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FOREST RENEWAL BC

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UNPUBLISHED REPORT

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Project Title: Disturbance Impacts on Key Processes in High Elevation Forests:
A Multiscale Approach
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Abstract

This project examined the interrelationships among natural disturbances and the associated mortality/renewal responses in trees and understory plant species diversity in subalpine forests of interior and coastal British Columbia. The research addressed both scientific and public sector concerns that future management strategies should more closely mimic natural processes.

The interior study was conducted in a 20,000 ha wilderness subalpine forest in southern Wells Gray Park. At the landscape scale, a low correlation between polygon attributes and physical terrain features indicated a weak linkage between historical disturbance patterns and topography. At the plant community scale, abiotic and disturbance variables explained relatively low percentages of total vegetation variation; greater variation was explained by soil chemistry pointing to the key role that soil properties play in subalpine forests. At the tree population scale, the size and age structures and radial growth rates of the two dominant species – *Picea engelmannii* and *Abies lasiocarpa* – were related to environment and disturbance conditions. The coastal study was conducted in *Tsuga mertensiana* - *Abies amabilis* dominated forests at four geographic locations: Mt. Cain, Tetrahedron Park, Cypress Provincial Park, and Lizzie Lake/Cerise Creek in Garibaldi Provincial Park. Vegetation variation and tree growth were related to environmental conditions in 7 habitat-types: closed forest, avalanche edge forest, avalanche track non-forest, scree forest, scree non-forest, parkland tree islands, and parkland heath.

The results from this project provide a valuable baseline for identifying, solving, and anticipating problems in high elevation forest renewal and biodiversity management. Benefits include improvements to the classification of high elevation plant communities, greater understanding of the quantitative linkages between forest vegetation, environmental factors, and natural disturbances, and the education and training of post-secondary students who will acquire the responsibilities for managing British Columbia's forests in the 21st century.

INTRODUCTION

Throughout this report, reference is made to the following four manuscripts that contain the major results of the project. The manuscripts are in preparation for publication in scientific journals and are referred to in the text by Roman numerals:

I Zhang, W., and G. Bradfield. Forest polygon features and topographic attributes of a subalpine landscape in Wells Gray Park, British Columbia, Canada.
II Bradfield, G., W. Zhang, and A. Arsenault. Multiscale study of a subalpine fir-spruce forest landscape in eastern-central British Columbia. 1. Plant community-environment relationships.
III Bradfield, G., and W. Zhang. Multiscale study of a subalpine fir-spruce forest landscape in eastern-central British Columbia. 2. Relationships of forest size and age structure to environmental factors.
IV Bradfield, G., and W. Zhang. Comparison of forest vegetation and tree growth at four subalpine sites in south-coastal British Columbia.

Concept and Rationale for the Research

Montane forests exhibit substantial differences from lowland forests in the nature and organization of biological diversity and natural disturbance regimes (Oosting and Reed 1952, Day 1972, Day and Monk 1974, Shea 1985, Kneeshaw and Burton 1997). In British Columbia, high elevation forests are more strongly influenced by storm, rockslide, and snow avalanche events, and less affected by fire and insects than lower elevation forests. Although vegetation descriptions and guidelines exist for classifying forest ecosystems according to the provincial biogeoclimatic system (Lloyd et al. 1990, Pojar et al. 1991), little is known about the role and importance of environmental variables in promoting and maintaining biological diversity within the various ecosystem units over a range of spatial and temporal scales.

A subalpine forest landscape is a complex mosaic of structural and compositional patches at different scales. Physical terrain conditions and disturbance influence the landscape patterns at all spatial scales, but the relative importance of the variables may differ from one scale to another (Gosz and Sharpe 1989). The resulting patterns are commonly shown as polygons on forest cover maps. At a landscape scale, ecological questions may relate to the types, sizes, and distribution of polygons in relation to landform and disturbance; alternatively, questions may be asked relating to the structure and dynamics of vegetation within polygons. These two approaches are complimentary in that each may identify process affecting the other. For example, a juxtaposition of different polygon types may be maintained by disturbances such as fire, rockslides, or avalanches. In general, the linkage between vegetation variation and polygon attributes has not been quantitatively addressed.

At "meso" spatial scales, forest vegetation patterns are largely determined by environmental conditions related to soil and topography, and to the influence of the prevailing disturbance regime (White 1979, Glenn-Lewin and van der Maarel 1992, Lertzman et al. 1996). There is a long tradition in community ecology of analyzing the correlations and interactions among environmental variables to gain insight into the underlying factors controlling vegetation variation. For a given forest landscape, a thorough analysis of vegetation patterns in relation to environmental conditions, including natural disturbance, is prerequisite to understanding the nature of the interactions occurring, and to implementing ecologically based options for management.

