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Treeline Dynamics on Southern Vancouver Island, British Columbia

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This paper describes the nature of treeline dynamics and upper-elevation tree establishment patterns on southern Vancouver Island, British Columbia. We examined tree growth, climate and seedling relationships at three upper-elevation locations using standard dendroecological approaches. Our data suggest that this habitat has experienced species-specific pulses of tree establishment that have had a major impact on the character of the local treeline boundaries. The stem data collected within quadrats at Gemini Mountain and Haley Bowl show that seedling establishment within the last three centuries was episodic and linked to historical climatic patterns. Successful mountain hemlock establishment in this setting is restricted to periods characterized by either cool summers and shallow winter snowpacks, or warmer than normal summers and moderately deep snowpacks. The establishment of amabilis and subalpine fir seedlings appears restricted to intervals with cool growing seasons and moderately deep seasonal snowpacks. Episodic seedling establishment in the 20th century has resulted in a gradual infilling of the local treeline and the development of a more structured parkland belt that is expected to have habitat implications for endangered Vancouver Island marmot.

Keywords: dendroecology, subalpine meadows, seedling establishment, tree rings, Vancouver Island, Vancouver Island marmot.

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Introduction

Little is known of the nature of long-term treeline dynamics on Vancouver Island. While regional palynological evidence suggests that treelines have responded to Holocene climatic changes (Pellatt and Mathewes, 1995), significant fluctuations in the position of treeline within the last millennium are less certain. Nevertheless, within the historical period, tree establishment in subalpine meadows has been recorded at many locations within the nearby Coast Mountains of British Columbia (Brink, 1959) and mountainous areas of Washington State (Fonda and Bliss, 1969; Franklin et al., 1971; Woodward et al., 1995; Rochefort and Peterson, 1996; Miller and Halpern, 1998).

This paper describes the nature of historical treeline dynamics and interactions in high-elevation meadows in the Insular Mountain Range of Vancouver Island. We have previously reported on treeline sites from northern and central Vancouver Island, where old-growth mountain hemlock *(Tsuga mertensiana)* and yellow-cedar *(Chamaecyparis nootkatensis)* trees range in age to 1200 years (Smith and Laroque, 1998a; Laroque and Smith, 1999). In contrast, our reconnaissance surveys at treeline on southern Vancouver Island suggest that the trees are far younger in this region and that there is evidence for recent episodes of meadow invasion by trees. While this characteristic was initially viewed as an artefact of a higher incidence of pre-settlement fires on the southern end of Vancouver Island (Parminter, 1991), extensive low-elevation fire history surveys (Schmidt, 1970) and fossil charcoal records (Brown and Hebda, 1998; Gavin, 1999) show that fires within the past few centuries were scattered and spatially limited. Based on these findings, we speculated that our observations might record a recent interval of treeline disturbance or migration. To investigate the climatic conditions which may have initiated these invasions, we examined the relationship between tree growth and climate using a standard dendroclimatological approach. Data on the age structure of the local treeline was also collected to describe the long-term dynamics of tree infilling and migration on two meadow ecosystems.

Methods

Study Sites

Investigations were completed within the Green Mountain Critical Wildlife Management Area on south-central Vancouver Island (Figure 1). This area extends from the Haley Lake Ecological

Reserve No. 117 northward to Gemini Peak in the Greater Nanaimo District Watershed. The three study sites, Green Mountain, Gemini Mountain, and Haley Bowl, are located along a northwest- to southeast-facing mountain ridgeline that rises more than 1200 m above the Nanaimo River valley (Figure 1). The sites transect an altitudinal transition between the coastal western hemlock biogeoclimatic zone (CWH) and the mountain hemlock biogeoclimatic zone (MH) (Klinka et al.,1991). While trees in the lower elevation CWH zone exhibit a continuous forest canopy, a transitional ecotone finds western hemlock *(Tsuga heterophylla)* and amabilis fir *(Abies amabilis)* forming localized subalpine meadow treelines at 1000 m asl. Vegetation close to the crest of the ridgeline is characterized by mountain hemlock trees and montane meadows composed of a patchwork of forbs (e.g., *Fragaria vesca, Veratrum viride),* shrubs (e.g., *Vaccinium* spp, *Juniperus communis)* or ferns *(Pteridium aquilinum)* (Milko, 1984; Milko and Bell, 1986). Shrubby krummholz to erect mountain hemlock tree islands mantle the summits of Green Mountain (1463 m asl), Gemini Mountain (1505 m asl) and Haley Bowl (1300 m asl).

