

Seedfall, Seed Germination, and Initial Survival and Growth of Seedlings of *Thuja plicata* in Southwestern British Columbia

Abstract

Reasons for the relative absence of *Thuja plicata* regeneration in the old growth *Thuja plicata* - *Tsuga heterophylla* forests close to Vancouver, British Columbia, were assessed by measuring seedfall and applying *Thuja* seeds to small plots. All measurements were replicated in two different sites. The small (0.5 m²) plots were established in 2 canopy cover conditions (clearcut and forest), 3 seedbed conditions (mineral soil, burned forest floor, and undisturbed forest floor), and 2 mammal and bird seed predation conditions (with and without). Each canopy cover, seedbed, and seed predation combination was replicated 15 times in each study site. Large numbers of viable seeds (>200/m²) fell in 1990/91 and again in 1994/95. Seed germination decreased in the order – burn > mineral soil > forest floor; forest > clearcut; and without predation > with predation. After 3 growing seasons, of the 100 seeds applied to each plot, an average of only 1-2 seedlings had survived. This number of surviving seedlings decreased in the order – burn > mineral soil > forest floor, and clearcut > forest, but was not influenced by predation. After 3 growing seasons, seedling growth tended to decrease in the order – burn > forest floor > mineral soil; clearcut > forest; and without predation > with predation.

It was concluded that the relative lack of regenerating *Thuja* seedlings in the study area forests was not due to a lack of viable seeds. Although a lack of suitable seedbeds and the presence of the forest canopy reduce the number of seedlings in undisturbed forests, this number should still be substantial. The observed relative lack of regenerating *Thuja* seedlings must therefore result from other factors which were not considered in the present study.

Introduction

Thuja plicata (western redcedar, hereafter abbreviated as *Thuja*) is a prominent tree species in the Coastal Western Hemlock zone forests of British Columbia (Krajina 1969). It is considered to have a high shade tolerance (Minore 1990). Although earlier work (Krajina et al. 1982, Minore 1990) suggested that it was less shade tolerant than its common associate, *Tsuga heterophylla* (western hemlock), more recent work in British Columbia suggests the opposite (Carter and Klinka 1992, Wang et al. 1994). Because of this shade tolerance and its longevity, it is considered to be a climax species (Minore 1990).

A climax species is expected to have an abundance of regenerating young seedlings within an old growth forest. Observations of *Thuja*-dominated old growth forests near Vancouver, B.C. suggested a relative lack of young *Thuja* seedlings. This led to a multifaceted study of the ecology of *Thuja* in these forests. One facet involved quantifying the structure of the forests. This was completed by Daniels et al. (1995) who confirmed that the forests contained extremely few *Thuja* trees less than 100 years old. A surprising lack of

Thuja regeneration has also been observed elsewhere in B.C., Alaska, and Idaho (Minore 1983, Parker and Johnson 1994). Based on measured irregular age class structures and occurrence of distinct peaks in age classes of *Thuja*, Daniels et al. (1995) concluded that conditions for *Thuja* regeneration had varied with time and hypothesized that regeneration peaks occurred following fire or windthrow events. Eis (1962) had also previously hypothesized that regeneration in these forests peaked following fire.

Some studies reported that disturbed seedbeds were preferred by *Thuja* for regeneration from seed (Minore 1990) and were consistent with the preceding hypothesis. The results of other studies, however, were inconsistent with the hypothesis. These studies, in U.S. inland northwest forests, found that decaying wood in contact with mineral soil could be the preferred seedbed in old *Thuja* forests (Parker, 1986), and that *Thuja* regeneration was more abundant in untreated areas than in mechanically treated or burned ones (Ferguson 1994). In forests close to Vancouver, Soos and Walters (1963) found that seedbed type had little influence on the quantity and rate of *Thuja* germination, but in clearcut areas germinant

survival was better on mineral soil and burned substrata than on decaying wood.

Recognizing that a study of stand structure alone, in conjunction with some of the *Thuja* germination contradictions in the literature, could not conclusively explain the dynamics of *Thuja* in the Vancouver region, we embarked on additional ecological studies of *Thuja*. Wang et al. (1994) have reported the influence of light on *Thuja* seedling growth. The present report focuses on the earliest stage of *Thuja* regeneration – seedfall, seed germination, and initial growth and survival of *Thuja* seedlings.

The objectives of the study were to determine for the Vancouver region forests 1) if the relative lack of regenerating *Thuja* seedlings was due to a lack of viable seeds, and 2) the influence of light, forest floor disturbance, and predation by birds and mammals on *Thuja* seed, germination, and initial growth and survival of *Thuja* seedlings.

Methods

Study Area and Field Work

Two study sites were established, one in Capilano watershed (Eastcap Creek) and another in Coquitlam watershed (Cedar Creek), two of Vancouver's water-supply watersheds managed by the Greater Vancouver Watershed District. The study sites are located 20 km north (Eastcap Creek), and 30 km northeast (Cedar Creek) of the city of Vancouver, British Columbia. Both sites were located within the Very Wet Maritime Coastal Western Hemlock biogeoclimatic subzone which is characterized by a perhumid, cool, mesothermal climate (Klinka et al. 1991). Both sites were on lower, concave slopes, averaging 10 - 15% slope, and contained coarse-skeletal Humo-Ferric Podzols (Canada Soil Survey Committee 1987) analogous to U.S. Typic Haplorthods (Soil Survey Staff 1975) derived from glacial till and underlain by granitic rocks. The Eastcap Creek site had an elevation of 500 m a.s.l. and a northerly aspect, while the Cedar Creek site had an elevation of 600 m a.s.l. and a southeasterly aspect.

Each study site contained a recent (≤ 3 years old) clearcut and an adjacent old growth forest with little *Thuja* regeneration but abundant overstory *Thuja*. The Eastcap Creek forest had a total basal area of 82 m²/ha comprised of 30 m²/ha of

Thuja, 50 m²/ha of *Tsuga heterophylla*, and 2 m²/ha of *Abies amabilis* (amabilis fir). The Cedar Creek forest had a total basal area of 173 m²/ha comprised of 159 m²/ha of *Thuja*, and 14 m²/ha of *Tsuga heterophylla*. The dominant and codominant layers of the tree canopy contained 18 stems/ha of *Thuja*, 265 stems/ha of *Tsuga*, and 42 stems/ha of *Abies* in the Eastcap Creek forest, and 83 stems/ha of *Thuja* and 158 stems/ha of *Tsuga* in the Cedar Creek forest. Tree regeneration in these forests (seedlings up to 100 cm high) comprised 36 stems/ha of *Thuja*, 10,670 stems/ha of *Tsuga*, and 5,670 stems/ha of *Abies* in the Eastcap Creek forest, and 224 stems/ha of *Thuja*, 7,390 stems/ha of *Tsuga* and 2,170 stems/ha of *Abies* in the Cedar Creek forest. Understory vegetation in the forests consisted of very sparse shrub and herb layers over a moss layer varying in cover from 0 to 90%. Shrub, herb and moss vegetation in the clearcuts was initially similar to that in the forest although herb and shrub cover increased during the study.

