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Age Distribution of Western Hemlock and Its Relation to Roosevelt Elk Populations in the South Fork Hoh River Valley, Washington

Abstract

The relationship between historical fluctuations of Roosevelt elk populations and the age structure of western hemlock was examined in two terrace forests in the South Fork of the Hoh River. Despite a dramatic decrease of elk between 1895-1910, no evidence was found for an increase in hemlock establishment during this period. Since 1700, hemlock establishment has remained low (1-6 trees per 2 ha per decade) on the lower terrace but increased in the upper terrace forests between 1830-1900. Neither age-class structure is consistent with the hypothesis that elk browsing on hemlock is so severe that trees become established when elk populations are low.

Introduction

Valley bottoms on the western slopes of the Olympic Mountains are noted for their tall, epiphyte-laden forests of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*). These alluvial stands contrast with many others in the coastal *Picea sitchensis* zone in their relative openness and successful reproduction of Sitka spruce (Franklin and Dyrness 1973, McKee *et al.* 1980).

The Roosevelt elk (*Cervus elaphus roosevelti*) is an important part of the valley ecosystems. Some reside permanently in the valleys, whereas many Roosevelt elk use these areas as winter range only (Jenkins and Starkey, 1980). Browsing by elk is known to have major effects on the structure and composition of plant communities (Sharpe 1956), and intense browsing has been noted by many authors (Bailey 1918; Murie 1934, 1935; Schwartz and Mitchell 1945; Sumner 1938).

Western hemlock reproduction is currently not as well represented as Sitka spruce in many of the alluvial forests, and differential browsing by Roosevelt elk has been proposed as an explanation. Western hemlock is a component of the elk's winter diet, but Sitka spruce is rarely browsed (Leslie and Starkey 1980).

A test of the elk-browsing hypothesis was suggested in 1978, when a disproportionate number of pole-sized (10-30 cm) western hemlocks were found during structural analysis of some alluvial forests (McKee *et al.* 1980). Since Roosevelt elk populations were known to have been low around 1900 (Jenkins and Starkey 1980; Taber and Raedeke 1980), this bulge in the western hemlock size-class distribution might be related to relative freedom from browsing. Assuming that elk ate western hemlock in the past, fewer elk could mean that more hemlocks escape destruction as saplings and grow into trees.

The study reported herein was designed to test this hypothesis by developing an age-

class distribution of western hemlocks and relating it to elk populations. The study was carried out in two river terrace forests of Sitka spruce and hemlock along the South Fork of the Hoh River in Olympic National Park. The results are, therefore, applicable only to that valley.

Study Area

The study sites are permanent sample plots established in 1978 within the valley of South Fork of the Hoh River on the western slope of Olympic National Park (Franklin 1980). The South Fork is a typical U-shaped valley of glacial origin, but has an unusually wide floodplain. The plots are located on the upper three of six terrace surfaces; the upper terrace plots characterized the forests found on surfaces five and six, but the lower terrace plots characterize forests on surface four (Swanson and Lienkaemper 1980). Soils on the lower terrace plots are haplaquepts, whereas those on the upper terrace plots are dystrochrepts (Joseph Means, pers. comm.). The climate is moist and mild, with mean annual precipitation near 320 cm and a mean annual temperature of 10°C (Franklin 1980).

Coniferous forests of Sitka spruce and western hemlock found on the river terraces have many notable features, including: (1) heavy cover of epiphytic plants (Franklin and Dyrness 1973); (2) a canopy layer that can exceed 85 m in height (McKee *et al.* 1980); and (3) despite the tall structure, an open canopy which allows a dense herb layer or tall shrub layer (or both) to develop. Upper and lower terrace plots had 142 and 64 trees ha⁻¹, respectively, and the estimated biomass for the same stands was 808 and 642 mt ha⁻¹ (McKee *et al.* 1980). "Nurse-logs" are the most important site of tree reproduction, with 88 to 97 percent of all seedlings starting on logs (McKee *et al.* 1980). Logs cover only a small fraction of the total surface; however, Graham (1980) found log coverage of 11 percent on the upper terrace and 6 percent on the lower terrace.