Dendroclimatological Analysis

High-elevation stands of mountain hemlock have considerable dendroclimatological utility (Smith and Laroque, 1998a; Gedalof and Smith, 2001) and offer an appreciable temporal scope for climatic reconstruction (Smith and Laroque, 1998b). In mid-August 1996, we identified a minimum of 20 mountain hemlock trees with limited bole and crown damage for sampling at each site (Figure 1; Table 1). Two cores were extracted at breast-height on each tree (ca. 180% apart) using a standard increment borer. Individual cores were air-dried, glued into slotted mounting boards, and sanded to a high polish in preparation for tree-ring measurement. The cores were visually crossdated with reference to a common set of marker or pointer years (Stokes and Smiley, 1968) and the annual ring-widths measured to ±0.01 mm using a WinDendroTM (Version 6.1b) digital image measurement system (Guay et al., 1992). Where ring boundaries were difficult to distinguish, a 40X stereo-microscope and Velmex-type stage measurement system were employed for verification. Signal homogeneity was ascertained using the COFECHA computer program (Holmes, 1983) and the individual core measurements were standardized using ARSTAN to remove any inherent age/growth trends (Holmes et al.,1986). A common time series was then developed by compiling the standardized site chronologies into a local master tree-ring chronology.

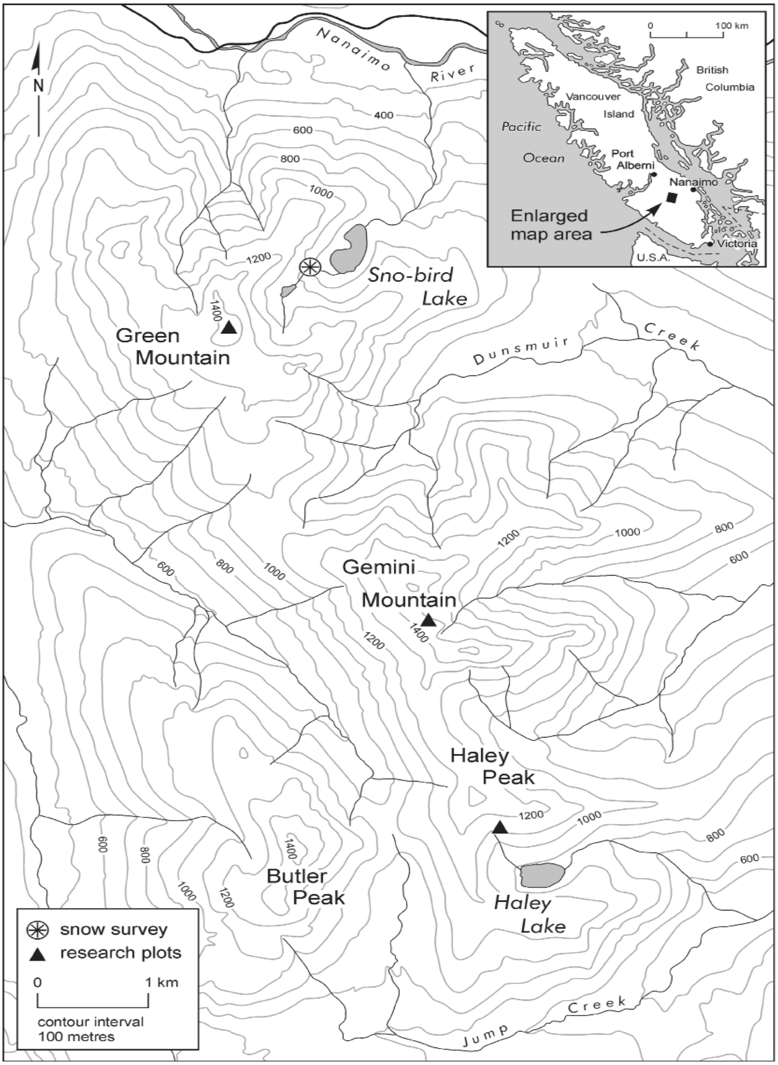

Figure 1 Map of the study locations and surrounding landscape on Vancouver Island.

