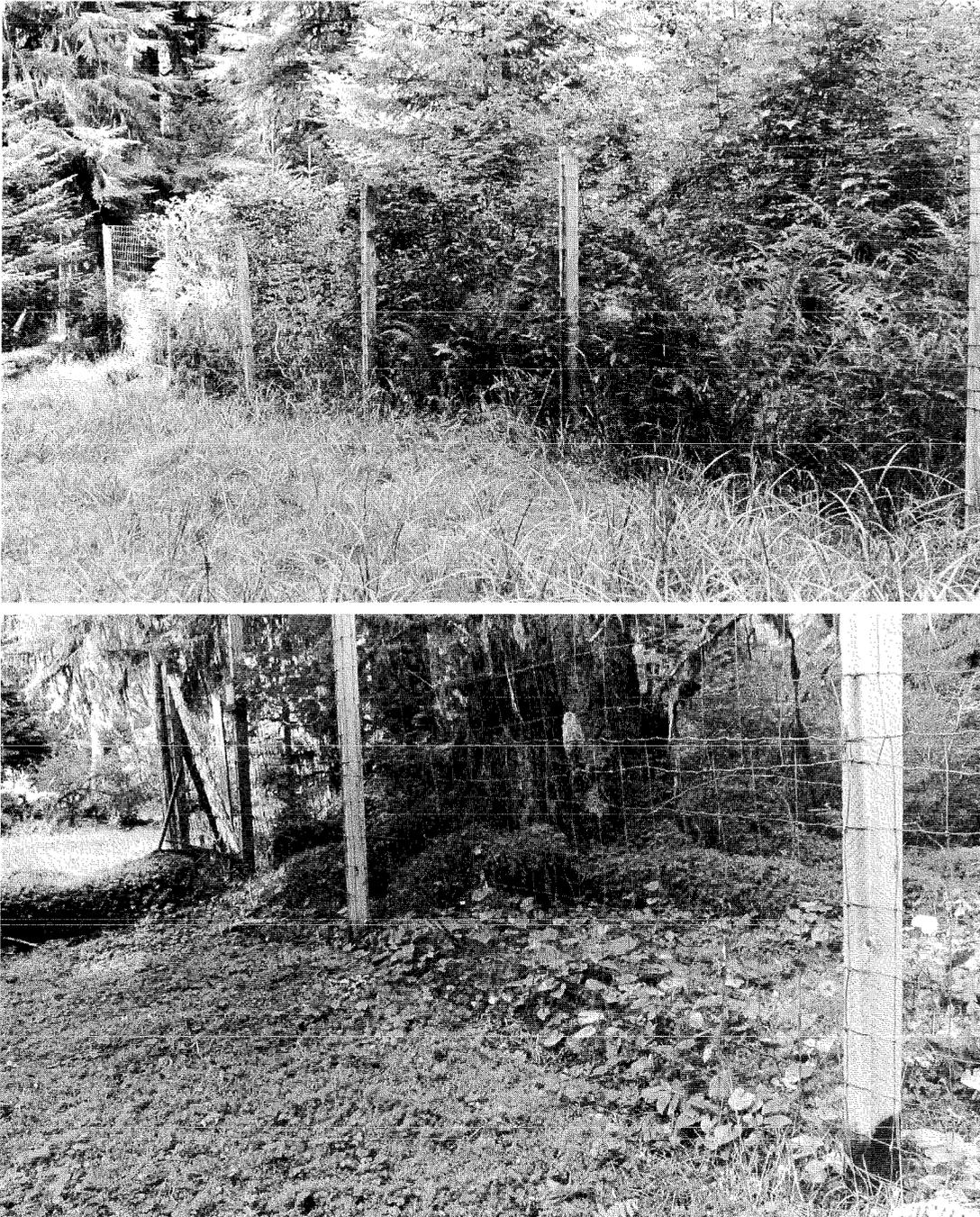
The general null hypothesis, that vegetation structure and composition were not significantly altered by ungulate herbivory, was investigated using a combination of line transect and plot techniques. Line transects were used to estimate the size and abundance of grass, moss, and shrub refugia patches throughout the 11-km<sup>2</sup> valley floor forests. After the grass and moss patch data had been compiled, plant community composition and standing crop inside and outside two 8-year-old 0.5-ha ungulate exclosures were compared by patch type using rectangular plots. Restricted randomization techniques were used in both transect and exclosure work to insure statistical validity and to improve accuracy of patch-size and distribution estimates (Grieg-Smith 1983).