Seedfall was collected in perforated plastic greenhouse trays (27 cm x 53 cm x 6 cm deep) lined with fiberglass insect screen. At each site the trays were placed at 20 m intervals along two transects 20 m apart, oriented at right angles to the forest-clearcut edge. Placement began 20 m either side of the edge, with 5 trays per transect in the clearcut and 5 in the forest. Thus, at each site a total of 10 trays was placed in the forest, and 10 in the clearcut. Trays were in place from August 1990 until June 1995. They were emptied every 2-4 weeks during the September-May period, or whenever possible during periods of snow, and every 6 weeks during the June-August period.

Seed germination was studied using small square plots, 0.5 m² in area. At each study site, plots were located randomly between obstacles (primarily decaying wood) both in the forest and in the clearcut, all plots being at least 30 m from the forest-clearcut edge. One third of the plots in each canopy cover situation were located on undisturbed forest floors, another third had all forest floor material removed to expose the surface mineral soil, and the last third were located on burned forest floors. The burned forest floor was achieved by piling woody debris < 7 cm diameter on the forest floor surface during dry periods in July - August, 1990, covering the debris with

plastic sheets, then burning with a hand-held drip torch in November, 1990, when the surrounding organic materials were very wet. Forest floor depths of burn (amount of forest floor burned by the fires) were monitored using 3 or 4 depth-of-burn pins in every second plot. Depths of burn ranged from 0 to 21 cm, but averaged 1.9 cm at Eastcap Creek and 1.0 cm at Cedar Creek based on 96 measurements per site. Undisturbed forest floor depths averaged 10-25 cm. Half of the plots of each seedbed type in each light situation were fitted with metal wire (1 cm mesh) cages to exclude mammal and bird, but not insect seed predators. Each canopy cover/seedbed/predation combination was replicated 15 times. Thus, there was a total of $- 2$ (study site) $\times 2$ (canopy cover) $\times 3$ (seedbed) $\times 2$ (predation) $\times 15$ (replicates) = 360 plots.

Seedbed and predation treatments were randomly allocated to the plots. All plots were prepared during July – August, 1990, and covered with fiberglass screen to exclude fresh seedfall immediately after preparation. Fiberglass screen was placed on the burned plots within a few hours of burning. Within a week of burning 100 *Thuja* seeds collected from nearby areas (B. C. Ministry of Forests Seed Center, seedlot number 10326) were scattered onto the ground surface in each experimental plot. Germination tests indicated these seeds had a viability of 89%.

The percentage of above-canopy photosynthetically active radiation reaching the ground surface in the forests was measured on a uniformly cloudy day in July and again in August, 1997, using a Decagon Devices, Model SF-40 sunfleck Ceptometer. Measurements were made every 5 m on a 50 x 50 m square grid containing the seed germination plots. Due to the lack of tree mortality in the plots during the 1991 – 1997 period and the relatively slow growth rates of vegetation in old growth forests, the August 1997 measurements are considered to represent light conditions during the study.

During the 1990/91 winter, tree blowdown in the Eastcap Creek forest resulted in the loss of 3 plots. Water erosion at Cedar Creek resulted in the loss of 2 plots in the forest and 13 in the clearcut. These plots were excluded from subsequent analysis. By mid-May, 1991, *Thuja* seedfall had declined to very low levels, so the fiberglass screens were removed from the plots. This occurred within

2 weeks of snow leaving the plots. The numbers of living and dead *Thuja* seedlings in each plot were counted once every 2-3 weeks until mid-September, 1991, with the final count for the year occurring on 17 October. At this time all living seedlings were marked with colored toothpicks to avoid confusion with seedlings from fresh seedfall in subsequent years. The metal seed predator exclosures were removed in August when predation was considered to have dropped to very low levels (T. Sullivan, Faculty of Forestry, University of B. C.; pers. comm.).

Seedlings were counted on 7 February, 1992, then again in late March and every 3-4 weeks until the end of October. In 1993, seedlings were counted on 22 April, then every 6-8 weeks until the end of September. Plots were weeded regularly, as needed, to eliminate plant competition as a variable influencing the results.

In October, 1993, all surviving seedlings had their basal diameters, heights, and crown volumes (greatest width (A) \times width at 90° to A \times height) measured.

Laboratory Work and Data Analysis

Seeds collected in the seedfall traps were dried at 25 - 30° C in the laboratory, separated from other litterfall, counted, then tested for viability on a germination table.

Data on the total number of seeds germinating and the number of living seedlings at each counting period were subjected to analysis of variance (ANOVA). In some instances, visual inspection suggested that datasets were not normally distributed and/or Bartlett's tests indicated variances were not homogeneous. These datasets were subjected to different transformations and the transformed data again subjected to ANOVA. Transformations improved normality and homogeneity of variances although occasionally variances were still not homogeneous. Seedling growth data were also subjected to checking for normality and homogeneity of variances prior to ANOVA. Logarithmic transformations were needed to improve normality and homogeneity of variances but some datasets could not be transformed in such a way as to meet the assumptions of ANOVA. The two study sites were not replicates as they had different aspects with noticeably different microclimates. Consequently, analyses of variance were 3 way factorials, with seedbed, light,

and predation as the 3 factors. All analyses were conducted separately for each study site using SYSTAT software (Wilkinson 1986).