Table 1 COFECHA statistical parameters for the mountain hemlock master chronologies from Green Mountain, Gemini Peak and Haley Bowl.

	Green Mountain	*Gemini Peak*	*Haley Bowl*	*Master Chronology*
Site characteristics				
Longitude	124° 20′ 25″W	124° 19′ 05″W	124° 18′ 45″W	—
Latitude	49° 03′ 20″N	49° 01′ 50″N	49° 00′ 30″N	—
Elevation (m asl)	1463	1505	1300	—
Dendrochronological characteristics				
Number of trees cored	20	23	23	66
Number of cores	40	46	46	132
Number of cores in series	29	43	31	103
Series correlation*	0.57	0.51	0.52	0.53
Autocorrelation value	0.6	0.69	0.66	0.64
Mean sensitivity	0.3	0.27	0.24	0.27
Crossdated Interval	1747-1996	1759-1996	1876-1996	1747-1996

*Significant at the 99% confidence interval at values over 0.33

The software program PRECON (Version 5.17) was used to determine the relationships between the master chronologies and monthly records of temperature and precipitation (Fritts, 1999). PRECON utilises a principal component analysis to maximize the climatic signal within a tree-ring series (Fritts et al.,1971) and calculates a response function that highlights the climatic variables most limiting to growth (Blasing et al., 1984). The climatic data required for the analysis were derived from the Nanaimo climate station (1902–1990), located approximately 35 km east of the study sites (Figure 1). To isolate the physiological influence of winter snowpacks, snow survey data from Sno-bird Lake (No. 3B16, B.C. Ministry of Environment,1966-1990), located one km from the study area (1100 m asl,), was included in our climatological analysis (Figure 1).

Habitat Analysis

In coastal British Columbia, treeline is commonly demarcated by a sharp transition from erect to krummholtz tree forms (Brooke et al.,1970). While this characteristic is apparent at a few sites in the study area (Demarchi et al., 1996), most treeline ecotones are distinguished by widespread seedling incursions (Figure 2). To study the age structure and spatial distributional of tree seedlings and saplings at these sites, we chose two locations within 2.5 km of each other for detailed study (Table 1). The Gemini Peak site is a montane meadow located on a south-facing slope (24–25°) at 1450 m asl (Figure 1 and 3). The Haley Bowl site is a subalpine meadow located north of Haley Lake on a south-facing slope (24–25°) at 1100 m asl (Figure 1). Despite the physical similarities between the two sites, spring snowmelt at Haley Bowl commonly occurs one month earlier than at the Gemini Peak site (Milko, 1984).

Figure 2 Photo showing saplings at the Green Mountain montane meadow site. The majority of the trees in the foreground are from a recent pulse of subalpine fir establishment in the 1970s. Immediately behind these trees is a cohort of subalpine fir established in the 1940s and 1950s and, in the background, an older cohort of mature mountain hemlock.

At each site, a 15 x 60 m cross-slope plot was established that straddled the local treeline-meadow ecotone, and included representative areas of established forest and meadow. The quadrats were subdivided into 5 x 5 m quadrats and an inventory was taken of the total number of stems belonging to one of three classes: tree, sapling, or seedling. Trees were defined as woody stems more than 2 m in height, saplings as stems between 0.25 to 1.99 m in height, and seedlings as stems less than 0.25 m in height. Age classes for the trees were determined by collecting increment cores at breast height, counting the annual growth rings and applying a sampling height correction factor (see McCarthy et al.,1991). For stems in the sapling and seedling classes, cross-sectional discs were collected at their base, categorized according to height, and their age calculated by counting the number of annual tree-rings present in each disc.

Figure 3 Photo of the subalpine meadow study site at Gemini Peak looking south. The subalpine fir trees behind the person in the centre of the image are from the 1940s and 1950s establishment pulse. Haley Peak is on the immediate left of the photograph and Butler Peak is across the valley to the immediate right.

