L. D. Daniels, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

P. L. Marshall, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

R. E. Carter, TimberWest Forest Ltd., P.O. Box 10017, 700 West Georgia Street, Vancouver, British Columbia, Canada V7Y 1A1

and

K. Klinka, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

Age Structure of *Thuja plicata* in the Tree Layer of Old-Growth Stands near Vancouver, British Columbia

Abstract

Age and diameter data were collected from 720 sound stumps (diameter ≥7.5 cm) of *Thuja plicata* (western redcedar) trees from 15 old-growth submontane cutover sites, within three watersheds near Vancouver, B.C. The relationship between age and dbh was quantified by regression analysis. The age structure on different sites was compared using age frequency distributions.

Regression models revealed weak, but still significant, relationships between age and diameter at breast height. Age distribution curves showed that the *Thuja* stands had been uneven-aged. The predominance of peak age classes indicated that establishment had been episodic and the populations were not in demographic equilibrium. We hypothesize that wind and fire disturbances and long-term climatic variation influenced the population dynamics and can explain the peaks observed in the age structures. Within the study area, *Thuja* populations are probably in a continual state of disequilibrium.

Introduction

Thuja plicata Donn ex D. Don (western redcedar) is a valuable species with commercial importance and ecological and aesthetic values. To manage the species requires knowledge of its population dynamics and the processes affecting regeneration and growth. Evaluation of stand structure yields information about regeneration and development (Lorimer 1985), but its value in understanding the dynamics of *Thuja* remains under-used (Oliver et al. 1988). Past studies have often been limited to interpreting diameter distributions (Schmidt 1955, Gregory 1957, Franklin and DeBell 1988, Keenan 1993), since age determination is difficult because of large size and frequent heartwood decay. Size can be used to interpret the population dynamics, but only when the relationship between tree age and size is strong (Lorimer 1985). Moreover, the age-size relationship has been shown to vary with site for some species, complicating interpretation of their dynamics (Veblen 1986, Stewart 1986). Of the studies cited, only Keenan (1993) reported the relationship between tree age and size. The value of diameter distributions for evaluating the dynamics of *Thuja* have yet to be critically assessed.

In this exploratory study, we provide the first replicated age analysis of *Thuja* in old-growth submontane forests of coastal British Columbia. Tree ages were determined from field counts of sound stumps from recently cut stands. We found the relationship between age and diameter at breast height (dbh) to be highly variable, making dbh a poor predictor of tree age. We derived age class distributions for 15 sites from which we generated three hypotheses regarding *Thuja* population dynamics and disturbance.

Methods

Study Sites

The study was conducted in the Capilano, Coquitlam, and Seymour watersheds, collectively 57,791 ha, located north of Vancouver, British Columbia. The study sites were in the Very Wet Maritime Coastal Western Hemlock biogeoclimatic subzone, within the perhumid, cool mesothermal climatic type (Klinka et al. 1991). Soils were steep-slope, coarse-skeletal, Ferro-Humic Podzols (Agriculture Canada Expert Committee on Soil Survey 1987) derived from colluvium and glacial till, and underlain by granitic rocks.

Fifteen study sites (A to O), five in each watershed, were selected for study. Each was a cutover area between 4 and 13 ha (Table 1). The sites were various aspects at elevations from 400 to 825 m, but all were on midslopes and had fresh to moist soil moisture regimes and medium soil nutrient regimes (Klinka et al. 1989). The stands had been cut since 1986, but were not slash burned. According to forest inventory, each had been dominated by *Thuja* >250 years old, but contained mature *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), and *Abies amabilis* Dougl. ex Forbes (Pacific silver fir). *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) had been present in four of the stands (E, J, M, and N). We considered these sites representative of *Thuja*-dominated stands in the three watersheds, because the cutovers were continuous with extant stands typical of the submontane forest.