At the tree population scale, important ecological questions relate to the growth patterns and population size/age structures of species in relation to biotic and abiotic environmental conditions. In western North America, subalpine forest ecology has long focused on coexistence mechanisms of the two dominant tree species, *Abies lasiocarpa* (subalpine fir) and *Picea engelmannii* (Engelmann spruce) (Hanson 1940, Stahelin 1943, Baker 1949, Oosting and Reed 1952, Day 1972, Krajina et al. 1982, Shea 1985, Eastham and Jull 1999, Huggard et al. 1999). Quantitative studies of overall population size/age structures and coexistence patterns in relation to different environmental variables are, however, lacking.

Objectives

In this project, the structure, composition, and dynamics of subalpine forests within two biogeoclimatic zones of British Columbia (interior ESSF, and coastal MH) were studied in relation to physical terrain conditions and natural disturbances. As the nature of subalpine forest ecosystems and disturbance regimes changes considerably between interior and coastal regions, different approaches were taken in the two geographic locations. In the interior (manuscripts I, II, III), studies were done at three different scales in a 20,000 ha wilderness area of montane/subalpine forest (>1300m elevation) in Wells Gray Park. At the landscape scale (I), the general objective was to quantitatively characterize the linkages among polygon features, physical terrain conditions, natural disturbances, and vegetation variation. At the "meso" scale (II), the objective was to quantify the importance of environmental factors in explaining variation in species composition within major vegetation groups and elevation zones. At the population level (III), the quantitative relationships between population size/age structures and growth responses of the dominant subalpine tree species were examined in relation to environmental conditions.

In the coastal region (IV), the intervals between large scale disturbances in high elevation forests are much longer than in the interior (MacKinnon and Trofymow 1998). Alternatively, disturbance and recovery processes operating on smaller spatial and temporal scales have been recognized (Lertzman et al. 1996). In addition to gap-phase dynamics, other landscape processes operating at larger spatial and temporal scales also play important roles in the structure and dynamics of high elevation forests in coastal British Columbia. Near treeline, "parkland" forest consisting of small islands of trees scattered in a heterogeneous landscape indicates that conditions are becoming too harsh for trees to establish (Brett and Klinka 1998). Natural disturbances from avalanches and rockslides also have significant impacts on vegetation patterns and tree growth at high elevation sites. Despite the prevalence of various types of natural disturbances in coastal forests (e.g. avalanches, rockslides), data are lacking on their effects on species composition and forest growth patterns. Therefore, this study was designed to investigate the variation in species composition and forest structure in habitats associated with subalpine parkland, avalanche, and rockslide affected sites at four locations in south-coastal British Columbia. In particular, the study focussed on the influence of type of habitat and geographic location on the growth and population/size structure of the two dominant high elevation tree species, *Abies amabilis* (Pacific silver fir) and *Tsuga mertensiana* (mountain hemlock).

METHODS

Study Areas

The study area in the British Columbia interior (I, II, III) was a 20,000 ha portion of southern Wells Gray Park (Fig.1). The area consists of a broad, mountainous plateau with steep sided valleys. At approximately 1300m a.s.l., the upper montane forests grade into subapline forests dominated by *Picea engelmannii* and *Abies lasiocarpa*. Whereas *P. engelmannii* is less common but attains larger sizes, *A. lasiocarpa* is more abundant in the canopy and understory layers. At approximately 2100m a.s.l., forests are replaced by subapline meadows, with talus and rock outcrop becoming the dominant landscape feature above ca 2300m. Throughout the study area, the forests have experienced a variety of natural disturbances: lighting strikes at high elevations cause numerous small fires every year; avalanche tracks and rockslides resulting from bedrock fracturing are common features on steep terrain; frequent windstorms cause uprooting and snapping of large trees. A large portion of the lower elevation transitional forest is regenerating from an extensive wildfire in 1926. A number of smaller fires during the 1950s affected parts of the mid-elevation subalpine forests.