An initial transect point was randomly chosen on an aerial photograph along the lowest 0.5-km of the river within the sample area. Fifteen additional transects were established along the river at 0.5 km intervals. Transects ran along the shortest compass line to the valley wall on both sides of the river. Patch intercept and transect lengths were measured using a small, belt-carried distance measuring device (a Walktox). We recorded patch intercept length, location, and patch type, and estimated

the area of grass and moss patches that intercepted the transect. Additionally, species composition and an estimate of perpendicular distance (10-m classes) from the transect to each shrub refugia was recorded following the methods of Burnham et al. (1980). A refugia was defined as a "safe" growth site where shrubs (primarily elderberry, *Sambucus racemosa* L. and salmonberry, *Rubus spectabilis* Pursh) grew to maturity and reproduced sexually without appreciable browsing from ungulates (i.e., flowers and (or) fruit were present).

Two 8-year old 0.5-ha exclosures built in 1980 (Fig. 2) were used to examine the effects of ungulate herbivory on forest vegetation. These 2.44 m high woven wire exclosures were located approximately 0.8 km apart in an old-growth Sitka spruce – western hemlock forest. One exclosure was on an older upper terrace, and the second was on a somewhat younger lower terrace. The upper terrace exclosure was located in a Sitka spruce – western hemlock stand with an understory of moss, oxalis, and huckleberry. Relatively small grass-dominated patches existed prior to exclosure construction (M.E. Harmon, Forest Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon, U.S.A., unpublished data). The lower terrace exclosure was in a Sitka spruce stand with an understory more or less equally split between G and M patches prior to construction (M.E. Harmon, unpublished data).

**Fig. 2.** Grass (top) and moss (bottom) patches inside and outside a 0.5-ha ungulate enclosure on the South Fork Hoh River, Olympic National Park.



The rationale for siting the two exclosures is noteworthy. A preliminary study by a team of forest ecologists in 1978 revealed two broad forest community types, Sitka spruce – western hemlock and Sitka spruce – vine maple. A permanent 2-ha plot was established at a representative site within each type to study stand dynamics over time; all live trees, snags, and logs were mapped (Franklin 1982). Only later was the decision made to exclude ungulates from a portion of these plots. This contrasts markedly with studies common in range and wildlife management, where exclosures are often deliberately located on the most heavily grazed sites available (e.g., Schwartz and Mitchell 1945).

We avoided the pitfall of establishing plots immediately outside exclosures (Hurlbert 1984) by randomly selecting patches along the transects for detailed measurements. Five transects, each within 1 km of at least one exclosure, were used to quantify understory vegetation. One to three sample blocks (depending on transect length) were measured on each transect, totaling 10 blocks per patch type. Each block contained four  $1 \times 4$  m plots located randomly within a patch that was at least  $20 \text{ m}^2$  in area.

Inside each exclosure we (1) identified G and M patches from photographs and data (M.E. Harmon unpublished) recorded

the year of fence construction (1980), (2) randomly selected five 5 × 5 m sample blocks per patch type, and (3) randomly selected four 1 × 4 m plots within each block. We avoided fence lines, existing permanent plots, and patch boundaries. Combined data from the two exclosures resulted in 10 blocks per patch type.

Understory cover was estimated for each species (grasses were lumped) to the nearest 1% in each plot using a gridded plot frame. Shrubs and saplings were sampled over the entire 1 × 4 m plot and ferns, on a 1 × 1 m quadrat nested within plot. Forbs and grasses were sampled on nested 1 × 1 m quadrats outside exclosures and on nested 0.5 × 0.5 m quadrats inside exclosures. Nested quadrat locations were determined using random numbers. Estimates of percent cover of bare mineral soil, rock, litter, and dead and fallen woody debris were also recorded.