Roosevelt elk are common, although no historical or current population estimates are available for the South Fork valley. Historical data suggests that elk were plentiful over the Olympic Peninsula until 1895. Rapid settlement during the 1890s led to a dramatic increase in hunting and a subsequent drop in elk numbers. By 1905, populations were so low that the state legislature declared a 10-year moratorium on elk hunting. In 1909, the Federal government set aside a reserve for the elk. The recovery of the elk was sufficiently rapid that heavy browsing of the vegetation was reported by 1915. A large elk die-off during the winter of 1916-17 may have been a consequence of this overbrowsing. Other sequences of population increase, overbrowsing, and population decrease evidently have occurred around 1933, 1937, 1949, 1956, and 1964, and may represent an important feature of elk population dynamics in the Olympic National Park (Jenkins and Starkey 1980).

Methods

Two 2-ha permanent sample plots were established in 1978 (Franklin 1980), one each on the upper and lower terraces. Trees over 5 cm diameter at breast height (dbh) were mapped, tagged, and measured for dbh on the plots at that time. Most of the western hemlocks were cored during the summer of 1981. Since we were interested primarily in trees less than 200 years old, few individuals over 90 cm dbh were cored (see Fig. 1). The cores were taken at breast height, numbered according to the tree tags, and stored

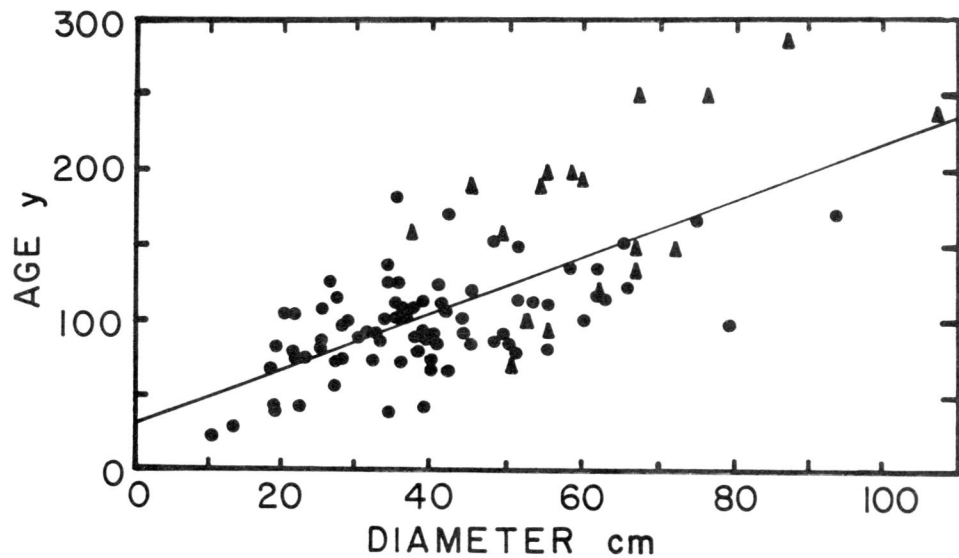


Figure 1. Relationship between diameter at breast height (dbh) to age at breast height (abh) for *Tsuga heterophylla* in upper terrace forest. Dots represent ages for trees without heartrot, while the triangles indicate trees with heartrot and estimated ages. The line drawn through the points was fitted by linear least-squares and is $ABH = 30.5 + 1.8 \text{ DBH}$, $r^2 = 0.46$, $N = 95$. DBH is in cm and ABH is in years.