Sampling Methods

We sampled both sound and decayed stumps at each study site. Decayed stumps had partially rotten heartwood, but had been alive when the stand was cut. The decayed stumps were measured to test the assumption that specific size classes were not missed in our analysis of sound stumps alone. Age counts on sound stumps ensured that full ages of trees were determined.

Two sampling designs were used: the first on four sites (A, C, D, and E); the other on the remaining sites. For the first design, two parallel lines on each study site divided the cutover area into three equal portions. Six sampling points were uniformly distributed along each line. The four sound *Thuja* stumps closest to each point were sampled, for a total of 48. At each of three randomly selected points, decayed stumps were

TABLE 1. Site descriptions and age summaries for *Thuja plicata* in the tree layer on 15 study sites (for each site, n = 48) and for sites stratified by location and aspect (for each location and aspect, n = 240)

Site	Aspect	Elev. (m)	Area (ha)	Age (years)					
				Mean	S.D.	Median	Min.	Max.	Range
Capilano									
A	NW	620	6.0	395	164	421	114	826	712
B	NE	580	10.8	305	150	291	95	727	632
C	N	550	9.7	504	174	491	160	1051	891
D	SW	790	6.1	294	153	256	93	757	664
E	S	600	12.5	316	184	263	75	915	840
Seymour									
F	E	500	6.0	451	196	436	101	985	884
G	N	425	6.7	369	145	351	120	678	558
H	W	825	8.4	356	165	346	128	768	640
I	E	800	6.1	295	145	284	93	875	782
J	SE	520	6.4	479	157	462	206	792	586
Coquitlam									
K	NW	500	9.7	421	181	374	139	814	675
L	W	400	4.3	318	138	273	150	670	520
M	S	700	12.1	424	120	432	146	806	660
N	SE	500	12.8	311	116	309	126	695	569
O	E	450	5.8	346	109	331	78	535	457
Location									
Capilano watershed				363	182	357	75	1051	976
Seymour watershed				390	175	367	93	985	892
Coquitlam watershed				364	143	339	78	814	736
Aspect									
North				399	175	405	95	1051	956
East/West				353	161	331	78	985	907
South				365	164	351	75	915	840

sampled within a circular plot with a radius equal to the distance to the outermost sound stump. A mean of 17.8 decayed stumps (S.D. = 11.45) were measured within each plot but this design was time-consuming. It was replaced with the second design, in which we located all sound *Thuja* stumps within each study site, from which 48 were randomly selected from the entire cutover area for measurement. From the 48 sound stumps, two stumps were randomly selected around which circular plots of 12 m radius were established. All decayed stumps within each circular plot were sampled.

Sampling was restricted to the tree layer, since the study was conducted on cutover areas. Stumps with a diameter ≥7.5 cm were assumed to be part of the tree layer, normally defined as trees of height ≥10 m (Luttmerding et al. 1990). At all stumps, we measured the diameter including the bark (cm) and the uphill and downhill vertical distances (cm) from the upper surface of the stump to the ground, to calculate mean stump height. Field counts of the annual rings on sound stumps determined the ages. For weathered stumps or those with poorly distinguishable rings, a V-gouge was cut into the stump to expose a fresh surface and a 10X hand lens was used to count the rings.

Data Analysis

We calculated dbh from mean stump height and diameter measurements using conversion tables (Demaerschalk and Omule 1978). The dbh of decayed stumps were evenly distributed and ranged from 18 cm to 312 cm, indicating that decay was not dependent on tree size. We did not miss trees of specific sizes by considering only sound stumps. Given the broad range in size of decayed stumps, we assumed no age cohorts were missed and the survey of sound stumps alone was an unbiased representation of the structure of *Thuja* in the original stands. Further analyses were conducted on data from sound stumps.

Age at stump height was corrected to total age (in 1991) by using the age of seedlings from the understory of extant stands nearby (Daniels 1994). Stumps were grouped into 50 cm height classes, then we added the mean seedling age for each height class to the stump age count to give the total tree age (Table 2).