### Standing crop

In addition to percent cover, several plant dimensions were recorded to estimate standing crop. Measurements included (1) basal stem diameter, height, and canopy diameter of each shrub or sapling, (2) length of each frond and height of ferns, and (3) average height of forbs by species and graminoids as a group. Equations relating plant characteristics (e.g., percent cover, basal stem diameter, frond length) to standing crop were developed from dry weight of plants clipped at ground level, dried 48 h at 50°C, and weighed to the nearest 0.01 g. Herbaceous plants were clipped in 0.25-m<sup>2</sup> quadrats; shrubs and saplings were clipped as individual plants and ferns as individual fronds. Equations for herbaceous species (forbs and graminoids) were developed using data from plots containing a broad range of cover values and, for ferns, single fronds of various lengths were clipped and weighed. Shrubs and saplings over a range of heights and diameters were clipped individually. Plant morphology differed greatly inside and outside exclosures, so separate equations were developed for plants inside and outside. Sampling was conducted when standing crop was near the summer maximum.

Algorithms for estimating standing crop from plant measurements were computed using stepwise multiple linear regression or simple linear regression (Norusis 1986). Selection of parameters and their transformations (e.g., ln dry weight) was accomplished using results of Alaback (1982, 1986) as a guide. Equations were selected on the basis of a high adjusted  $r^2$  and a visual inspection of residual plots until a linear result was achieved (Draper and Smith 1966).<sup>5</sup> The lowest  $r^2$  was 0.43, but most ranged from 0.75 to 0.94 ( $p \leq 0.05$ ). Total standing crop and prediction limits (Sokal and Rohlf 1981) were computed for each species and summed by vegetation group (i.e., shrubs, saplings, ferns, forbs, graminoids, and mosses).

### Statistical analysis

Data were evaluated using the Kruskal–Wallis nonparametric ANOVA (Norusis 1986) at  $p \leq 0.05$  because sample sizes were small ( $n = 10$  blocks). Transect means for patch intercept length, number of patches per transect, richness of patch types per transect, and equitability (i.e., a measure of relative diversity;  $H'$  of Whittaker 1975) of patch types per transect were compared under the null hypothesis of no significant difference between transects by geographic location (e.g., north vs. south of the river, upper river vs. lower river).

Block means ( $n = 10$ ) were used to compare patch types inside and outside exclosures. Vegetation characteristics included percent cover by species, percent cover of nonliving components (litter, large woody debris, bare soil, and rock), and percent cover by vegetation group (i.e., shrubs, ferns, etc.). We also compared species richness, percent similarity (Whittaker 1975), and equitability. The null hypothesis was that no significant differences existed in vegetation parameters by patch types inside or outside exclosures.

The small sample sizes used in these analyses and the conservative nature of the Kruskal–Wallis test (Sokal and Rohlf 1981) can limit the inferences from these data. Despite this, the “power efficiency” of the test is 95.5% of the parametric ANOVA (Siegel 1956).

Refugium densities were determined using the program TRANSECT (Burnham et al. 1980). The program, originally designed to estimate density of bird nests, uses a Fourier series estimator based on distances from a transect; it seemed an ideal way to calculate the density of refugia in the SFH. We estimated the density of refugia by species and all refugia combined.

## Results

### Patch distribution and abundance

A total of 183 G and 202 M patches were intercepted along 14 534 m of transects in the SFH. The intercept length of G patches ( $18.7 \pm 22.9$  m, mean  $\pm$  SE) was less than the intercept length of the M patches ( $45.7 \pm 64.4$  m;  $p \leq 0.0001$ ). There was no difference in the number of G ( $12.2 \pm 6.6$ ) and M ( $13.5 \pm 5.9$ ) patches per transect, which indicated that the smaller G patches were interspersed within a matrix of M patches. Transects also intercepted very small numbers of patches in high water table areas that were dominated by horsetail (*Equisetum* spp.), yellow skunk cabbage (*Lysichiton americanum* Hultén & St. John), or slough sedge (*Carex obnupta* Bailey).