in plastic straws for 2 to 4 weeks until rings could be counted. Cores with very slow growth rates were aged with the aid of a hand lens. Heartrot made 35 percent of the cores incomplete. Ages of these trees were estimated by assuming that the innermost decade of growth represented the growth rate of the missing part of the radius and that the first ring lies in the center of the bole cross section. To estimate the total age of an individual, years required to reach breast height were assumed to be 10. Trees were grouped into decade age groups for analysis. The age structure of small hemlock (5 cm dbh) was estimated in each plot by separating individuals into 5-year age classes based on bud scars and branch whorls. A regression of age against branch whorls for hemlock indicated a close relationship between the two variables ($\text{age} = 1.44 + 0.94 \text{ whorl numbers}$, $r^2 = 0.79$, $N = 26$, $p < 0.01$). Plants with repeated browse damage were assumed to be older than bud scars would indicate. In each terrace plot, hemlocks were examined in eight, 50 m by 1 m belt transects. Relative estimates of elk population size for the Olympic Peninsula are based on Taber and Raedeke (1980). Precipitation and temperature data between 1914 and 1980 for the Forks, Washington, weather station were compiled from U.S. Weather Bureau summaries (1914-1980).

Results and Discussion

The age structure of western hemlock on terraces does not appear to correspond well with estimated elk population sizes (Fig. 2). More hemlocks do not appear to have become established when elk densities were lowest. On the lower terrace forest peaks of western hemlock establishment occurred during the decades of 1880, 1840, and 1800; but until 1900, the overall pattern was of two to six trees per 2 ha established per decade. On the upper terrace there was a period of heavy establishment (8 to 21 trees per ha per decade)

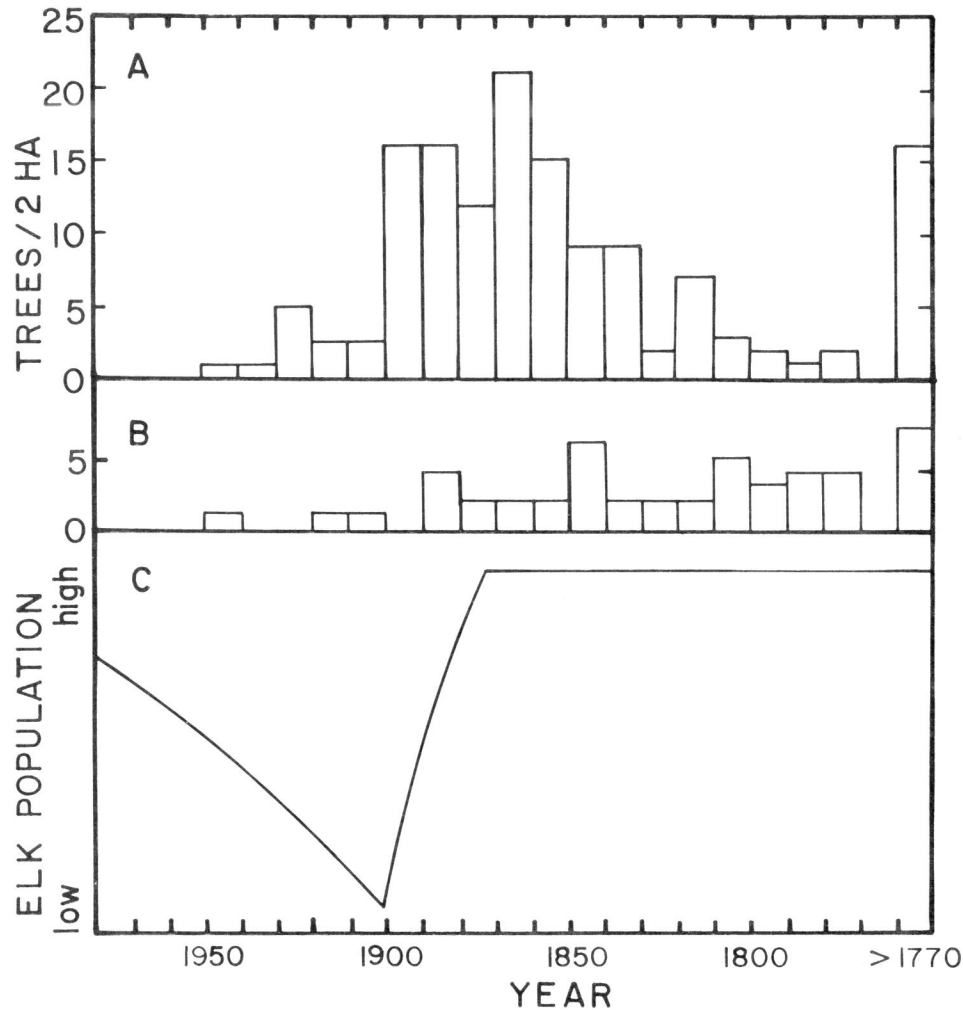


Figure 2. Density of *Tsuga heterophylla* by decade age classes for upper and lower terrace stands as a function of elk population fluctuations recorded for the Olympic Peninsula. A. upper terrace B. Lower terrace C. Relative fluctuations in elk populations.