To quantify the relationship between age and dbh we derived site-specific regression equations and a general equation, for all sites combined. Both age and dbh were logarithmically transformed to provide a function describing the relationship between age and size of *Thuja* trees ($\log_{10}[\text{age}] = b_0 + b_1 \times \log_{10}[\text{dbh}]$) which met the assumptions of regression analysis (Zar 1984). The standard error of the estimate (SEE) for each transformed model was back-transformed to present its variation in original units (years). For all statistical tests, significance was set at $\alpha = 0.05$.

Age frequency distributions (50-year classes) were prepared for each study site and for all data combined. All trees ≥900 years old were included in a single class. The mean class frequency and its standard deviation was calculated for each distribution. We defined "peak" age classes as those with class frequencies greater than the mean frequency plus one standard deviation, and compared the occurrence of peaks among sites.

Results

The ages of sound stumps ≥7.5 cm dbh ranged from 75 to 1051 years; mean ages for sites ranged from 294 to 504 years; and median ages from

TABLE 2. *Thuja plicata* seedling ages by height class. To calculate total age of trees, the mean seedling age corresponding to stump height was added to the field count of stump age.

Height (cm)	No. of stumps	No. of seedlings	Seedling ages (years)			
			Mean	S.D.	Minimum	Maximum
≤50	142	119	17	6.76	5	45
51 - 100	361	71	25	8.78	11	48
101 - 150	172	16	31	10.73	16	52
151 - 200	37	5	33	8.56	23	42
201 - 250	8	4	44	15.97	24	62

256 to 491 years. The mean ages within Capilano, Seymour, and Coquitlam watersheds were 363, 390, and 364 years, respectively. Means for north, east/west, and south aspects were 399, 353, and 365 years, respectively (Table 1).

The range and standard deviation of mean ages for all study sites were high (Table 1). The variability in ages was also reflected in the age-size regression models. Although these models indicated that size explains a statistically significant proportion of the variation in age, the relationships were weak. The R^2 values of age on dbh ranged from 0.32 to 0.79 and the corresponding SEE's ranged from 67 to 137 years for the site-specific models. The general regression equation was statistically significant ($R^2 = 0.65, p \leq 0.001$); however, its SEE of age on dbh of 109 years was high (Figure 1).

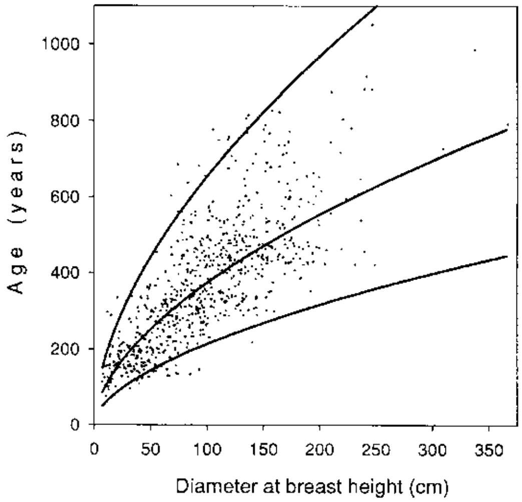

Figure 1. Relationship between age and dbh for *Thuja plicata*. The middle curve marks the regression line [$\log_{10}(\text{age}) = 1.435 + 0.568 \log_{10}(\text{dbh})$]. Upper and lower curves mark the regression line ±1.96 SEE, including 95% of observations (n = 720).

The age class distributions showed the *Thuja* in the tree layer were uneven-aged with ranges from 457 to 891 years on each site. The age class distribution for all *Thuja* trees combined showed the highest class frequencies between 150 and 500 years. Peak classes were the 200 (200 = upper limit of class from 151 to 200 years), 350, 450, and 500 year classes (Figure 2). Examination of age class distributions by study site (Figure 3) showed five sites (A, D, E, H, and L) to have had peaks in the 200 year class; eight sites (D, F, G, H, I, K, N, and O) to have had peaks in the 350 year class; and ten sites (A, B, C, E, F, G, H, I, J, and M) to have had peaks in one or both of the 450 and 500 year classes. Ten sites (A, B, D, E, F, G, H, I, J, and N) had more than one peak, with up to 350 years between peaks. Nine sites (A, B, D, E, I, L, M, N, and O) had three or fewer *Thuja* older than 600 years.