Comparisons of transect means for patch intercept length, number of patches, proportion of G and M patches, and equitability of patch types among areas (i.e., north, south, upper valley, lower valley) revealed no significant geographic differences on the SFH valley floor. Moreover, the exclosure sites appeared to indeed be representative of understory conditions throughout the study area.

A total of 356 shrub refugia were tallied along SFH transects. Salmonberry and elderberry were most common, accounting for 93.5% of the refugia (Table 1). There were an estimated 428 and 245 refugia/km<sup>2</sup> that contained salmonberry and elderberry, respectively. Refugia often contained both species. Four other species, western thimbleberry (*Rubus parviflorus* Nutt.), cascara buckthorn (*Rhamnus purshiana* DC.), fool’s huckleberry (*Menziestia ferruginea* Sm.), and goatsbeard (*Aruncus dioicus* (Walt.) Fern. var. *acuminatus* (Rydb.) Haravar.) were rarely encountered. Refugia were observed most frequently on root mats of fallen trees or behind barriers created by a matrix of fallen trees in excess of 2 m in diameter (Fig. 3). Comparisons of the mean number of refugia per transect, mean number of refugial species per transect, and the number of refugia per metre of transect length revealed no significant geographic variation.

### Exclosures

We found no significant differences in total cover; cover by group (i.e., forbs, graminoids, mosses, ferns, shrubs, and

<sup>5</sup> Regression equations for each species may be purchased from The Depository of Unpublished Data, Document Delivery, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

**Table 1.** Frequency, density, and canopy area of shrub refugia along transects in the South Fork Hoh River valley.

Shrub species	No. of refugia		Density*		Canopy area (m <sup>2</sup> ) <sup>†</sup>		
	<i>n</i>	(%)	Mean	SE	Mean	SE	Range
Salmonberry	245	68.8	428.4	44.1	11.3	29.6	1–400
Elderberry	89	25.0	245.9	55.0	15.6	20.1	1–100
Thimbleberry	15	4.2	—	—	6.1	8.5	1–30
Cascara	5	1.4	—	—	11.5	16.5	1–40
Goatsbeard	1	0.3	—	—	—	—	—
False azalea	1	0.3	—	—	—	—	—
Total	356						

\*Number of refugia per square kilometre from Fourier series estimator results of the program TRANSECT (Burnham et al. 1980).

<sup>†</sup>Shrub canopy area per refugium (m<sup>2</sup>).

**Fig. 3.** Shrub refugia composed of elderberry and salmonberry on a Sitka spruce root mat in the South Fork Hoh River, Olympic National Park.

saplings); species richness by plot; species richness of forbs, ferns, and shrubs; and equitability between the two exclosures (within patch type). Consequently, we pooled data for the two exclosures by patch type.

The null hypothesis was rejected in numerous comparisons involving G patches and provisionally accepted for most comparisons involving M patches (Table 2). Significant differences existed in mean total cover and mean cover by vegetation group between grazed and protected G patches. Inside exclosures, G patches had significantly more total

cover ( $p = 0.0413$ ), more fern and shrub cover ( $p = 0.0284$ ,  $p = 0.0002$ , respectively), and less graminoid cover ( $p = 0.0002$ ) than outside. Mean total cover and cover of forbs was greater in fenced than unfenced M patches (total cover,  $p = 0.0494$ ; forb cover,  $p = 0.0413$ ). There were no differences in cover of nonliving components inside and outside exclosures for either G or M patches.

Total standing crop of G and M patches was greater in fenced than unfenced plots (Fig. 4, Appendix). Shrubs and graminoids in G patches exhibited opposite patterns with

**Table 2.** Mean percent cover of living and nonliving components in grass and moss patches inside and outside two 8-year-old ungulate exclosures on the South Fork Hoh River ( $n = 10$  blocks per patch type inside and outside).