Results and Discussion

Seedfall

During the study, high seedfall years occurred in 1990/91 and 1994/95 (Figure 1). The number of viable seeds reaching the ground surface in the forests was >200 seeds/m² at Eastcap Creek and >1000 seeds/m² at Cedar Creek during the study. This shows that the low density of *Thuja* seedlings in the forests can not be attributed to a lack of viable seeds. Most *Thuja* seeds are reported to escape bird and animal predation (Minore 1990) and viable seeds, if they do not germinate, may enter the forest soil seed bank. Studies of seed banks in western North American forests containing *Thuja* have found viable *Thuja* seeds present (Harmon and Franklin 1995, McGee and Feller 1993, Yearsley 1993). Even if germination is unlikely after a year in the seedbank (Minore 1990), the widespread presence of viable *Thuja* seeds in soil seedbanks further suggests that the low number of *Thuja* seedlings in *Thuja* forests can not be attributed to a lack of viable *Thuja* seeds.

Seed Germination

The total numbers of seeds germinating (Table 1) were only slightly greater than the maximum numbers of living germinants recorded (Figures 2-4). The trends in numbers for seedbed, light, and predation, were identical for both study sites. The only significant first or second order interaction for both study sites was between seedbed and predation. However, in neither case did this interaction alter the observation that, for both study sites, the numbers of seeds germinating decreased in the order - burn>mineral soil>forest floor in both the presence and absence of predation. The interaction only influenced the relative magnitude of the differences.

Thus, germination decreased in the order - burn>mineral soil>forest floor; forest>clearcut; and without predation>with predation. Germination was also greater at Cedar Creek than at Eastcap Creek. At Cedar Creek, the average total number of seeds germinating per plot for burned plots in the forest without predation was 80, and close to the potential maximum of 89. Greater germination at Cedar Creek is consistent with the greater quantities of *Thuja* present in the Cedar Creek forest. In the field, germination was greater in the forest than in the clearcut. The forested plots

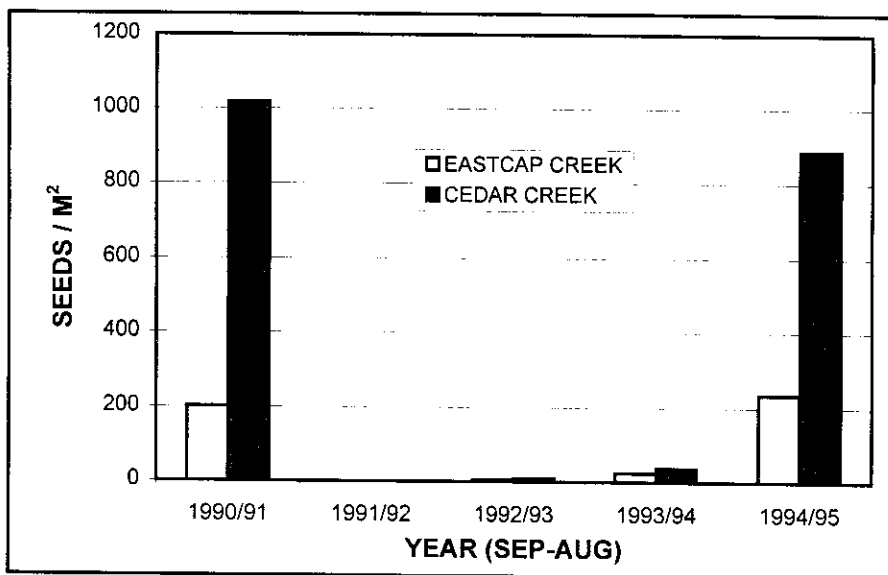


Figure 1. Annual (1 September - 31 August) number of viable seeds falling in the forests in each of the two study areas.

TABLE 1. Mean total number of germinating seeds per plot, and results of analyses of variance.

Environmental parameter	Eastcap Creek	Cedar Creek
1. Seedbed (S)		
Mineral soil	13 (1) ^b	34(3) ^b
Burned forest floor	25(2) ^c	59(4) ^c
Undisturbed forest floor	8(1) ^a	15(3) ^a
Significant interactions	S x P	S x P
2. Canopy Cover (C)		
Forest	18(2) ^a	43(3) ^a
Clearcut	14(2) ^b	27(3) ^b
Significant interactions	none	none
3. Predation (P)		
Without	18(2) ^a	46(3) ^a
With	14(1) ^b	24(3) ^b
Significant interactions	S x P	S x P

For a given area and environmental parameter, different superscripts indicate significantly different ($P < 0.05$) numbers of seedlings per plot. Standard errors are given in parentheses.

received 1 - 12% (average 4% at Cedar Creek and 2% at Eastcap Creek) of the photosynthetically active radiation received by the clearcut plots. The fact that laboratory germination can be improved by exposing seeds to light (Li et al. 1994) suggests that the influence of the forest canopy on light is outweighed by its influence on other environmental factors, with respect to *Thuja* seed germination.

Seedling Survival

Numbers of living seedlings peaked early in the first growing season with 74-93% of total mortality occurring during the first growing season (Figure 5). Mortality during the first winter dropped to 4-22% of the total, while mortality during the next 2 years accounted for only 1-11% of the total at Eastcap Creek and 1-4% of the total at Cedar Creek (Figure 5). Seedling survival after 3 growing seasons varied from almost 0 (forest floor seedbeds at Cedar Creek) to 11% (clearcuts at both study sites) of the number of seeds that germinated. On average, only 1 and 2 seedlings of the potential 89 per plot, at Eastcap and Cedar Creeks, respectively, survived the first 3 years.

The two time periods with the greatest mortality in the present study were 25 June - 10 July and 20 August - 17 October, 1991, (Figures 2-4) and they coincided with low rainfall periods. Only

4 mm of rain during a 14 day period in the June-July sampling interval, and 2 mm of rain during a 32 day period in the August-October sampling interval were recorded at a weather station located at a similar elevation 9 km southeast of the Cedar Creek site. This weather station recorded 33 - 97 mm of rain during each of the other sampling intervals and no less than 37 mm of rain during any other 14 day period in the 1991 growing season. Surface soil temperatures were not measured but no stem lesions were seen above the ground line (cf. Gashwiler 1971), suggesting water deficits, rather than heat, as the major cause of mortality. Minor, but unquantified amounts of frost heaving and frost damage were observed, contributing to the winter period mortality. Most mortality, however, was probably attributable to water deficits during the first growing season, which is consistent with previous studies of *Thuja* seedling survival (Gashwiler 1971, Soos and Walters 1963) and with the known preference of *Thuja* for moister sites (Krajina 1969).

Low survival of seedlings during the first growing season has been reported previously for *Thuja* (Gashwiler 1971, Minore 1990, Soos and Walters 1963). Drought and high soil temperatures have been the primary causes of this mortality. High temperatures and drought are unlikely in forests. There, low survival is more likely a result of shade-induced poor root growth resulting in inadequate supply of water and nutrients to seedlings (Minore 1990).