In the coast region (IV), four geographic locations in south-coastal British Columbia were selected for study: Mt. Cain (50°13'N, 126°18'W), Tetrahedron Park (49°37'N, 123°37'W), Cypress Provincial Park (49°25'N, 123°12'W), and Lizzie Lake (50°08'N, 122°23'W) - Cerise Creek (50°20'N, 122°25'W) in Garibaldi Provincial Park (Fig. 1). Elevation ranges sampled at the four locations were 1140m to 1610m (Mt. Cain), 1105m to 1610m (Tetrahedron), 1080m to 1320m (Cypress), and 1320 to 1720m (Lizzie Lake - Cerise Creek). The dominant tree species at all locations were *Tsuga mertensiana* and *Abies amabilis*, with other species including *Thuja plicata* (western redcedar), *Tsuga heterophylla* (western hemlock), and *Chamaecyparis nootkatensis* (Alaska yellow cedar) also present but in lesser amounts. All locations fall within the Mountain Hemlock (MH) biogeoclimatic zone, except that the Lizzie Lake/Cerise Creek location occurs in the transition to the Engelmann Spruce-Subalpine Fir (ESSF) zone, where *P. engelmannii* and *A. lasiocarpa* attain greater importance (Pojar et al. 1991).

Sampling

Data collection on landscape polygons (I)

Following the general approach outlined by the Ecosystems Working Group (1995), polygons were mapped onto 1:15,000 aerial photos (1992) covering an extensive portion of the study area in southern Wells Gray Park. Each polygon identifies an ecosystem unit of relatively homogeneous vegetation structure, topography, and soil features. Sixty-eight center points were systematically distributed at roughly 8cm intervals across the aerial photos. Two sizes of concentric circular plots, 3cm and 5cm in diameter on the aerial photos (corresponding to ca. 450m and 750m on the ground), were used for recording data on polygon features and terrain conditions. The two plot sizes allowed for testing effects of "size of observation window" on the assessment of landscape complexity. Polygon features recorded in each plot included types of polygons contained, relative coverage of each type, boundary types (Rescia et al. 1997), and length of each boundary type. Nine indices of polygon diversity and complexity were calculated based on the measured variables. In total, 15 variables (both measured and derived) were used for characterizing polygon features.

A corresponding data set with information on physical terrain features and natural disturbances was also assembled for the aerial photo plots. Physical terrain features were measured from topographic (TRIM) maps at 1:20,000 and 1:10,000 scales. Derived indeces of "aspect favourability" and "slope favourability" (Beers et. al. 1966), area-weighted according to the terrain conditions in each plot, were calculated to examine effects of potential solar radiation on polygon attributes. Information on natural disturbance was obtained from ground vegetation plots sampled within polygons (see next section), or from aerial photo interpretation.

Forest vegetation sampling (II, III, IV)

During the 1995/96 field seasons in Wells Gray Park (II, III), 134 forest vegetation plots spanning a broad range of topographic and natural disturbance conditions were sampled at 21 site locations. Sites were selected to include a broad coverage of forest and natural disturbance conditions within the study area. Depending on the variation present at each site, 2-9 circular plots, each 20m in diameter, were pseudo-randomly selected for vegetation sampling. An additional 70 vegetation plots were sampled in 1997 to augment the information available for interpreting polygon types.

During the 1997/98 field seasons in coastal British Columbia (IV), 143 vegetation plots were sampled within 7 types of habitats recognized in the field: closed subalpine forest, avalanche edge forest, avalanche track non-forest, scree forest, scree non-forest, parkland tree islands, and parkland heath. Within each habitat-type recognized, plots were subjectively located to cover the major features of vegetation variation. Circular plots (20m diam.) were used for sampling forest vegetation; non-forest vegetation was sampled using reduced plot sizes of 4m x 4m, or 2m x 2m, depending on plant size and vegetation heterogeneity.

An initial topographic and physiognomic description for each plot was made including information on elevation, slope, aspect, mesoposition, percentage cover and height of canopy trees, intermediate trees, saplings, shrubs, seedlings, herb, moss, litter, and other ground surface features. Disturbances were qualitatively noted by type as fire, windthrow, rockslide (i.e scree) and avalanche. Fire evidence noted included fire scars on fallen logs and trees, and the occurrence of charcoal on the ground and in the soil. Soil pits were described in alternate plots in the Wells Gray study area (II, III), and in each of the coastal plots (IV). A detailed soil chemical analysis (forest floor and upper mineral horizons) was undertaken for 44 plots in the transition zone from upper montane to lower subalpine forests in Wells Gray Park (III).

Percentage cover of all understory herbaceous species and tree seedlings were estimated within plots. Tree stems >10cm DBH were recorded by species and DBH. For dead stems, the stage of decomposition and extent of top breakage also were recorded. Saplings (<10 cm DBH) were enumerated by species in two DBH size classes: 1-5cm, and 5-10cm. As with trees, separate tallies were recorded for living and dead saplings. Adjusted percent coverage values of tree species in plots were calculated by multiplying the relative importance values by the total percent canopy cover of all trees in each plot.