Understory component	Grass patches				Moss patches			
	Inside		Outside		Inside		Outside	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Graminoids	2.8 <sub>a</sub>	15.7	29.7 <sub>ab</sub>	11.0	12.8	17.7	11.9 <sub>b</sub>	12.2
Forbs	29.1	18.0	56.1	12.2	43.7 <sub>a</sub>	20.2	26.5 <sub>a</sub>	17.1
Mosses	43.0 <sub>a</sub>	30.7	15.9 <sub>b</sub>	7.8	70.1 <sub>a</sub>	21.3	71.1 <sub>b</sub>	26.5
Ferns	44.4 <sub>ab</sub>	29.1	17.8 <sub>a</sub>	14.5	18.7 <sub>b</sub>	14.2	16.3	16.7
Shrubs	40.2 <sub>a</sub>	24.5	2.9 <sub>ab</sub>	4.9	25.2	13.4	13.0 <sub>b</sub>	10.9
Small trees	4.6	6.2	0.4	0.5	4.3	7.0	1.0	1.2
Total	164.2 <sub>a</sub>	45.0	122.3 <sub>a</sub>	16.4	164.5 <sub>b</sub>	36.3	129.8 <sub>b</sub>	33.2
Bare soil	0.0		0.3	0.5	0.0		tr	
Rock	0.0		tr		0.0		0.0	
Litter	26.5	16.2	13.7	6.6	14.6	12.5	16.5	13.0
Wood	0.9	2.8	0.6	2.0	tr		3.0	5.9

Note: Numbers on the same line with the same letter are significantly different at  $p \leq 0.05$  (Kruskal–Wallis ANOVA). tr, trace.

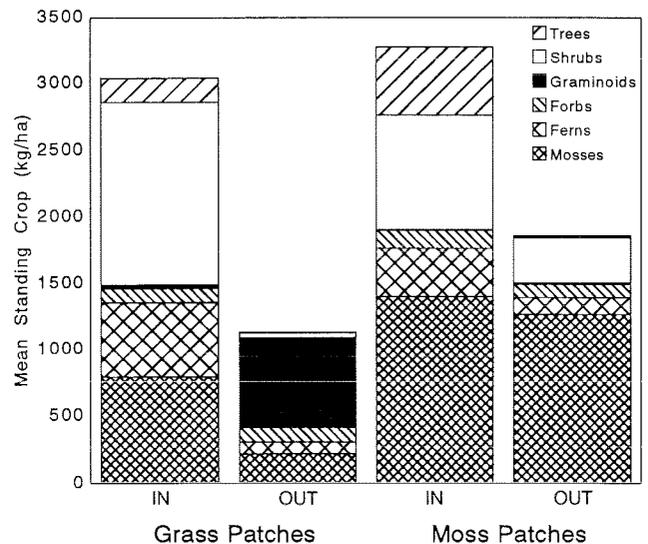
respect to the exclusion of ungulate herbivory; shrubs had a mean standing crop of 1369.5 kg/ha inside and 36.0 kg/ha outside exclosures, while graminoid standing crop was 29.7 kg/ha inside and 671.9 kg/ha outside. Standing crop of shrubs in M patches was also greater inside (856.2 kg/ha) than outside (340.9 kg/ha) exclosures, but graminoid standing crop was low both inside (7.4 kg/ha) and outside (11.1 kg/ha). Tree sapling and fern standing crop was greater inside than outside for both patch types, and mosses had greater standing crop inside than outside only in G patches. Forb standing crop was similar inside and outside exclosures for both patch types.

Species richness and equitability differed between exclosed and unexclosed vegetation and between patch types. Total species richness and species richness of forbs (Fig. 5) was significantly greater in unfenced than fenced G patches ( $p = 0.0006$ , total;  $p = 0.0016$ , forbs). Additionally, forb richness was greater in G than M patches both inside ( $p = 0.0307$ ) and outside exclosures ( $p = 0.0006$ ). Equitability (Table 3) of the forb component in G patches was also greater inside than outside exclosures ( $p = 0.0233$ ), while equitability of the shrub component in G patches was less than that of M patches both inside ( $p = 0.0139$ ) and outside ( $p = 0.0370$ ) exclosures. Forb equitability of unexclosed G patches was greater than forb equitability of M patches outside exclosures ( $p = 0.0065$ ).