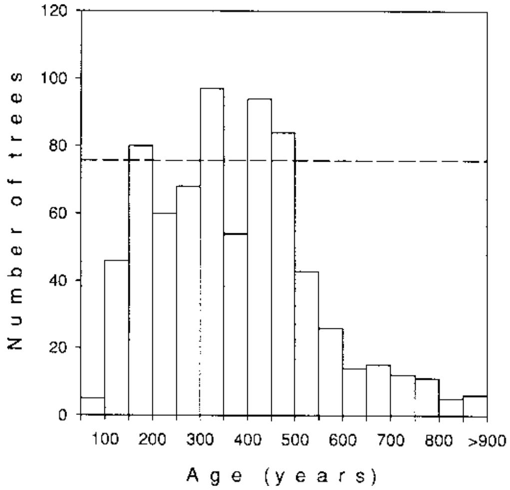

Figure 2. Age frequency distributions of 720 *Thuja plicata* in the tree layer on 15 study sites. The x-axis shows the upper limits of 50 year classes. The broken line marks the mean class frequency + 1 standard deviation of the mean; classes with frequencies above this line are "peak" classes.

Discussion

Age-Size Relationship

The age and size of the trees we observed agreed with those reported previously (Franklin and Hemstrom 1981, Beese and Sanford 1992, Keenan 1993). Although there was a general trend of increasing age with tree size, dbh was a poor predictor of tree age and the accuracy of predictions decreased with increasing tree size (Figure 1). Tree diameters provided general information about the range of tree ages on a site, as suggested by Keenan (1993), but diameter distributions did not clearly depict changes in *Thuja* populations with time. Inconsistent relationships between age and size have been shown for other species (*e.g.*, Stewart 1986).