Measurement of tree population age structure and growth responses

Increment cores were obtained from trees of each species selected without bias within fixed size classes in each plot. The size classes were 20cm DBH intervals from 10cm up to 110cm; trees >110cm DBH were sampled as a single group. Cores were taken as close as possible to the tree base to account for the slow growth rates in subalpine forests. Two-centimeter thickness cross section disks (two disks per species) were cut at ground level within each size class (1-5cm, 5-10cm) of saplings. Cores and cross section disks were collected separately for living and dead stems. Ages were determined by visually counting annual rings under a dissecting microscope. Also recorded were synchronous growth events in the patterns of annual rings (e.g. narrow and wide rings, suppression and release events).

In Wells Gray Park (III), a total of 913 tree increment cores and 909 saplings disks were obtained, representing 9% and 21% of all saplings and trees recorded in all plots. In the coastal study area (IV), a total of 976 cores and 550 disks were collected.

Data analysis

Polygon heterogeneity and relationships to landscape features (I)

The aerial photo plot data sets containing measurements on the polygon attributes (15 variables) and the corresponding topographic/disturbance features (23 variables) were analysed separately with Principal Component Analysis (PCA). In each case, PCA of a correlation matrix was performed because of the mixed measurement scales of the original variables. The first PCA axis of each data set was used as the major factor which accounted for most of the variance among the variables. Within-set and between-set correlations of variables with the first PCA axis of each data set were used to evaluate the degree of linkage between polygon and landscape features.

Three main polygon-types that occurred widely throughout the Wells Gray study area (FA, FR, and FV) were analysed for relationships between vegetation heterogeneity, stage of forest development, and environmental conditions. Vegetation data sets for the polygons were assembled by grouping together ground vegetation plots that were representative of the polygons. Polygon-type FA is subalpine forest with *Menziesia ferruginea* as the dominant understory species, and was represented by four forest development stages: FA4 (sapling), FA5 (young), FA6 (mature), and FA7 (old). Polygon-type FR is subalpine forest with *Rhododendron albiflorum* as the dominant understory species; two developmental stages, FR6 (mature) and FR7 (old), were common in the study area and were analysed separately. Polygon-type FV contains young and old subalpine forest with *Valeriana sitchensis* as the understory character species. The use of single and multiple stages of vegetation development in the polygon analyses enabled the effect of time on compositional variation to be determined.

Within-polygon habitat variability (i.e. beta diversity) was estimated by the degree of species compositional turnover (scaled in standard deviation units) along the first axis of a Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980, Økland 1986; Beckéus 1993; Zhang 1998). The DCAs were run using the program CANOCO (ter Braak 1987, 1990). Vegetation-environment relationships within polygons were analyzed to determine: 1) the importance of individual environmental and disturbance variables in accounting for the observed variation in species composition, and 2) categories of environmental and disturbance variables (including stages of forest development) that best explain species variation.

Multivariate analysis of vegetation variation (II, IV)

The major vegetation-types in the Wells Gray study (II) were determined using the polythetic-divisive classification technique, TWINSPAN (Hill 1979). In assessing the nature and strength of the vegetation-environment relationships, both the effects of changing the sampling scale on the results, as well as the linkages of species composition to abiotic and biotic environmental factors were examined. The effects of sampling scale were examined by analyzing vegetation-environment relationships within three data sets of differing size: the full data set (n=134, "all plots"); a sub-set comprised of only those plots from continuous subalpine forest (n=59, "mid-elevation plots"); a sub-set with only those plots from upper-montane to lower-subalpine transition forests for which soil chemistry data were available (n=43, "soil plots"). Within each data set, the relationships between species composition and the abiotic and biotic variables were analysed using the program package CANOCO.

Graphical summaries (i.e. ordination scatter plots) of the main relationships between vegetation variation and environmental variables were produced for the Wells Gray (II) and coastal study areas (IV). In the relatively confined Wells Gray study area, DCA was used to summarize overall variation in the species cover data, with environmental variables included in a subsequent step by regression analysis on the DCA axes. In the more geographically diverse coastal study area, Canonical Correspondence Analysis (CCA, ter Braak 1986) was used to assess vegetation-environment relationships. In this case, geographic location was used as a covariable in CCA in order to avoid the influence of unique, location specific effects on the assessment of vegetation variation. As well, only those abiotic variables determined to be significant from forward selection analysis were used "actively" in the CCA; biotic variables were included "passively" by means of a subsequent regression analysis on the CCA axes. This method ensured that the ordination results displayed the primary influence of abiotic factors on patterns of variation in species composition.