Results

Dendroclimatology

Comparative dendrochronological statistics for the chronologies from each site are given in Table 1. The data suggest that the radial growth behaviour of mature mountain hemlock trees at all three sites is similar. Series correlation is a measure of the common signal (degree of homogeneity) contained in a stand of trees (Holmes et al., 1986). The narrow range of positive correlations (0.51-0.57), signifies that each series contains a relatively homogeneous environmental signal. Sensitivity provides a measure of between-ring variability (Fritts, 1976) and the positive values recorded (0.24-0.30) are characteristic of climatically sensitive mountain hemlock chronologies on Vancouver Island (Smith and Laroque, 1998a, 1998b; Gedalof and Smith, 2001). Autocorrelation is a measure of correlation between successive growth rings from one year to the next. The positive values from our chronologies (0.60-0.66) suggest that tree growth at these sites is conditioned by factors in preceding growth years. Recognition of a common between-site growth signal allowed us to compile the data with confidence into a single, regional, master chronology (Table 1; Figure 4).

Figure 5 illustrates the climate-growth relationships revealed by a response function analysis of the master chronology. The analysis indicates that 60 percent of the annual variance in mountain hemlock growth can be explained by climatic factors (46%) and prior growth characteristics (14%). The climate variables with the strongest influence on mountain hemlock radial growth include mean April temperature and total August precipitation (Figure 5). Both variables are positively correlated ($r = 0.46$, $p< 0.05$) with the growth index. Warm temperatures in April are assumed to accelerate spring bud burst (Owens, 1984) and activate earlywood growth, while higher August precipitation reduces summer drought conditions and prolongs the growing season (Peterson and Peterson, 1994).

The negative correlations between radial growth and previous June temperature can be explained by summer drought effects that limit photosynthetic production and initiate higher respiration rates (Peterson and Peterson, 1994). The negative relationship with November and December precipitation illustrates a suppressive growth response to above-normal snowpacks that limit the length of the growth period. Smith and Laroque (1998a) found that when seasonal snowpacks on Vancouver Island exceed four metres in depth, mountain hemlock radial growth is significantly reduced, regardless of the growing season temperature. An examination of snow survey data from Sno-bird Lake confirmed the relationship of November and December precipitation to spring snowpack totals and substantiates the negative correlations between winter precipitation and annual growth of mountain hemlock.

Treeline Structure

Figure 6 presents a generalized vegetation map of the Gemini Mountain and Haley Bowl quadrats. The vegetation units serve as a framework for a schematic illustration of the spatial distribution