Survival was poorest in forest floor seedbeds, being almost 0% at Cedar Creek (Figure 2). Numbers of living seedlings always decreased in the order - burned forest floor > mineral soil > forest floor, for both study sites. Mortality during the first year was sufficiently high that during the second and third years, there were generally no significant differences in the numbers of living germinants between any of the seedbed types at Cedar Creek or between the mineral soil and forest floor seedbeds at Eastcap Creek. Not only did more seeds germinate on the burned seedbeds at Eastcap Creek (Table 1) but survival was also greatest on these seedbeds (Figure 2). At Cedar Creek, greater germination on the burned seedbeds was offset by greater mortality on these seedbeds than on mineral soil seedbeds (Figure 3) accounting for the lack of a statistically significant difference in the numbers of surviving germinants between these seedbed types. These

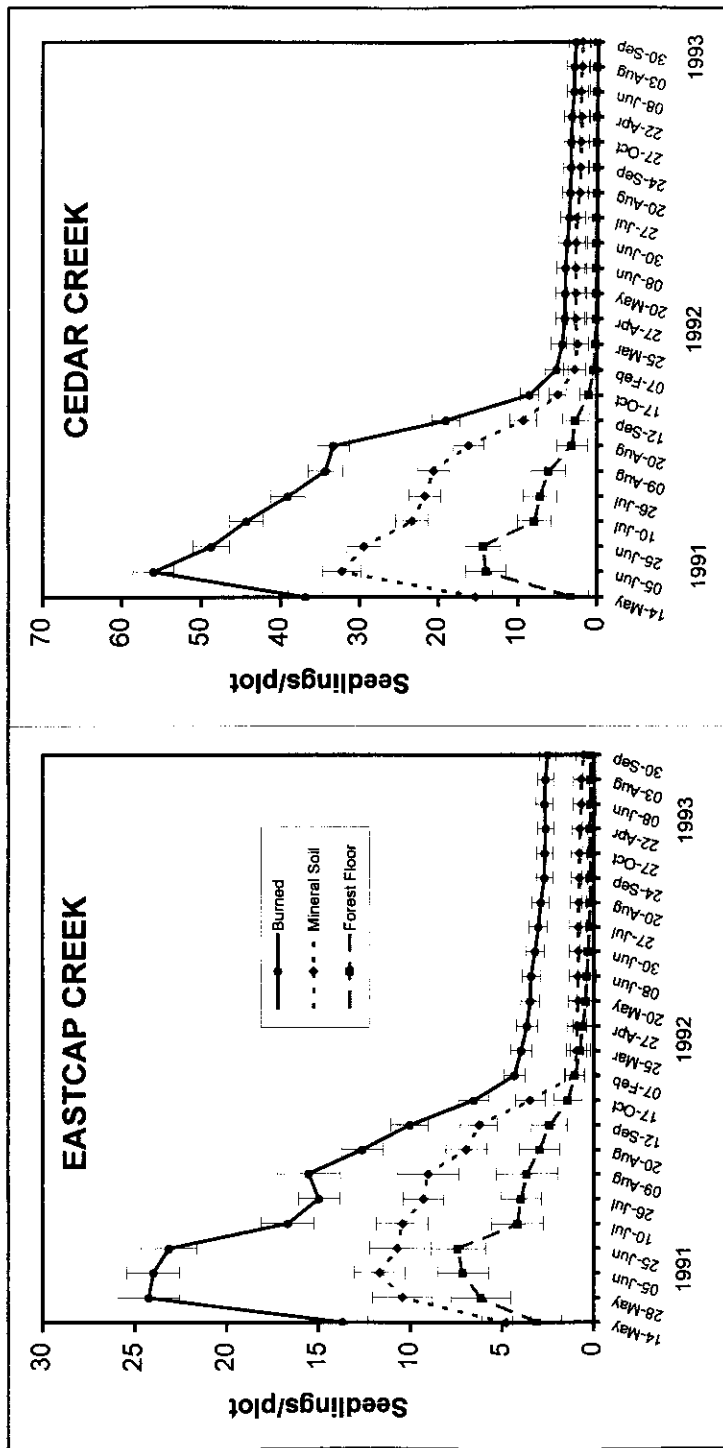


Figure 2. Mean number of living seedlings per plot as a function of time at each study site for each of the three seedbeds.