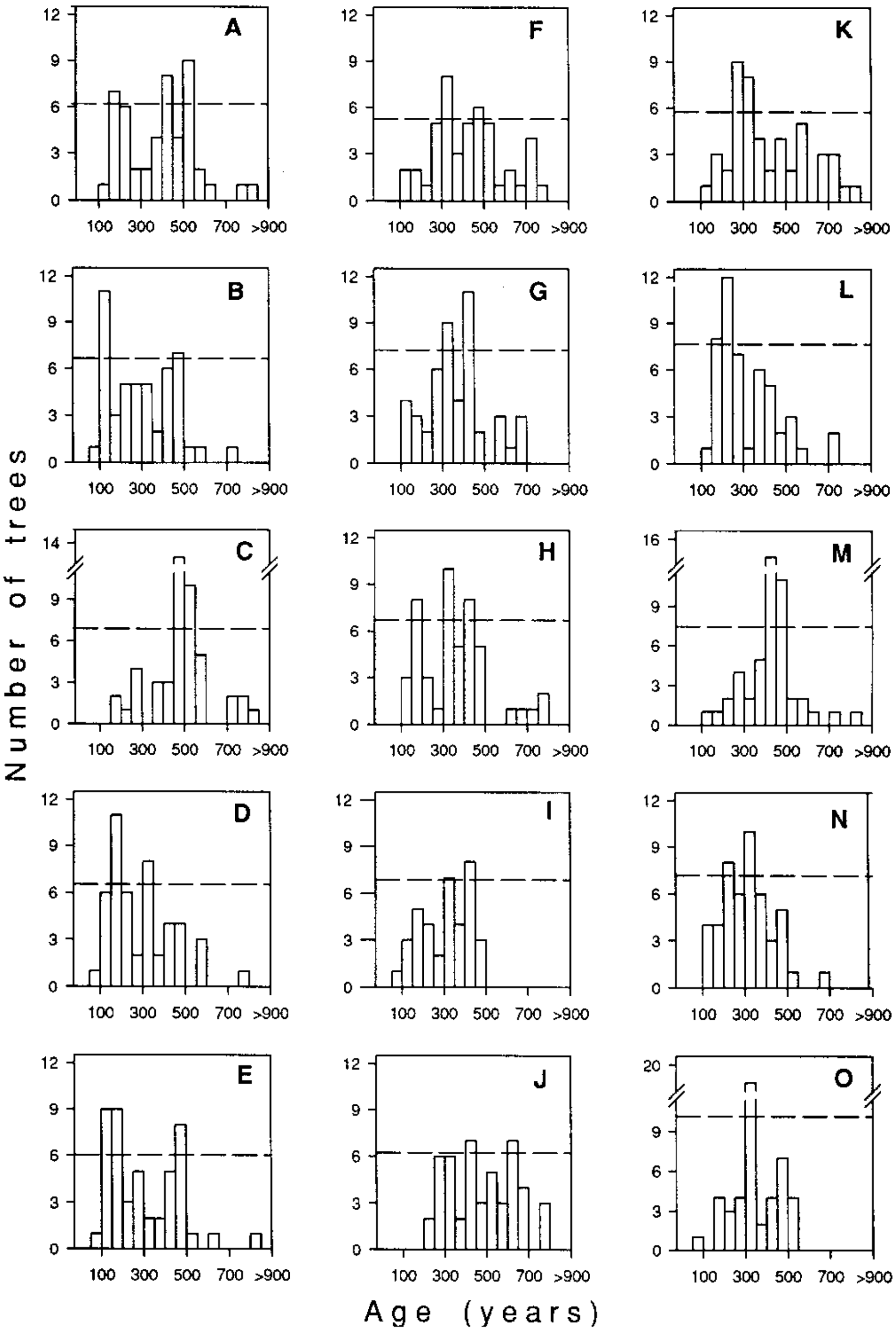

Figure 3. Age frequency distributions of *Thuja plicata* in the tree layer of study sites A to O. The x-axes labels show the upper limits of 50-year classes. The broken lines mark the mean class frequencies + 1 standard deviation of the mean; classes with frequencies above this line are "peak" classes.

Age Distributions

The low frequency of trees <100 years old resulted from the arbitrary minimum diameter of 7.5 cm used to define the tree layer of the sites and did not indicate a lack of regeneration on the sites. Delayed recruitment to the tree layer is consistent with *Thuja*'s tolerance of shade (Carter and Klinka 1992) and the slow replacement of canopy trees in old-growth forests in the coastal region (Lertzman and Krebs 1991, Spies et al. 1990).

The peaks in the age class distribution (Figures 2 and 3) indicated that establishment and mortality within *Thuja* populations have been variable during 800 years. From diameter distributions, it has been inferred that *Thuja* has low recruitment, but high survival in all size classes (Franklin and DeBell 1988, Keenan 1993). Theoretically, the corresponding age distributions should show high adult (canopy tree) survivorship with increased chance of death at the end of the life span. This theoretical distribution assumes that recruitment and mortality have been constant over time, *i.e.* that the population was at demographic equilibrium (Harcombe 1987). But, *Thuja* is evidently not at demographic equilibrium within the study area.

The age distributions of individual study sites (Figure 3) reflect sporadic mortality and regeneration episodes. They suggest the influence of disturbances of various magnitudes and extents. For example, disturbances of high intensity can reduce structural complexity by eliminating existing age classes in parts or all of a stand (Hemstrom and Franklin 1982). At least nine sites (A, B, D, E, I, L, M, N, and O) in the study area appeared to have been affected by such disturbances. Disturbances affecting stands *ca.* 600 to 700 years ago could explain the lack of *Thuja* trees greater than 600 years of age, although the life span of *Thuja* can be greater than 1000 years (Franklin and Hemstrom 1981, Keenan 1993).