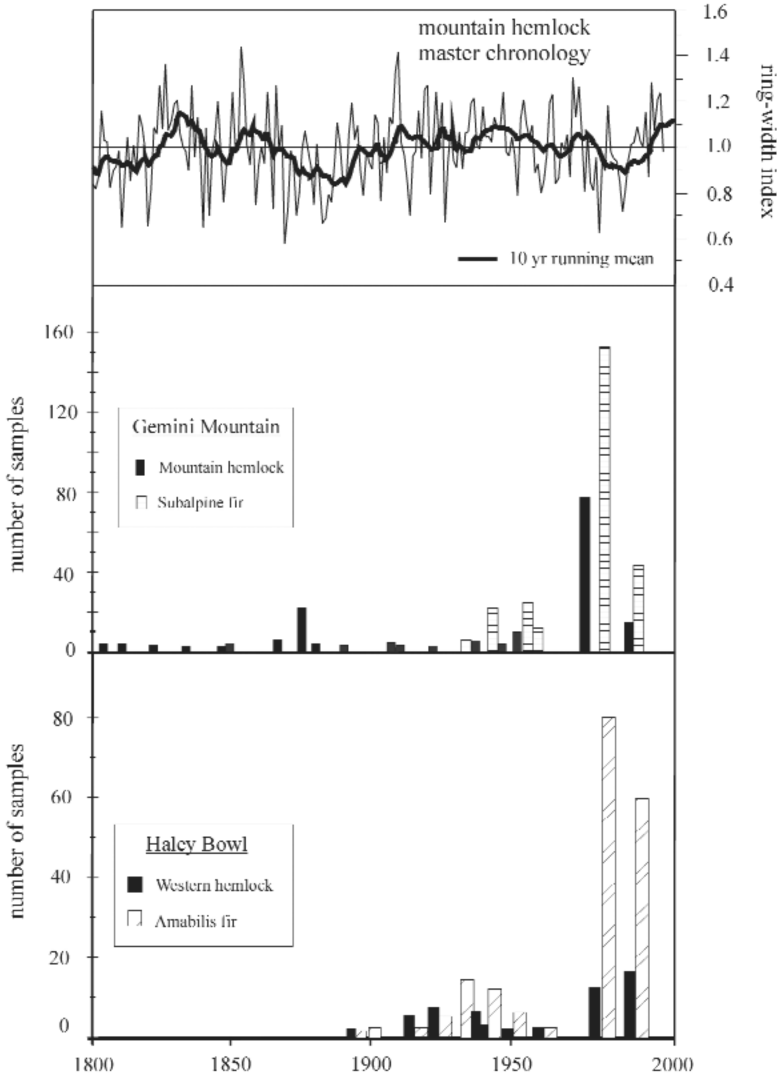

Figure 4 The master mountain hemlock tree-ring chronology and species-age data from Gemini Mountain and Haley Bowl. Not ethe difference in scale for the histogram data from Gemini Mountain to Haley Bowl.

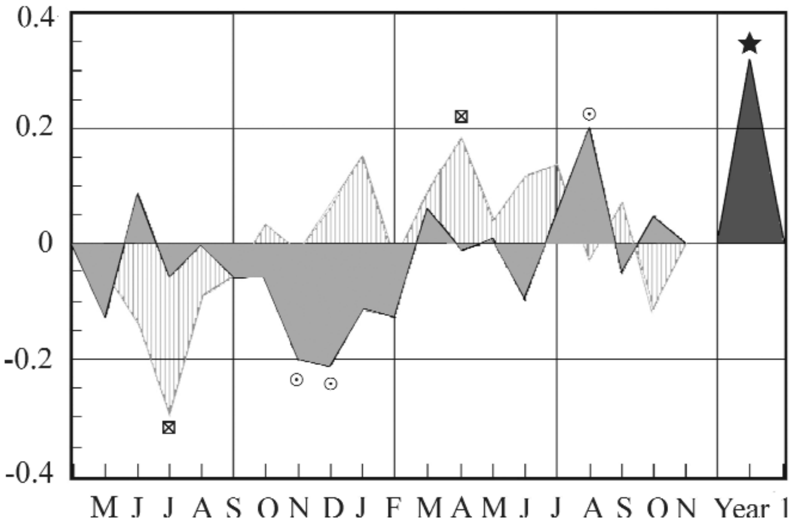

Figure 5 The response function analysis from the mountain hemlock master chronology and the Nanaimo climate station. Variables significant at the 95 percent interval are indicated by either the square (precipitation) or the circle (temperature) in the month that is significant. The star signifies that the previous year's growth is also significant at the 95 percent confidence interval.

of mapped stems in the two plots. The differences in species representation between the two sites are obvious. At Haley Bowl, amabilis fir (n = 157 stems) and western hemlock (n = 50 stems) dominate the sample plot (Table 2). In contrast, subalpine fir (n = 245 stems) and mountain hemlock (n = 149 stems) dominate the Gemini Mountain plot (Table 2).

At Gemini Mountain, the subalpine meadow is intersected along the southwestern section of the quadrat by treeline (Figure 6a). Tree cover within this area is dominated by mountain hemlock trees and saplings of mixed ages. The ecotone ascends upslope into a heather meadow that is dominated by a mix of mountain hemlock and subalpine fir seedlings and saplings. The plot extends eastwards to intersect a heather meadow and end in a forb-dominated meadow.

At Haley Bowl, the subalpine meadow plot extends westwards from the local treeline through a bracken fern *(Pteridium aquilinium)* meadow to a forb-dominated meadow in the central axis of the basin (Figure 6b). Treeline within the plot is distinguished by a clustering of tree islands consisting of mixed-age amabilis fir and western hemlock trees. Isolated islands surrounding standing snags and fallen coarse woody debris are dominated by either amabilis fir or western hemlock seedlings and saplings (Figure 6b).