Forest structure and tree growth in relation to environment (III, IV)

Relationships between stand age (determined as the oldest tree sampled in a plot), average radial growth rates, and environmental variables were examined using Pearson correlations (III). Average radial growth rates of trees were determined as the average width of annual growth rings. For the two major tree species in the coastal data (*A. amabilis* and *T. mertensiana*), relationships between growth rates and habitat-types were examined using Analysis of Covariance (ANCOVA) with DBH as a covariable in the analysis (IV). This method enabled direct comparison of differences in growth rates between tree species in the same habitat-type, and for the same species in different habitat-types.

Linear regressions of tree age on DBH were run for different species in plots grouped by vegetation types in Wells Gray Park (III). In the coastal study (IV), age vs DBH regressions were performed for trees grouped by the different habitat-types recognized. Where necessary, data transformation was applied to the DBH measurements to equalize the residuals (IV), or to correct error variances (III).

Three size structure data sets were compiled for the Wells Gray study, one for all tree species combined, and one each for *A. lasiocarpa* and *P. engelmannii* (III). The importance of environmental variables, singly and in eight groups (e.g. topography, disturbance, surface features, etc.), in explaining variation in forest structure was examined by forward selection in CANOCO. The analyses were performed using the data on living tree stem densities within 20cm DBH intervals.

RESULTS

Forest polygon features in relation to physical terrain and disturbance (I)

Of the total of 203 polygon types identified in the aerial photo plots, 89% occurred with low frequency (<10%) and low total coverage (48%) across the landscape. The most common polygon types were FR, FV, and FA, collectively covering nearly 49% of the total area sampled. The highest number of polygon types recorded per plot was 18 for the large plots, and 10 for the small plots. Polygon boundary types and total boundary lengths varied greatly among plots; however, the indeces of overall polygon structural diversity showed relatively low variation among plots.

No significant correlations were detected between the first PCA axis of the polygon attributes and the individual physical terrain variables. Moreover, the first PCA axes from the two data sets also were uncorrelated. These results suggest that the major factors determining polygon complexity are not related to topographic features in the Wells Gray Park study area.

Beta-diversity (i.e. degree of species compositional change) within five main polygon types ranged from 3.1 to 4.3 standard deviation units (Table 1). The old growth forest polygon type (FR7) had the lowest beta diversity. The young forest polygon type (FR45) and the types with multiple structural stages (FA and FV) had higher beta-diversity, suggesting that vegetation heterogeneity declines with time. Total variation in the species data explained by significant environmental variables was highest in the young forest polygon types (e.g. 55% for FR45), and lowest (19%) in the old forest polygon type (FR7). These results suggested that the direct influence of environmental variables on species composition declines as forests mature.

The total variance in species composition explained by forest structure variables was less than 30% (Table 2). Variance explained was higher in the FA and FR polygon types (22-29%) than in the FV type (12%). Among the individual structural variables, canopy height and coverage of shrub and herb layers explained the highest amounts (5-20%) of variation in all types.

Forest vegetation-environment relationships (II, IV)

In Wells Gray Park, 11 community-types were derived from the TWINSPAN classification of plots. In the first division of TWINSPAN, the high and middle elevation *Abies - Picea* forests (community-types 1 to 7) were separated from the lower elevation, montane-subalpine transition forests with greater presence of *Pinus contorta* (lodgepole pine; community-types 8 to 11). A DCA ordination showing the extent to which the TWINSPAN community-types are related to variation in several common species and significant environment and disturbance factors is given in Fig. 2. The regression of selected environmental variables on the DCA axes showed that elevation and degree of fire disturbance were oppositely correlated with axis 1. Axis 2 was mainly related to solar radiation (expressed as heat index), and degree of disturbance from rockslides and windthrow. In general, most community-types were tightly clustered within the DCA, although community-types 1, 3, and 6 showed higher variation along the second axis indicating greater heterogeneity related to disturbance within those types. In the CCA of the coastal data (IV), vegetation varied continuously from closed forest to avalanche and scree meadows, with considerable overlap in species composition among the different habitat-types (Fig. 3). The main abiotic gradients related to the vegetation patterns were LFH depth and soil moisture (both increasing into closed forest), and elevation (increasing into the meadows).