between 1830 and 1900. This period does not correspond well to the hypothesized elk decline between 1890 and 1910. One peak in hemlock establishment on the upper terrace could be related to a decline in elk during the 1930's, but the absence of such a pulse on the lower terrace indicates factors other than elk are controlling hemlock establishment.

Hemlocks less than 20 years old show a reverse-j shaped population-age structure (Table 1.) Survival rates of 54 to 64 percent per yr were calculated by assuming that a constant percentage survive each year during the 5-year age classes.¹ These low survival rates may be caused by a number of factors, including seasonal water stress and low nutrient availability on logs (especially less decayed ones), competition, and elk browsing. Elk kill plants by repeated browsing of tops as well as by pulling root systems out of

TABLE 1. Age structure of *Tsuga heterophylla* less than 5 cm dbh for upper and lower terrace levels. Each number is based on eight, 50 m by 1 m belt transects.

Age class (years)	Density* (number/50 m ²)	
	Upper terrace	Lower terrace
0-5	51.37 ± 49.64	50.00 ± 47.98
5-10	2.37 ± 0.71	1.50 ± 2.14
10-15	0.25 ± 0.16	0
Total	53.99 ± 50.60	51.50 ± 48.87

*Mean ± standard deviation.

logs. Studies using small exclosures (Dee Boesma, pers. comm.) have confirmed that elk reduce hemlock survivorship.

Alternative explanations of the western hemlock age distribution other than elk include small mammals, fire disturbance, windstorm, or climatic changes. Other mammals, such as mountain beaver (*Alpodontia rufa*) or snowshoe hare (*Lepus americanus*), may also influence hemlock reproduction and therefore reduce the correlation between elk populations and hemlock age structure. Although there was no evidence of fire in these plots (McKee *et al.* 1980), other terrace forests in the area have burned. Graham (1980) failed to find evidence for a large blowdown on either terrace, so this disturbance seems to be an unlikely explanation.

Climatic changes also are an unlikely explanation. First, if climatic changes were important, they were interacting with some other factors, since there is little correspondence between hemlock peaks in establishment in the upper and lower terraces. Second, climate changes, as reconstructed from tree rings for the Columbia River Basin (Fritts *et al.* 1979), do not match changes in hemlock age classes. For example, Fritts *et al.* (1979) found precipitation 20 mm over the 1901-70 mean for the 1850's, and precipitation 20 mm below the mean for the 1860's. Yet both decades were similar in hemlock establishment on the upper terrace. Finally, there has been no consistent long-term change in climate in terms of precipitation or temperature that corresponds to the decrease in *Tsuga* establishment since 1930 (Fig. 3).

At present we hypothesize that the pulses in *Tsuga* for the two terraces are associated with some phases of stand development, such as canopy openings or seedbed, which could be secondarily influenced by elk and climate. Establishment of western hemlock would be sensitive to the abundance of rotten wood (McKee *et al.* 1980) and changes in light regime. During the period of 1830 to 1900, one or both of these conditions may have been more favorable in the denser upper terrace stand. Fluctuations on the lower terrace were probably minor. A detailed analysis of stand history, such as that done by Henry and Swan (1974), would be very revealing in this regard. Finally, we want to emphasize that there may be a poor correspondence between hemlock establishment and historical elk population fluctuations in other watersheds. The results of this study suggest that age and not size structure should be examined before any relationships are assumed between elk and tree establishment.