Table 2 Total number of seedlings, saplings, and trees found within each 15 x 20 quadrat, by species.

Location	mountain hemlock				subalpine fir			
	seed	sap	tree	total	seed	sap	tree	total
Gemini Peak								
Subplot A	12	62	57	131	4	68	8	80
Subplot B	6	12		18	30	71	40	141
Subplot C					5	10	9	24
Total	18	74	57	79	39	149	57	245

Location	western hemlock				amabilis fir			
	seed	sap	tree	total	seed	sap	tree	total
Haley Bowl								
Subplot A	10	2	8	20	9	11	7	27
Subplot B	1	2	5	8	19	7	6	32
Subplot C	4	7	7	18	29	63	6	98
Total	15	11	20	46	57	81	19	157

Age-structure analysis of the stems in each plot shows some marked differences (Figure 4). At Gemini Mountain, subalpine fir seedlings and saplings account for 54 percent of the total stems present, while 38 percent of all stems were mountain hemlock (Table 2). In the Haley Bowl plot, amabilis fir seedling and sapling stems account for 68 percent of all stems, and western hemlock seedlings and saplings have only a minor presence (17%).

The oldest trees sampled in our survey consisted of an isolated stand of 10 mountain hemlocks on Gemini Mountain. While these trees ranged in age from 200 to 237 years, the next oldest trees, by species, were limited to a 102-year old amabilis fir, an 88-year old western hemlock, and a 68-year old subalpine fir. These data confirm that relatively young stems characterize both treeline settings, and based on our plot inventories, require ca. 37 years to reach breast height.