Explanatory power of environmental variables (II, IV)

The total variance in species composition explained by topography in the three groups of plots in the Wells Gray study (II) was greater than that explained by disturbance and surface features (Table 3). The total variance explained by individual abiotic variables was generally low (<5%); only elevation and fire presence attained significance in all three groups of plots. In the group of soil plots, the chemistry of organic and mineral horizons explained substantially greater vegetation variation (73%) than any of the other abiotic variables tested. Biotic variables were generally more successful than abiotic variables (except for soil chemistry) in accounting for compositional variation. Among the biotic variables, shrub cover and maximum tree size in the sampling plots explained the greatest amount of variance in species composition indicating a combined effect of current and historical factors on species composition.

In the coastal study (IV), 35% of the total variance in the species data was cumulatively explained by 26 abiotic variables (Table 3). Geographic locations and topographic features each explained 8% of the total variance. Elevation, slope/aspect, soil moisture, and depth of soil organic horizons all showed significant relationships with species composition. Differences among habitat-types explained only 7% of the total variance in the species data, in agreement with the strong overlap among habitats in the CCA results (Fig. 3). Among the biotic variables, densities of snags, saplings, and small living trees explained a significant amount (16%, $p<0.05$) of the total variance in the species data indicating a link between mortality and recruitment processes and changes in species composition. Additional variance explained by canopy cover, total basal area, and maximum DBH was low.

Tree ages and environmental correlates of growth rates (III, IV)

Stand ages ranged from 64 to 398 years in the Wells Gray study area (III). As expected, the youngest stands occurred in the montane-subalpine transition zone (64-260 years) which had been partially burned in the extensive fire of 1926. Significant correlations with stand age were found for total tree basal area (Pearson $r=0.44$, $p<0.001$, $n=134$), and canopy height ($r=0.43$, $p<0.001$). A weak relation between DBH and age was apparent for both *A. lasiocarpa* and *P. engelmannii.*

Variation in average ring width was related to differences among species, stem sizes, and environmental conditions. On average, ring widths for *A. lasiocarpa* were narrower than for *P. engelmannii* up to 50cm DBH; for stems larger than 50cm DBH, *P. contorta* had the widest rings in all size class (III). For small to mid-size *A. lasiocarpa*, ring width was positively correlated with DBH and aspect favourability (Table 4) indicating that larger trees grow faster, possibly because of the competitive advantage gained for resources such as light and soil nutrients. Average ring width in small to mid-size *A. lasiocarpa* was negatively correlated to elevation and canopy cover, indicating that radial growth rate declines with increasing climatic severity and increasing shade. For small to mid-size *P. engelmannii*, positive correlations between average ring width and aspect favourability, fire disturbance, and shrub cover support the contention that *P. engelmannii* is favoured by disturbance.

In the coastal study (IV), significant but weak relationships between radial growth rates of trees and elevation were detected for *Abies amabilis* ($r = -0.02$, $p=0.05$) and *Tsuga mertensiana* ($r = -0.20$, $p < 0.001$). Correlations between average radial growth rates and slope and aspect (as summarized in the aspect favourability and heat indeces) were, however, non-significant. Using DBH as a covariable ($p<0.001$), radial growth rates differed between *A. amabilis* and *T. mertensiana* ($p<0.001$), and among the types of habitat recognized ($p<0.001$). Moreover, the interaction term between species and habitat-types also was marginally significant ($p<0.05$) indicating the dependence of growth rates on habitat conditions. Average radial growth rates were generally higher for *A. amabilis* than for *T. mertensiana.* For both species, average radial growth rates were significantly lower in parkland sites than in other types of habitats recognized. The average growth rate for *T. mertensiana* was lower ($p<0.001$) in closed forest than in avalanche edge and scree forest, indicating that trees may benefit from resources released from nearby disturbances. Relatively strong relationships ($r^2 > 0.5$) were detected by linear regression analysis between age and DBH for five tree species in coastal subalpine habitats; however, age variation generally increased with tree size.

Forest structure-environment relationships (III)

The variation in tree densities within a range of size classes in the Wells Gray plots that could be explained by groups of environmental variables is summarized in Table 5. The variance explained from forward selection across all environmental variables was lower in the "all plots" group (9-15%), than in the high-elevation (18-25%), mid-elevation (24-25%), and transition zone (30-44%) subgroups. Among the separate groups of environmental variables, disturbances, topographic features, site locations, and community-types accounted for up to 49% of the variation in densities of living trees. Lower amounts of variation were accounted for by surface features, snag densities, and densities of opposing species (i.e. fir versus spruce). In the combined group of all plots (n=134), the use of plant communities and site locations as explanatory variables accounted for the greatest amounts of forest structural variation (13-27%). Site location explained more structural variation than community-types in the mid and high-elevation zones.