## Discussion

The role of ungulates in affecting forest understory vegetation in the SFH was appreciable. Ungulates influenced understory vegetation at valley-floor, vegetation-patch, and within-patch scales. Our data support the contention that ungulate herbivory has far-reaching effects on the structural and functional characteristics of these old-growth temperate rain forests (Jenkins 1981; Leslie and Starkey

**Fig. 4.** Mean standing crop of understory vegetation inside and outside ungulate exclosures in the South Fork Hoh River, by patch type.

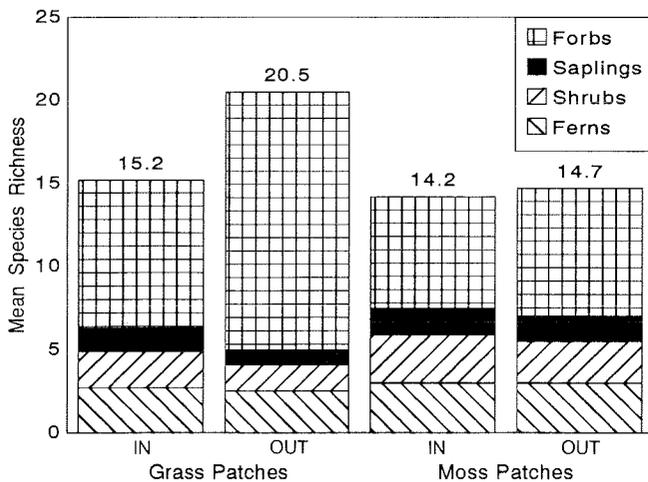


1982; Woodward et al. 1994). While this would not be an exceptional result in nonforest systems, it contrasts with reports of herbivory in forests as a series of intermittent insect outbreaks (Schowalter 1985), animal damage (Oliver and Larson 1990), or as food for herbivores (Danell et al. 1991). Recent work on moose (*Alces alces* L.) in boreal forests (McInnes et al. 1992; Pastor et al. 1993; McLaren and Peterson 1994) indicates that this view may be changing. Our study shows that native ungulates are a major ecological force shaping vegetation patterns in old-growth coniferous forests.

**Table 3.** Mean equitability ( $H'$ ) within understory vegetation components of grass and moss patches inside and outside ungulate exclosures on the South Fork Hoh River.

Understory component	Inside				Outside			
	Grass patches		Moss patches		Grass patches		Moss patches	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Forbs	0.51 $a$	0.20	0.41	0.11	0.70 $ab$	0.16	0.40 $b$	0.22
Ferns	0.24	0.13	0.30	0.14	0.22	0.17	0.24	0.17
Shrubs	0.17 $a$	0.13	0.33 $a$	0.20	0.09 $b$	0.14	0.23 $b$	0.16
Saplings	0.14	0.17	0.15	0.12	0.09	0.12	0.18	0.11

Note: Numbers with the same letter in the same line are significantly different at  $p \leq 0.05$  (Kruskal–Wallis ANOVA).

**Fig. 5.** Mean species richness in grass and moss patches inside and outside two ungulate exclosures on the South Fork Hoh River.

Eight years of ungulate exclusion in the SFH resulted in significant structural differentiation of vegetation in G patches and less change in M patches. Patches dominated by grass in 1980 had lower species richness and were dominated by ferns and shrubs 8 years later. The resulting patch type does not exist in the presence of ungulates unless it is protected by several large windthrown logs. Additionally, after 8 years of protection, the number of seedlings and saplings inside exclosures indicated that G patches will eventually become forest with a greater density than occurs in the presence of ungulate herbivory. M patches, on the other hand, may incur fewer changes in the absence of ungulates, or changes may require longer to develop. We observed that mosses had a greater “spongy” textured layer inside exclosures, but we did not measure this attribute. Competition with mosses and understory herbs is known to hinder tree reproduction in Sitka spruce – western hemlock forests (Harmon and Franklin 1989). Changes in the ubiquitous moss layer, although a comparatively slow process, may also have long-term effects on forest structure.