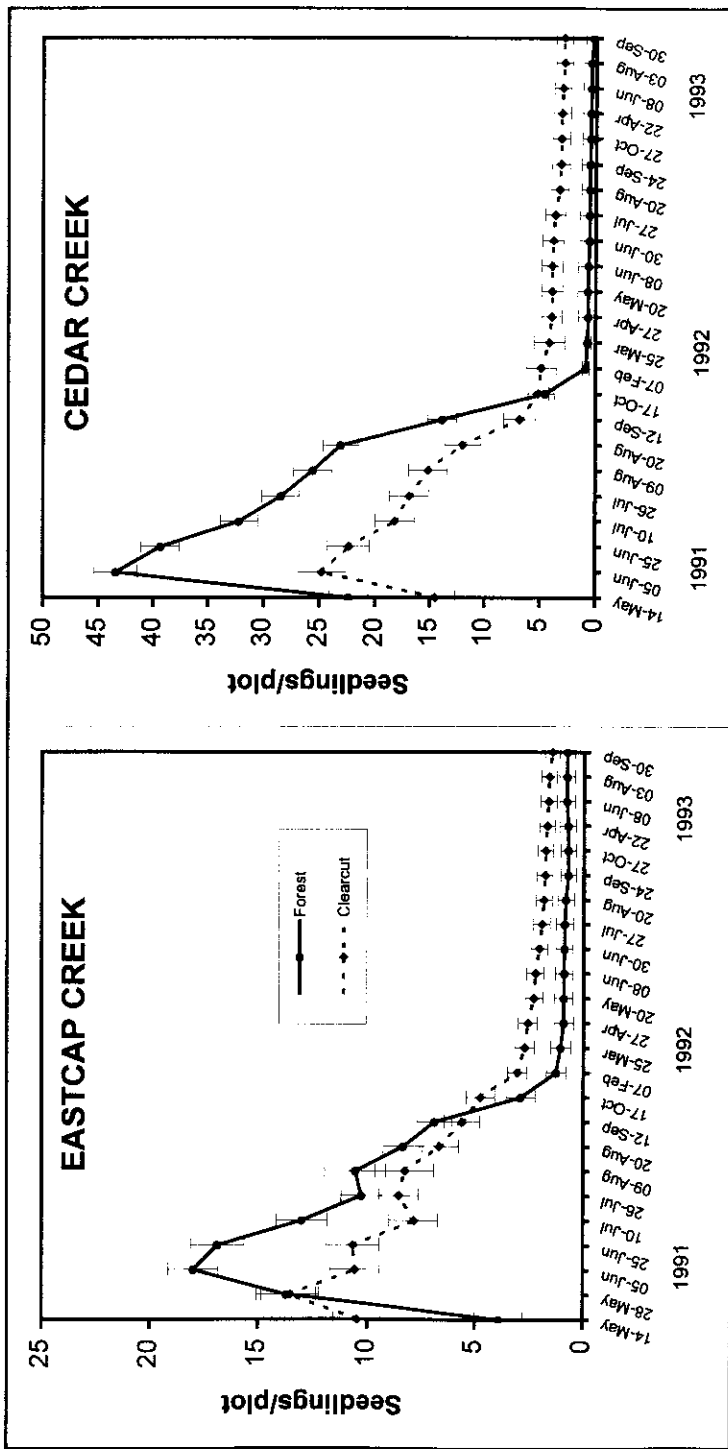


Figure 3. Mean number of living seedlings per plot as a function of time at each study site for the forest and clearcut areas.

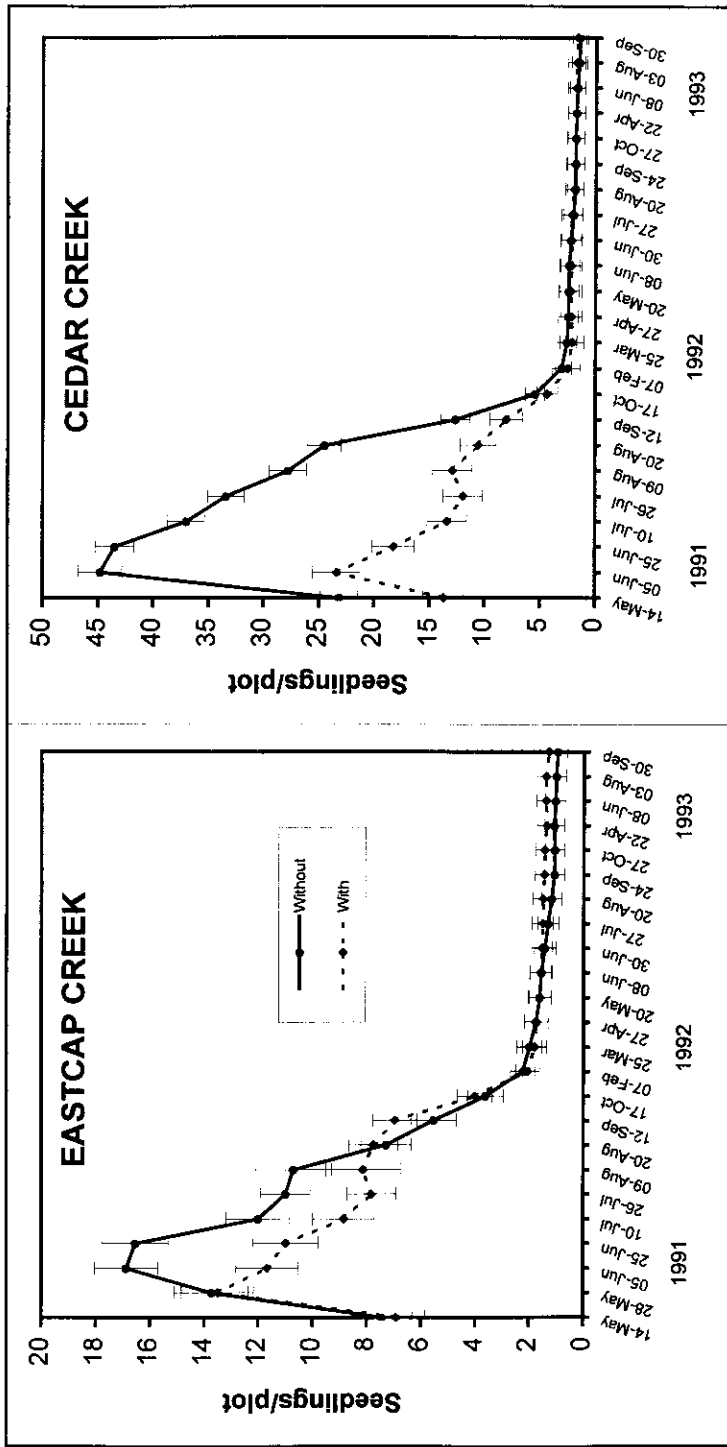


Figure 4. Mean number of living seedlings per plot as a function of time at each study site for the plots with and without vertebrate seed predators.