In contrast to high intensity stand-level disturbances, small scale disturbances, such as windthrow, can facilitate continuous establishment and result in a spread of ages among trees (Beese and Sanford 1992) similar to those observed here. The predominant influence of wind in coastal old-growth forests in the region is becoming widely recognized (Lertzman and Krebs 1991, Spies et al. 1990). Moreover, the broad, flat, discontinuous distributions of diameters for *Thuja* from plots of 0.25 to 0.4 ha (*e.g.* Gregory 1957, Keenan 1993) indicate the influence of small scale disturbances on *Thuja* dynamics. From these diameter distributions we can assume that the establishment of trees is intermittent (although exact years of establishment cannot be predicted with certainty), even at relatively small spatial scales.

Age Class Peaks

The irregular age class structures and occurrence of distinct peaks indicate that the conditions for *Thuja* regeneration within stands is variable through time. Interestingly, peaks occurred during the same 50-year classes at different sites and within different watersheds. This suggests that the conditions conducive to *Thuja* regeneration were effective at a local level and influenced a number of sites during the same periods. We offer three hypotheses relating these peak age classes to pulses of fire disturbance and climatic variation of the past.

Fire. We hypothesize that fire has influenced the study sites, altering stand structure and facilitating *Thuja* regeneration. The three periods of peak *Thuja* regeneration, 1491-1591, 1641-1691, and 1791-1841 are synchronous with high fire periods identified in the Pacific Northwest (Figure 4). During 1491-1591, "fire episodes," periods of high fire frequency (*sensu* Morrison and Swanson 1990), occurred in the Oregon Cascades (Cook-Quentin and Deer sites in Morrison and Swanson 1990) and major fires burned in mainland British Columbia (Eis 1962), Vancouver Island (Schmidt 1970), Desolation Peak (Agee et al. 1990) and Mount Rainier National Forest (Hemstrom and Franklin 1982). The 1450-1540 fire episode of the Olympic Peninsula (Henderson et al. 1989) overlaps with this period. During 1641 to 1691, fires burned in all of the cited areas, except the Deer site in Oregon. One major fire and three significant fires burned in the Bitterroot National Forest, and three significant fires burned in Yellowstone National Park during the same period (Table 2 in Heinselman 1978). The most recent peak in *Thuja* age distributions concurs with high fire periods in the Oregon Cascades (Morrison and Swanson 1990), Mount Rainier National Forest (Hemstrom and Franklin 1982), Vancouver Island (Schmidt 1970) and the mainland of British Columbia (Eis 1962). The presence of charcoal in the soil, fire scarred trees, and the codominance