DISCUSSION

Landscape scale polygon-environment relationships (I)

The first PCA axes of the polygon and physical terrain data sets were useful summary variables for comparing complex landscape features. The results suggest that, although strong correlations exist among individual variables within the two separate groups, correlations between groups are weak. Thus, to the extent that polygons represent landscape scale patterns of forest recovery following historical disturbances, there does not appear to be a straightforward relationship between natural disturbances and physical terrain.

The only significant relationship detected between polygons and terrain features was that between total polygon boundary length and the first PCA axis of the terrain data. The length of polygon boundaries is a function of the number and shapes of polygon patches on the landscape. Such boundaries are key features at the landscape scale, and have been linked to ecological processes influencing biotic and abiotic conditions that affect overall biodiversity (Forman and Godron 1988, Wiens et al. 1985, Holland et al. 1991, Metzger and Muller 1996, Rescia et al. 1997).

The effects of disturbance on patterns of polygon complexity depend, in part, on the pre-existing patterns (i.e. before the disturbance occurred), and on the extent of the disturbance (i.e. total area affected). For example, in a heterogeneous landscape, a large scale fire disturbance may decrease pattern complexity, whereas smaller scale disturbances may increase complexity in a relatively homogeneous landscape.

The polygon units in this study were delineated to represent dominant patterns of forest and landscape structure on 1:15,000 aerial photographs. As such, polygons can not be expected to reflect changes in understory vegetation where factors determining the distribution and abundance patterns of plant species are operating at much finer scales. Although elevation, slope, aspect, and forest structure all may contribute to the habitat requirements of understory plants, the results suggest that polygons are too coarse for use as indicators of variation in subalpine plant communities.

Forest vegetation-environment relationships (II, IV)

The results from the Wells Gray study indicate a moderate degree of correlation between vegetation patterns, site locations, and land form features (II). Elevation was the overriding "complex" environmental variable explaining variance in species composition and abundance patterns. At least three reasons may account for the low degree of vegetation variation explained by disturbance: (1) the main environmental variables to which plants are adapted vary independently of disturbance; (2) the primary measurement of disturbance used in this study (i.e. presence/absence) was not sensitive enough to detect fine scale disturbance responses of plants; (3) as disturbance has both spatial and temporal dimensions in its impact on vegetation, it tends to produce non-equilibrium states which are difficult to detect through analysis (Aplet et al. 1988). Further research along each of these avenues is called for before definitive management recommendations can be made about the role of disturbance in subalpine forests.

The major fire return intervals in wet, coastal subalpine forests are believed to be considerably longer than in drier, interior subalpine forests (IV). Assuming that stand age reflects the intervals between major disturbances, the increase in stand age from the coast/interior (MH/ESSF) transition sites at Lizzie Lake and Cerise Creek, towards the more oceanic sites at Mt. Cain and Tetrahedron, agrees with findings from other studies where geographical trends in forest age have been described (Lertzman and Krebs 1991). This study also demonstrated an inverse relationship between stand age and vegetation heterogeneity (DCA results, not shown here). Because of the confounding effects of stand age and distance from the coast, however, this pattern is open to more than one interpretation: it may reflect a developmental gradient whereby vegetation heterogeneity decreases with time; alternatively, it may reflect a lower degree of habitat heterogeneity in sites closer to the coast.

Variation in tree growth rates (III, IV)

Average radial growth rates of trees varied among species, individuals of different sizes, and environmental conditions. The faster growth of *P. engelmannii* than *A. lasiocarpa* in Wells Gray Park (III) agreed with the findings of Schmid and Hinds (1974), Peet (1981), and Shea (1985) in Colorado. In the coastal study (IV) the results suggested that *A. amabilis* grows faster than *T. mertensiana.* In many cases, trees exhibited their fastest radial growth at intermediate ages and sizes, possibly reflecting tradeoffs in resource allocation through different stages of development.

Considerable variation in growth rates of small trees was apparent in both interior and coastal study areas. Both *A. lasiocarpa* and *P. engelmannii* are reported to be shade tolerant species; however, the frequent occurrence of negative correlations (especially for small trees) between growth rate and canopy cover (or canopy height) suggested that both species could grow faster on sites receiving greater solar radiation.

In general, climatic suitability for tree growth gradually declines towards treeline in subalpine forests. Under closed forest conditions, growth rates of individual trees reflect the dynamics of neighbouring biotic and abiotic environments. For example, faster growth rates in saplings and small trees have been attributed to small scale disturbances from falling trees (Lertzman and Krebs 1991), and clearcuts (Brett and Klinka 1998).