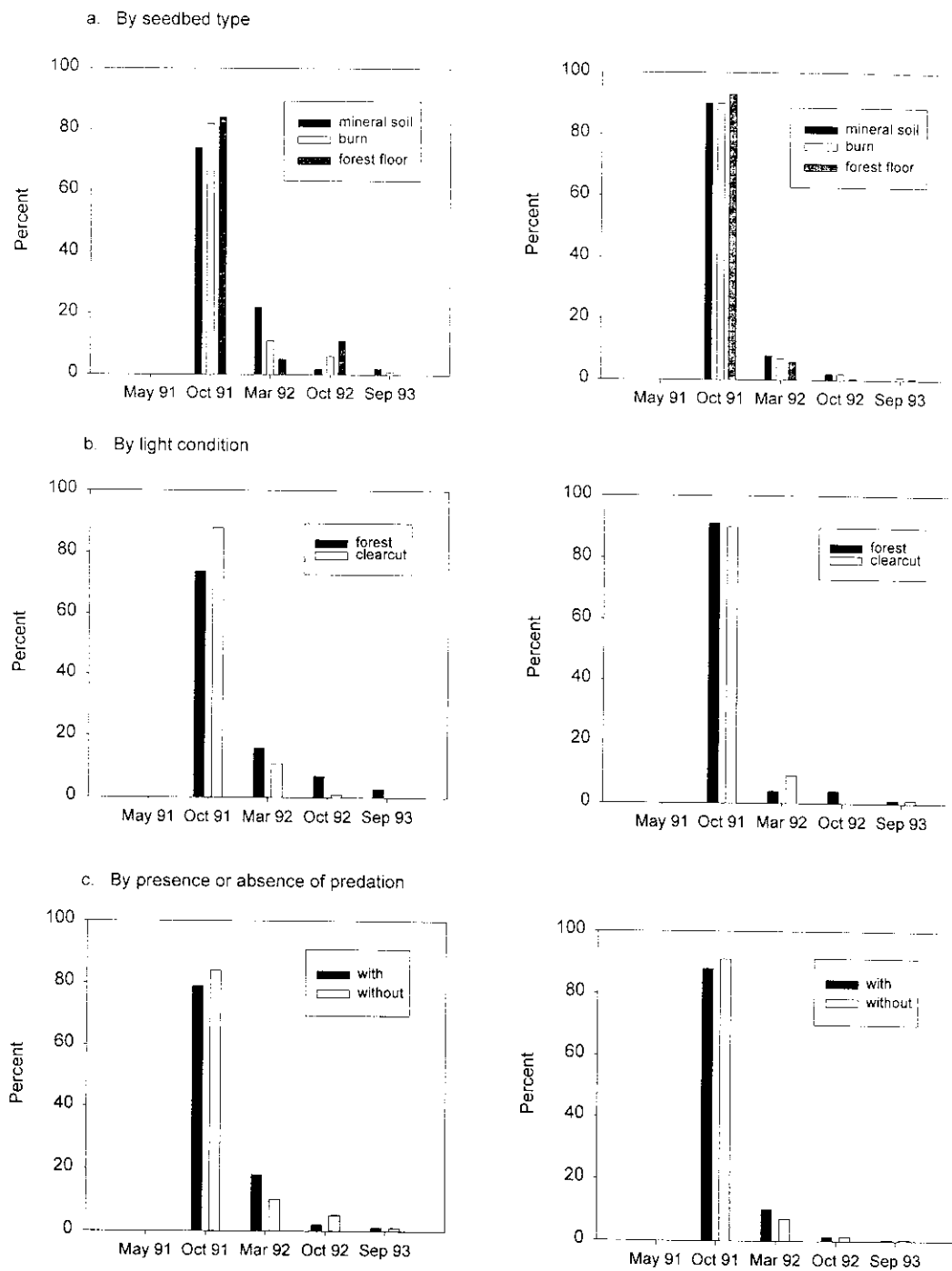


Figure 5. Mortality of seedlings expressed as a percentage of the total mortality during different time intervals during the first three years. Results for Eastcap Creek are on the left, and for Cedar Creek on the right. The time intervals are—

May 91 = 14 May – 5 June, 1991

Oct 91 = 6 June – 17 October, 1991

Mar 92 = 18 October, 1991 – 25 March, 1992

Oct 92 = 26 March – 27 October, 1992

Sep 93 = 28 October, 1992 – 30 September, 1993

results were not affected by any first or second-order interactions.

Although germination was greater in forest than in clearcut plots at both study sites during the first growing season (Table 1), the reverse trend for survival occurred at both study sites during subsequent years (Figure 3). This resulted in greater numbers of living seedlings in the forest plots during the first growing season, but greater numbers in clearcut plots during the second and third growing seasons (Figure 3). The significant differences in the numbers of living seedlings between the two canopy covers were generally more pronounced at Cedar Creek than at Eastcap Creek. By the end of the third growing season, differences were statistically significant only at Cedar Creek, with, again, no first or second order interactions.

Minore (1990) concluded that disturbed mineral soil seedbeds were a major requirement for regeneration from *Thuja* seed. He considered that burning favored *Thuja* seed germination by creating more mineral soil seedbed sites. In the present study, none of the burned plots had exposed mineral soil. No burned plot had a forest floor that was less than 3 cm thick during the first growing season. Burned forest floors in the study area were clearly the most desirable seedbed for *Thuja*. Greater numbers of *Thuja* seedlings on burned forest floor seedbeds and in clearcut rather than forest plots, suggest that *Thuja* has evolved to regenerate following disturbances which produce either mineral soil or burned forest floor seedbeds and/or expose them to greater amounts of light. In drier and hotter summer environments in the U.S. Pacific Northwest, seedling mortality from high surface temperatures in clearcuts suggests partial shading may enhance seedling survival (Gashwiler 1971, Haig et al. 1941). The influence of partial shading was not assessed in the present study, however.

The 100 seeds per plot produced 0.18 and 0.04 surviving seedlings after 3 growing seasons in undisturbed forest floor in the Eastcap and Cedar Creek forests, respectively. When applied to the number of viable seeds falling in the forest (Figure 1) this would suggest approximately 4,000 – 14,000 surviving *Thuja* seedlings per ha, 3 years after a good seed year. Even allowing for loss of seed as a result of seedfall onto rock or log surfaces, which cover approximately 30% of the

ground surface in the forests of the study area (Song 1997), a substantial number of seedlings should still survive. Observations of considerably fewer *Thuja* seedlings suggest other factors, such as pre-logging wildlife browsing or understory plant competition, have influenced *Thuja* regeneration in the undisturbed old growth forests of the study area.

Predation significantly decreased the numbers of seeds germinating (Table 1), but greater mortality occurred in the plots without predation (Figure 4). This resulted in no significant influence of predation on numbers of surviving seedlings from August (Eastcap Creek) or October (Cedar Creek) of the first growing season to the end of the study (Figure 4). It is unclear why greater mortality occurred in the predator exclusion plots. These results suggest that bird and mammal seed predation may be occurring but this has little effect on the numbers of living *Thuja* seedlings beyond the first growing season.

Seedling Growth

Mineral soil was generally the poorest seedbed for growth at both study sites, although not all growth differences between seedbed types were statistically significant (Table 2). At Eastcap Creek, the best seedling growth was found on undisturbed forest floors while at Cedar Creek, seedling growth tended to be the best on burned forest floors, although for the latter area there were no significant growth differences between burned and undisturbed forest floors. The seedbed x predation interactions for height and basal diameters did not change interpretations of the results. Growth was least on mineral soil seedbeds for both predation situations, but it was statistically significantly less only when predators were present.