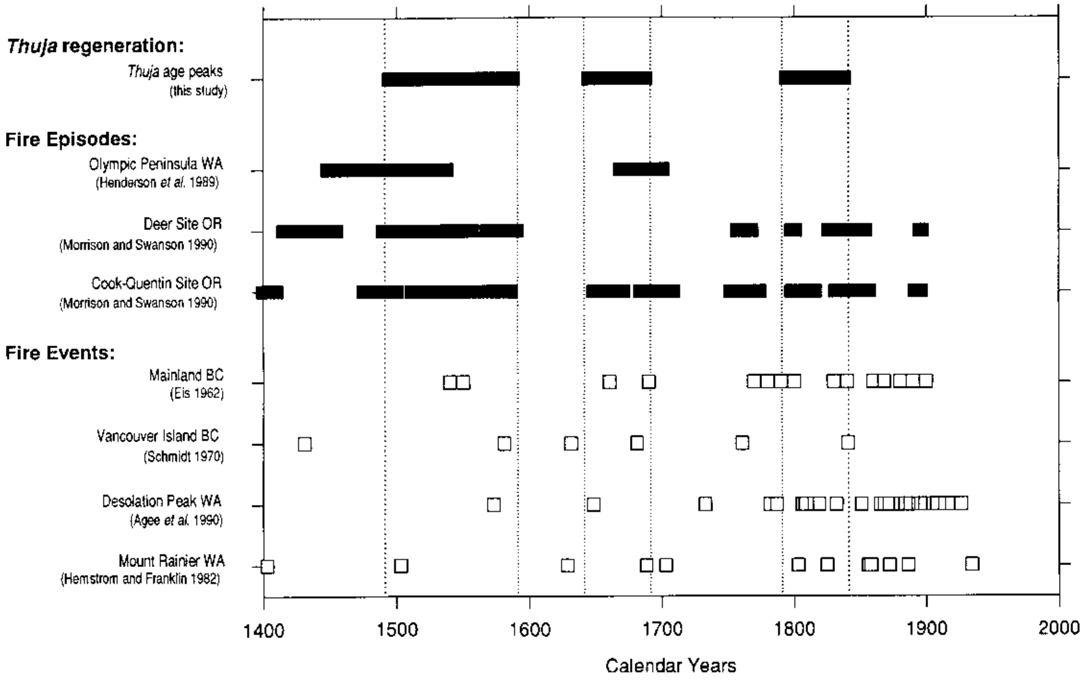

Figure 4. Chronology of *Thuja plicata* age peaks and fire disturbances in the Pacific Northwest. The left column identifies study areas and sources. Peak periods of *Thuja plicata* regeneration are represented by solid bars bounded by the vertical broken lines. Fire episodes greater than 1 year are represented by solid bars. Open squares show single years during which fires burned.

of intolerant *Pseudotsuga menziesii* in *Thuja* stands, provides strong evidence for our assertion that fire has affected the study area. However, we emphasize the need to document the fire history and fire regimes in the study area.

Climate. An alternate hypothesis to explain the observed age structures is the influence of a variable climate (Henderson and Brubaker 1986). Climate reconstruction from the Cascade Range, Washington (Graumlich and Brubaker 1986) show three periods of cooler than average summer temperatures (1600-1650, 1700-1760, and 1860-1900), each punctuating the periods of high *Thuja* establishment (Figures 2 and 4). Cooler climate might have reduced the success of *Thuja* establishment and recruitment, resulting in relatively low frequencies in corresponding age classes. It is evident from the current elevation distribution of *Thuja* and its decreasing vigour and abundance in montane forests, that cooler climate and shorter growing seasons are not conducive to *Thuja* establishment and growth (Minore 1990). Moreover, dendroecological findings from the study area show diameter growth of *Thuja* is significantly affected by temperature (Dobrý et al. in press). As the climatic variations identified by Graumlich and Brubaker (1986) probably affected a large region (Brubaker 1980), including our study area, we cannot discount the influence of historic climate variation on *Thuja* demographics.

Climate-Fire Interaction. A third hypothesis is that climate and fire interact and have affected *Thuja* demographics, now reflected in age structures. A relationship between climate and fire episodes in the Pacific Northwest has been postulated by Franklin et al. (1988), Hemstrom and Franklin (1982), Henderson et al. (1989), and Agee (1993). But the nature of the climate-fire relationship remains unclear. For example, high intensity fires ca. 600 to 700 years ago have been attributed to the warmer drier climate of the Medieval Optimum (1000-1300, Henderson et al. 1989), while other authors report cooling trends associated with low sunspot activity which are synchronous with fire periods (e.g. Agee 1993, Henderson et al. 1989).

Conclusions

From age frequency distributions, we have shown that the populations of *Thuja* in the study area were uneven-aged but were not in demographic equilibrium. We conclude that single-tree to stand-level disturbances were manifest in the age distributions. Considering the longevity of *Thuja* and the spatio-temporal scales at which wind, fire and climate affect the forests within the Pacific Northwest, it is improbable that *Thuja* will arrive at demographic equilibrium within the study area, even after long periods. Better knowledge of disturbance history and disturbance regimes within British Columbia's coastal forests are needed to improve our understanding of *Thuja* population dynamics.

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