Ungulates restricted the distribution of sexually reproducing individuals of certain shrubs to refugia on the

valley floor. Our observations suggested that this was not true on valley walls, where shrubs were more abundant and elk use was considerably less intense. Even on the valley floor, however, refugia were abundant, mainly because of the occurrence of frequent fallen trees and logs, which cover about 10% of the ground in these old-growth forests (Graham and Cromack 1982; Harmon and Franklin 1989). The distribution of refugial shrubs may reflect the effects of ungulate herbivory as well as a requirement for seedling establishment on mineral soil, an uncommon commodity in these forests except on root mats of fallen trees and active gravel bars.

The occurrence of partial refuges (i.e., refugia) has contributed to our understanding of the dynamics of predator–prey systems in patchy environments (the aggregative response of Begon et al. 1986). However, partial refuges usually considered herbivores as prey, not predators. Our work extends the concept of refugia to herbivore–plant systems. We predict that plant refugia will be found to be important in the dynamics of many long-established grazing systems.

Overall, ungulates maintain much of the characteristic understory structure of the valley floor. Analysis of early exclosure studies also supports this interpretation (Woodward et al. 1994). The course of stand development and succession in the SFH would seemingly be altered substantially (in direction and (or) rate) in the absence of ungulate herbivory, a likelihood that has received some attention (Franklin et al. 1982; Harmon and Franklin 1983). Additionally, the applicability of McNaughton’s (1984) “grazing lawn” hypothesis to forest understory has confirmed that elk actually maintain high-quality graminoids as a concentrated food source in the SFH (Happe 1993).

An additional hypothesis, which emphasizes the interactive nature of forests and ungulates, needs investigation. We suggest that chronic, abiotic disturbances to the forests (e.g., windthrow) may influence ungulate (particularly elk) population levels. If elk populations are indeed limited by their food supply (Jenkins 1981; Leslie and Starkey 1982), and since G patches are important feeding sites (Happe 1993), then the availability and composition of these patches are of considerable significance to the herbivores. When a large tree dies and falls (opening the forest canopy), the availability of light and nutrients change dramatically in

patches on the forest floor (Franklin et al. 1987). It seemed to us that this was probably the first step toward development of the herbaceous, graminoid-dominated understory. Windthrow produces new sites that may be subsequently modified to G patches that are maintained by elk herbivory. Thus, forest structure and processes may be closely linked with ungulate population levels at the individual plant, patch, landscape, and ecosystem levels.

The dynamics and patterns of patches in biotic communities have received renewed attention in the last 15 years (e.g., Paine and Levin 1981; Pickett and White 1985; Levin 1992). Composition and size of patches in forest communities have been variously attributed to disturbance regimes (Runkle 1982; Platt and Strong 1989; Pastor and Broschart 1990; Phillips and Shure 1990), edaphic factors (Beatty 1984; Beatty and Stone 1986; Pastor and Broschart 1990), ectomycorrhizal association (Connell and Lowman 1989), competitive interactions (Frelich et al. 1993), and light (Ustin et al. 1984; Denslow et al. 1990). Herbivory is known to contribute to patch formation and maintenance in grasslands (Belsky 1986; Day and Detling 1990; Hobbs and Mooney 1991) and has been shown to interact with physical forces such as isostatic rebound (Hik et al. 1992). Our studies extend these concepts by suggesting links between patch dynamics, ungulates, tree-fall gaps, and the structure of old-growth coniferous forests.

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**Appendix****Table A1.** Estimated mean standing crop (kg/ha) with lower and upper prediction limits by vegetation group inside and outside two ungulate exclosures on the South Fork Hoh River.

Vegetation group	Grass patches						Moss patches					
	Inside			Outside			Inside			Outside		
	Prediction limits			Prediction limits			Prediction limits			Prediction limits		
	Mean	Lower	Upper									
Mosses	789	344	1452	217	61	779	1398	728	2156	1263	349	4570
Ferns	563	529	602	87	35	204	366	249	596	128	44	249
Forbs	107	37	384	109	24	313	137	51	499	101	51	201
Graminoids	30	18	68	672	216	2089	7	6	23	11	3	35
Shrubs	1370	1332	1407	36	27	50	856	811	904	341	293	405
Trees	179	163	200	6	5	10	511	488	543	14	12	36
Total	3038			1127			3276			1858		