Some of the differences in these results between Eastcap and Cedar Creek may be an artifact of the small sample size for seedlings in undisturbed forest floors. These small sample sizes were the result of the low seed germination and seedling survival rates in the forest floors. It can be stated with more confidence that seedling growth was better in burned than in mineral soil seedbeds, with the differences being more pronounced at Cedar Creek.

Seedlings generally grew better at Cedar Creek than at Eastcap Creek, even on undisturbed forest floor seedbeds (Table 2). This better growth

TABLE 2. Mean heights, basal diameters, and canopy volumes of *Thuja* seedlings at the end of the third growing season, and results of analyses of variance.

Environmental parameter	Eastcap Creek				Cedar Creek			
	Height (cm)	Basal diameter (mm)	Canopy volume (cm ³)	n	Height (cm)	Basal diameter (mm)	Canopy volume (cm ³)	n
1. Seedbed (S)								
Mineral soil	9.1 (1.3) ^b	1.1 (0.1)	838 (245) ^a	42	9.7(1.3) ^a	1.5 (0.2) ^b	1507 (546)	40
Burned forest floor	9.2 (0.6) ^a	1.4 (0.1)	918 (170) ^b	136	18.8 (0.9) ^a	2.5 (0.1) ^a	4491 (678)	164
Undisturbed forest floor	14.6 (2.3) ^a	1.7 (0.1)	3114 (1671) ^a	14	17.3 (0.9) ^a	3.1 (0.5) ^b	2488 (1150)	6
Significant interactions	none	none	none		S x P	S x P	none	
2. Light (L)								
Forest	3.7 (0.1) ^b	0.6 (0.0) ^b	18 (3) ^b	55	3.0 (0.2) ^b	0.3 (0.0) ^a	11 (3) ^b	39
Clearcut	12.0 (0.6) ^a	1.6 (0.1) ^a	1479 (246) ^a	137	20.2 (0.8) ^a	2.8 (0.1) ^a	4744	171
Significant interactions	none	none	none		none	none	none	
3. Predation (P)								
Without	10.4 (0.9)	1.5 (0.1) ^a	1533 (399) ^a	79	17.8 (0.9)	2.5 (0.1) ^a	4472 (800)	135
With	9.1 (0.6)	1.2 (0.1) ^b	730 (124) ^b	113	15.7 (1.4)	2.0 (0.2) ^b	2773 (500)	75
Significant interactions	none	none	none		S x P	S x P	none	

For a given area, growth measure, and environmental parameter, different superscripts indicate significantly different ($P < 0.05$) magnitudes of growth. An absence of superscripts indicates no significant differences in growth. Standard errors are given in parentheses.

n = number of observations.

can be attributed to the warmer climate and nutrient richer forest floors at Cedar Creek *Thuja* grows better in the warmer portions of the Coastal Western Hemlock biogeoclimatic zone in southwestern B.C. (Kayahara et al. 1997) and the Cedar Creek Mormoder forest floors have lower C/N ratios and greater mineralizable N contents than the Leptomoder forest floors at Eastcap Creek (Fons and Klinka 1998). The mineral soils at both sites are poorer growing sites for *Thuja* than burned or undisturbed forest floors. This may be due to poorer nutrition or water supply in the mineral soil. Regardless of the reason, an increase in growth (from mineral soil to forest floor) is likely to be enhanced in the better growing environment of Cedar Creek.

Trends in seedling growth with light were quite clear and identical at both study sites. Seedling growth was better in clearcuts than in forests. The same result has been found for *Thuja* seedlings planted in the study sites (Wang et al. 1994). Adams and Mahoney (1991) found that naturally regenerated *Thuja* seedlings in Idaho grew best in partial shade and that growth was reduced more by below-ground competition than by competition

for light. Competing vegetation was removed from all plots in the present study on all seedling counting occasions during the growing season. This was necessary primarily in the clearcuts where herb and shrub species regenerated prolifically. The roots of trees and shrubs, however, would have been present to a greater extent in the forests than in the clearcuts. The competition environments of the study plots were not quantified. Consequently, it is unclear whether competition would have been greater in the forests or the clearcuts. However, seedlings grew better in mineral soil seedbeds in the clearcuts than in the forests. In these seedbeds below-ground competition would have been minimal as many roots were destroyed when the seedbeds were prepared. Furthermore, after 3 years, 9 plots had more than 10 *Thuja* seedlings present. Two of these plots contained 57 and 59 seedlings, respectively. Although there were no visible indications that competition between seedlings in these plots had affected seedling growth, the ANOVA was rerun excluding data from these 9 plots. The results were still identical to those presented in Table 2. Consequently, although we have not been able to definitely exclude the effects of below-ground competition, our data and

observations suggest that light had an important influence on *Thuja* seedling growth in our study area, with greater growth in the higher light levels in clearcuts rather than in forests.

Predation also appeared to influence growth with greater growth in plots where vertebrate predators were excluded (Table 2). However, seedbed interacted with predation at Cedar Creek such that basal diameter differences were statistically significant only on mineral soil seedbed plots. *Thuja* seedlings in plots without predator exclusion screens would have been available to herbivores. Deer, which are present in the study area, are known to browse *Thuja* seedlings heavily (Minore 1983). Curran and Dunsworth (1988) considered that damage from browsing may be the most important stand establishment problem for *Thuja* in coastal British Columbia. Thus, it is likely that browsing on the *Thuja* seedlings in plots without predator exclusion screens retarded aboveground seedling growth in relation to that in plots surrounded by screens. It is unclear why differences were statistically significant only on mineral soil seedbeds at Cedar Creek, unless this is partly an artifact caused by the small sample size ($n=6$) on forest floor seedbeds, and partly due to the greater visibility of seedlings on the mineral soil seedbeds.

Conclusions

We conclude that the relative lack of *Thuja* seedlings in the forests of the study area was not due to a lack of viable seeds. Although a lack of suitable seedbeds and the presence of the forest canopy reduces the number of seedlings in undisturbed old growth forests, this number should still be substantial. The observed relative lack of *Thuja* seedlings must result from other factors, such as pre-logging wildlife browsing or understory plant competition, which were not investigated in the

Literature Cited

- Adams, D. L., and R. L. Mahoney. 1991. Effects of shade and competing vegetation on growth of western redcedar regeneration. *W. J. Appl. For.* 6: 21-22.
- Canada Soil Survey Committee. 1987. The Canadian system of soil classification. 2nd ed. Agric. Can. Publ. No. 1646, 164 pp.
- Carter, R. E., and K. Klinka. 1992. Variation in shade tolerance of Douglas-fir, western hemlock, and western red cedar in coastal British Columbia. *Forest Ecol. Manage.* 55: 87-105.

present study. Investigation of these factors is warranted if the relative lack of *Thuja* regeneration is to be explained.