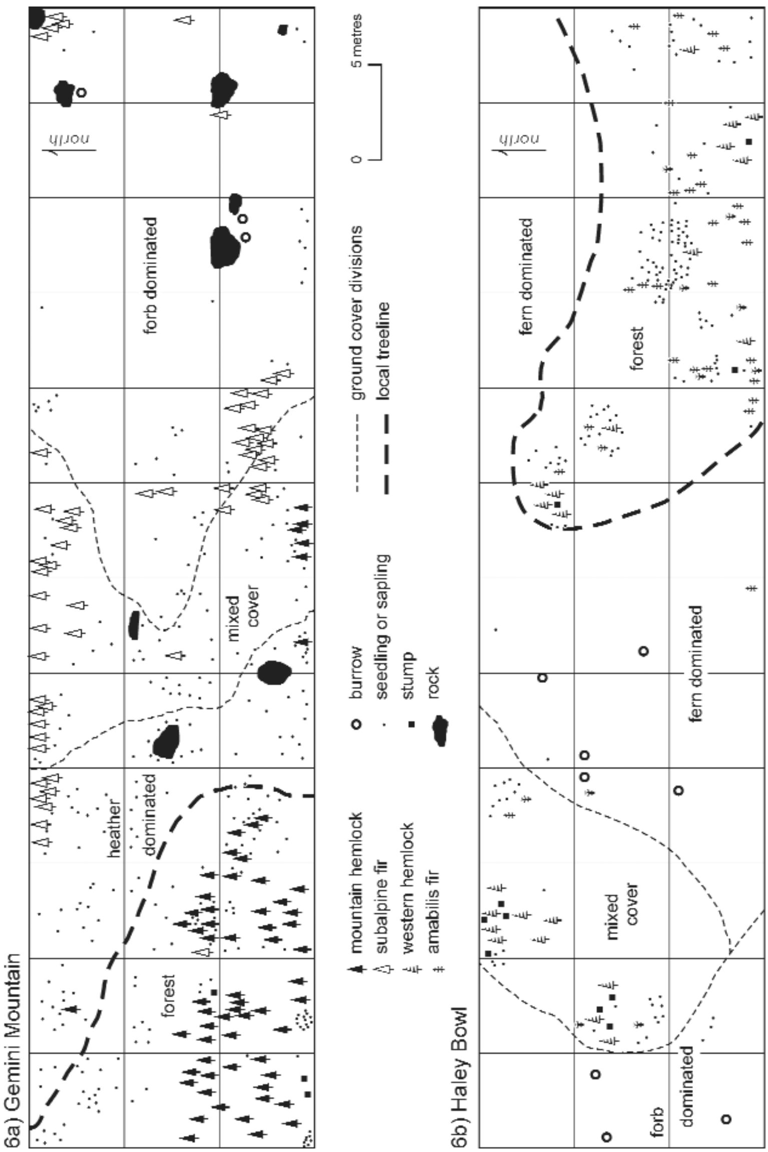

Figure 6 Schematic diagram showing the ground cover divisions and seedling, sapling and mature tree distribution int he study plots at 6a) Gemini Mountain and 6b) Haley Bowl. Note that for illustrative purposes the seedling and saplings have been collapsed into one category.

Discussion

Analyses of increment cores from the three summit sites show that trees in these stands range in age from 120 to 250 years (Table 1). While higher than normal rates of radial growth characterized the 1830s, early 1840s, early 1860s, the first half of the 20th century and the mid-1980s; markedly reduced rates of radial growth occurred during the early 1800s, late1860s to 1890s, and the late 1970s to the early 1980s (Figure 4). Our dendroclimatological assessments show that these variations reflect the influence of short-term climate variability, specifically those influencing growing season temperatures and seasonal snowpack totals (Smith and Laroque, 1998a).

The origin of the cohort of older trees could not be definitively determined. Based on data collected in Strathcona Provincial Park on Vancouver Island (Smith and Laroque, 1998a; Laroque and Smith, 1999), it could be argued they are the consequence of either an 18th century treeline advance, a successional response to a late 17th century fire or, in the case of Haley Bowl, recurrent snow avalanching (Milko and Bell, 1986). While the evidence remains ambiguous, the presence of charcoal at Gemini Peak (Milko, 1984) and the bracken fern meadows at Haley Bowl do suggest this cohort of trees is related to regeneration after a historic stand-destroying fire (Demarchi et al., 1996).

Analysis of increment core data from the meadows at Gemini Mountain and Haley Bowl revealed evidence for several intervals of seedling establishment (Figure 4). At Gemini Mountain, two notable periods of mountain hemlock establishment in the 1870s and 1950s are now recorded by stands of erect trees. Pulses of subalpine fir seedling and sapling establishment describe corollary events in the 1940s, mid-1960s, and mid-1980s. At Haley Bowl, while numerous western hemlock seedlings were established in the interval between the 1910s and the early 1930s, significant amabilis fir establishment did not begin until the mid- to late-1930s (Figure 4). These marked intervals of seedling establishment are broadly comparable to those recorded elsewhere within the Pacific Northwest region (Brink, 1959; Fonda and Bliss, 1969; Franklin et al.,1971; Heikkinen, 1984; Woodward et al., 1995; Miller and Halpern, 1998).

The stem data collected within the quadrats at Gemini Mountain and Haley Bowl show that long-term seedling establishment was episodic. Analysis of possible climatic factors responsible for these episodes indicates a strong association between establishment and summer temperature, as well as seasonal snowpack levels. For instance, at Gemini Mountain, episodes of mountain hemlock establishment are concurrent with periods of enhanced radial growth in the master mountain hemlock chronology (Figure 4). In contrast, subalpine fir establishment appears more closely related to lengthy intervals of reduced ring-width growth in mountain hemlock (Figure 4). Similarly, the data from Haley Bowl show western hemlock establishment was enhanced during periods of increased ring-width in mountain hemlock and that amabilis fir seedlings were successfully established during intervals of below-normal mountain hemlock growth.

These data support the findings of Little et al. (1994) and Woodward et al. (1995), which suggest that coniferous seed production and seedling establishment success is directly attributable to particular climate regimes. In this study, our stem/age data show that mountain and western hemlock seedlings establish and survive during conditions considered optimal for radial growth in mountain hemlock trees. Based on these findings, we suggest that successful mountain hemlock establishment in this setting is restricted to periods characterized by either cool summers and shallow winter snowpacks, or warmer than normal summers and moderately deep snowpacks. This finding supports the results of previous researchers in the region (e.g., Brink, 1959; Franklin et al., 1971; Agee and Smith, 1984).