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¹The exact calculation is as follows: percent survival = $\left(\frac{\text{number at } t+1}{\text{number at } t} \right) 0.20$

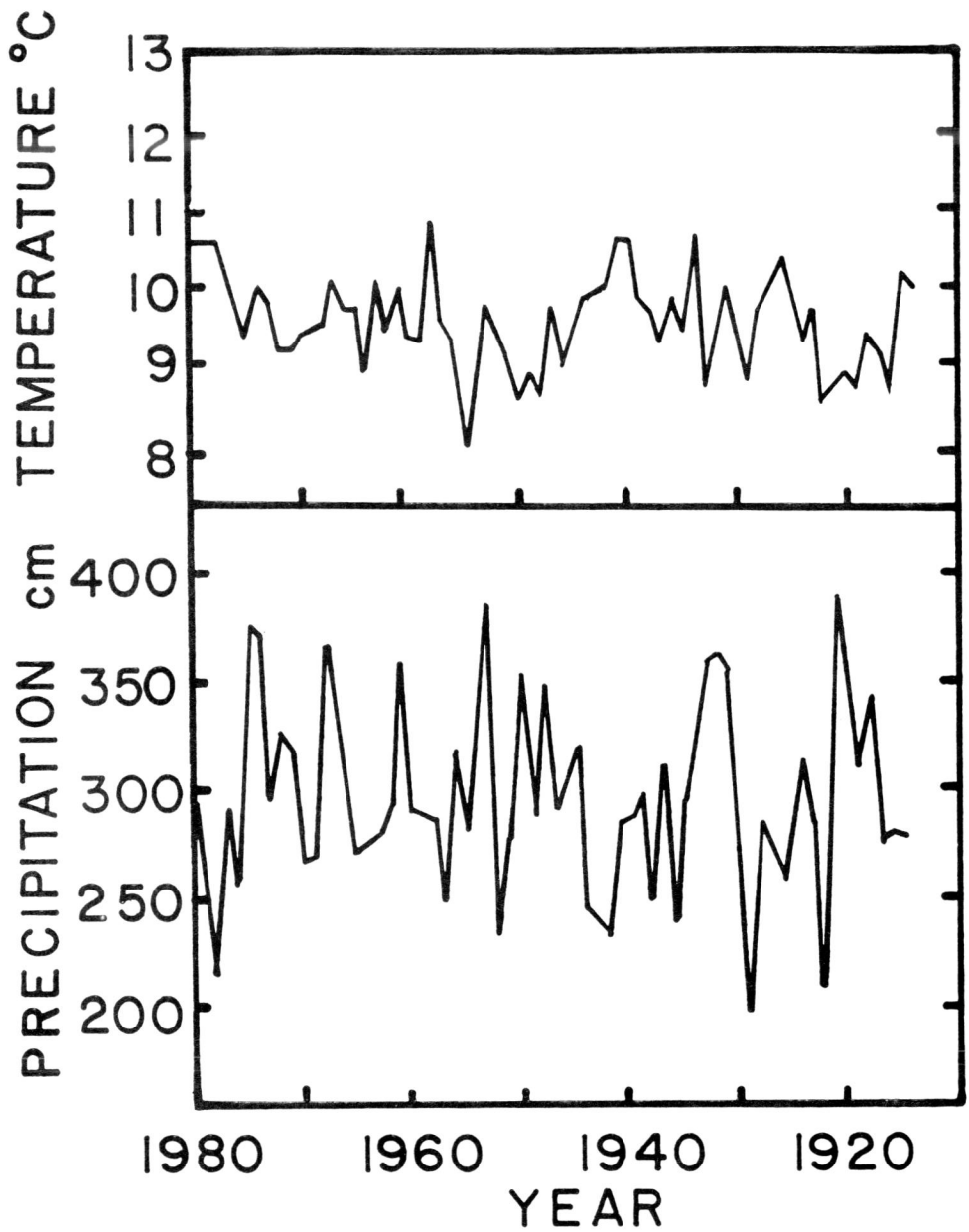


Figure 3. Mean annual temperature and total annual precipitation between 1914 and 1980 for Forks, Washington.

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