The results of the present study also support the hypothesis of Daniels et al. (1995) that regeneration peaks of *Thuja* in the study area forests occurred following fire or windthrow events. Daniels et al. (1995) were not able to discount the influence of a variable climate in explaining *Thuja* regeneration peaks. The more abundant germinants in the experimental plots, and *Thuja* regeneration in the warmer Cedar Creek forest than in the cooler Eastcap Creek forest is also consistent with this. However, the low number of germinants and poor survival of seedlings on forest floor seedbeds even in the warmer Cedar Creek forest suggest that *Thuja* regeneration is more responsive to seedbed conditions than to small changes in temperature. However, the effects of major changes in temperature (i.e., increases of $>5^{\circ}\text{C}$ in annual or growing season mean daily temperature) are still uncertain. Climate is certain to influence *Thuja* regeneration indirectly through its influence on fire incidence. Warmer, drier climates will increase fire incidence and lead to greater *Thuja* regeneration, unless the fires are so severe as to kill the mature *Thuja* trees over large areas and thus eliminate the *Thuja* seed source.

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- Curran, M. P., and B. G. Dunsworth. 1988. Coastal western redcedar regeneration: problems and potentials. *In* N. J. Smith (Compiler). *Western red cedar—does it have a future?* Conference Proceedings. Faculty of Forestry, University of B.C., Vancouver, B.C. Pp. 20-32.
- Daniels, L. D., P. L. Marshall, R. E. Carter, and K. Klinka. 1995. Age structure of *Thuja plicata* in the tree layer of old-growth stands near Vancouver, British Columbia. *Northwest Sci.* 69: 175-183.
- Eis, S. 1962. Statistical analysis of several methods for estimation of forest habitats and tree growth near Vancouver, B.C. Forestry Bulletin No. 4. Faculty of Forestry, University of British Columbia, Vancouver, B.C.

- Ferguson, D. E. 1994. Natural regeneration following timber harvest in Interior cedar - hemlock - white pine forests. In D. M. Baumgartner, J. E. Lotan, and J. R. Tonn (eds.) Interior - cedar hemlock - white pine forests: ecology and management Conf. Proc. Cooperative Extension, Washington State University, Pullman Wa. Pp. 239-247.
- Fons, J. and K. Klinka. 1998. Chemical and biotic properties and temporal variation of moder humus forms in the rain forest near Vancouver, British Columbia. Can. J. For. Res. 28: in press.
- Gashwiler, J. S. 1971. Emergence and mortality of Douglas-fir, western hemlock, and western redcedar seedlings. Forest Sci. 17: 231-237.
- Haig, I. T., K. P. Davis, and R. H. Weidman. 1941. Natural regeneration in the western white pine type. U.S.D.A. For. Serv. Tech. Bull. 767, Northern Rocky Mountain For. Res. Exp. Sta., Missoula, Montana, 99 pp.
- Harmon, J. M., and J. F. Franklin. 1995. Seed rain and seed bank of third- and fifth- order streams on the western slope of the Cascade Range. Res. Pap. PNW-RP480. U.S.D.A. Forest Service, Pac. Northwest Res. Stn., Portland, Or. 27 p.
- Kayahara, G.J., K. Klinka, and A. C. Schroff. 1997. The relationship of site index to synoptic estimates of soil moisture and nutrients for western redcedar (*Thuja plicata*) in southern coastal British Columbia. Northwest Sci. 71:167-173.
- Klinka, K., J. Pojar, and D. V. Meidinger. 1991. Revision of biogeoclimatic units of coastal British Columbia. Northwest Sci. 65: 32-47.
- Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecology of Western North America 2 (1): 1-147, Department of Botany, University of B. C., Vancouver, B.C.
- Krajina, V. J., K. Klinka, and J. Worrall. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Faculty of Forestry, University of British Columbia, Vancouver, B.C. 131 p.
- Li, X.J., P.J. Burton, and C.L. Leadem. 1994. Interactive effects of light and stratification on the germination of some British Columbia conifers. Can. J. Bot. 72: 1635-1646.
- McGee, A., and M. C. Feller. 1993. Seed banks of forested and disturbed soils in southwestern British Columbia. Can. J. Bot. 71: 1574-1583.
- Minore, D. 1983. Western redcedar—a literature review. Gen. Tech. Rep. PNW-150. U.S.D.A. Forest Service Pac. Northwest For. Res. Exp. Stn., Portland, Or. 70 p.
- _____. 1990. *Thuja plicata* Donn ex D. Don. In R. M. Burns, and B. H. Honkala (eds.) Agriculture Handbook: 654, U.S.D.A. Forest Service, Washington, D. C. pp. 590-600.
- Parker, T. 1986. Ecology of western redcedar groves. Ph.D. Thesis, University of Idaho, Moscow, Idaho.
- Parker, T., and F. D. Johnson. 1994. Cedar groves: the ultimate old growth. In D. M. Baumgartner, J. E. Lotan, and J. R. Tonn. (eds.) Interior Cedar - hemlock - white pine forests: ecology and management Conf. Proc. Cooperative Extension, Washington State University, Pullman, Wa. Pp. 53-55.
- Soil Survey Staff. 1975. Soil taxonomy. U.S. Dep. Agric. Handbook 436, 503 pp.
- Song, X. 1997. Relationships between coarse woody debris and understory vegetation in six forest ecosystems in British Columbia. M.S. Thesis, Faculty of Forestry, University of B.C., Vancouver, B.C. 109 p.
- Soos, J., and Walters, J. 1963. Some factors affecting the mortality of western hemlock and western red cedar germinates and seedlings. University of B.C. Fac. For. Res. Pap. 56.
- Wang, G. G., H. Qiang, and K. Klinka. 1994. Growth of *Thuja plicata* seedlings along a light gradient. Can. J. Bot. 72: 1749-1757.
- Wilkinson, L. 1986. SYSTAT. The system for statistics. SYSTAT Inc., Evanston, Illinois.
- Yearsley, H. K. 1993. Forest floor seed banks and their response to slashburning in some forest ecosystems in south central British Columbia. M. Sc. Thesis, Faculty of Forestry, University of B. C., Vancouver. B. C. 136 p.

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