The establishment of amabilis and subalpine fir seedlings in this setting appears restricted to intervals with cool growing seasons and moderately deep seasonal snowpacks. This may be linked to the ability of firs to germinate under snow (Zhong and van der Kamp, 1999), which greatly increases the length of the growing season and may serve to reduce the detrimental impact of late-season drought (Livingstone and Black, 1986). Interestingly, these same conditions are known to inhibit both mountain hemlock seedling establishment (Brett and Klinka, 1998) and mountain hemlock radial growth (Smith and Laroque, 1998a; Gedalof and Smith, 2001).

Implications for the Endangered Vancouver Island Marmot

These findings may have implications for ongoing efforts to ensure the future of the endangered Vancouver Island marmots. The Vancouver Island marmot *(Marmota vancouverensis)* is endemic to Vancouver Island and is listed as an endangered species by both the British Columbia and Canadian governments (Bryant, 1997). Annual counts confirm that fewer than 40 animals remain within a

40 km^2 area between Lake Cowichan and the Nanaimo Lakes (Bryant, 2001).

Bryant and Janz (1996) have shown that Vancouver Island marmots have distinctive habitat preferences and that subalpine and montane meadows, like those at Gemini Mountain and Haley Bowl, are essential for their survival. Unfortunately, meadows like these are extremely rare on Vancouver Island (Demarchi et al., 1996) and would be seriously endangered by a prolonged interval of tree invasion (Milko, 1984; Nagorsen et al., 1996).

We report with some concern, then, our data describing recent tree invasions which may be threatening the limited natural habitat of the Vancouver Island marmot (e.g., Krannitz and Kesting, 1997). We also note that the full consequences of these invasions are often delayed. Our tree-ring data show that seedlings take ca. 37 years to reach a height of 1.5 m, after which radial growth and apical extension are marked. This growth pattern appears correlated to the impact of snow burial on seedlings (e.g., shortened growing season) and the ability of taller trees to metabolize prior to snowmelt (Fry and Phillips, 1977; Oquist, 1983; Tesky et al., 1984; Carter et al., 1987). As a consequence, we expect that maturation of the seedlings established in the mid-1970s and the early 1980s, will result in a rapid closure of many meadow sites within the next ten to twenty years. This process is already evident in the montane meadow on Gemini Mountain, where a cohort of isolated mountain hemlock trees that established in the 1870s, and a cohort of subalpine firs that established in the1940s–1950s, have developed into stands of self-seeding tree islands. These continuing losses of habitat to tree invasion of high-elevation meadows may seriously compromise the future of the Vancouver Island marmot.

Conclusions

This study provides insight into the influence of climate and disturbance on treeline in southern Vancouver Island. The modern treeline found along the Green Mountain-Haley Bowl ridgeline likely developed following a stand-destroying fire in late 17th or early 18th centuries (Milko, 1984). Following regeneration of trees and establishment of a stable treeline, a lengthy interval with minimal recruitment followed. The scarcity of establishment in the 19th century is attributed to late-lying snowpacks, characteristic of the latter stages of the Little Ice Age climate regime (c.f. Magee and Antos, 1992; Rochefort and Peterson, 1996; Smith and Laroque 1996). The effects of these climate conditions would include increased seedling and sapling mortality from both snow creep and recurrent snow avalanche activity (Milko and Bell, 1986).

Distinct episodes of seedling establishment in the 20th century have resulted in a transformation of the local treeline. While the establishment of seedlings has infilled both sample plots, the most notable change has occurred within the montane meadow at Gemini Mountain. Meadow infilling at this site by subalpine fir records a prolonged invasion in the early 1940s and mid-1950s (Figure 4). The situation at Haley Bowl subalpine meadow is slightly different, with marked seedling establishment focussed either at the modern treeline or adjacent to the outlying tree islands (Figure 6b). While this activity could eventually result in a gradual closure of the treeline canopy and the development of a more structured parkland belt (Brooke et al.,1970), periodic snow avalanches at this site will likely continue to reinforce the heterogeneous character of the Haley Bowl treeline (Milko, 1984). The continued establishment, infilling, and maturation of trees in subalpine and montane meadows on Gemini Mountain and Haley Bowl are almost certain to have a detrimental impact on the limited habit of the Vancouver Island marmot.

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