In harsh environments at high elevations, tree growth rates are slow and individuals rarely attain large size. After fire, tree regeneration in subalpine forests is slower than in lower elevation forests (Hemstrom and Franklin 1982, Agee and Smith 1984).

Regression analysis indicated a weak linear relationship between age and DBH for *A. lasiocarpa* ($0.17 < r^2 < 0.23$) and for *P. engelmannii* ($0.03 < r^2 < 0.21$) (III). Other studies also have shown a significant but weak relationship between diameter and age (Steijlen and Zackrisson 1987, Johnson and Fryer 1989, Tappeiner et al. 1997). In a study of subalpine forests in Colorado, Shea (1985) suggested that height was a better predictor than radius (i.e. DBH) for tree age; however, r-square values remained low.

Variation in tree size structure in relation to disturbance (III)

Size structure variation in *P. engelmannii* was greater than in *A. lasiocarpa*, and was more strongly related to disturbances than to physical terrain conditions. Moreover, *P. engelmannii* had proportionally higher basal area than *A. lasiocarpa* in post-fire sites in the montane-subalpine transition zone, suggesting that fire disturbance would increase the dominance of *P. engelmannii.* These observations are consistent with the hypothesis that *P. engelmannii* is more sensitive to disturbance and, consequently, exhibits greater variety in size structure across the landscape.

The relationship between the size structure of forest trees and natural disturbances is widely recognized (Van Wagner 1978, Oliver 1981, Veblen et al. 1989). Regeneration processes are strongly influenced by forest overstory structure, including the occurrence of gaps. It is not only the frequency and intensity of disturbance, but also the type of disturbance that may affect tree size structure. Moreover, it is important to recognize that different types of disturbances may interact leading to changes in forest structure and composition that are difficult to predict (Veblen et al. 1994).

SUMMARY AND CONCLUSIONS

Objectives achieved by this project:

- Systematic inventory of subalpine forests at coastal (MH) and interior (ESSF) sites to evaluate effects of fire, wind, rockslide, and avalanche events as components of the overall natural disturbance regime.

- Quantification of variation in forest structure, plant species composition, and plant community diversity along gradients of site, topographic, and disturbance conditions.

- Evaluation of size/age structures and growth rates of subalpine tree species in relation to geographic locations, habitat-types, and components of the natural disturbance regime.

- Description of sampling and analytical methods useful for assessing ecosystem integrity in all regions of British Columbia.

Benefits resulting from this project:

i) Data sets

The field data sets collected during this project are included in electronic form with this report. In total, a complete record of vegetation, environmental, and natural disturbance conditions has been acquired for 353 plots spanning high elevation interior (ESSF), coast/interior transition (MH/ESSF), and coastal (MH) forests.

Interior (ESSF): This forest type has been sampled at 21 site locations in southern Wells Gray Park. Natural disturbance regimes sampled include windthrow, rockslide, fire, and avalanche. A total of 177 forest plots have been sampled including high elevation ICHmw3 (12 plots), ESSFwc2 (52 plots), ESSFvv (101 plots), and ESSFvv parkland (12 plots). A total of 26 plots in high elevation, non-forest vegetation have been sampled including ESSFvv meadow (24 plots), and ESSFvv avalanche shrub (2 plots).

Coast/interior (MH/ESSF) transition: This forest type has been sampled at two sites east of Lilooet Lake (Cerise Creek and Lizzie Lake). Natural disturbance regimes sampled include windthrow, avalanche, and rockslide. A total of 31 forest plots, and 12 non-forest plots (2 meadow, 10 avalanche) have been sampled.

Coast (MH): This forest type has been sampled on the southern mainland coast (Cypress Park, Tetrahedron Park), and on northern Vancouver Island (Mt. Cain Recreation Area). Natural disturbance regimes sampled include windthrow, rockslide, and avalanche. A total of 80 forest plots, and 27 meadow/shrub/heath plots have been sampled.

A total of 2022 increment cores and sapling disks from Wells Gray Park, and 1526 cores/disks from coast and coast/interior transition sites have been examined for age structure and suppression/release events in subalpine forests.

ii) Correspondence with Forest Renewal BC's investment priorities

The information gained in this project has direct application for restoring and maintaining the ecological integrity and environmental sustainability of montane and subalpine forests in coastal and interior British Columbia.

Specific benefits from the project include:

- The field data and research results are being used for revisions to "A guide to site identification and interpretation for the Kamloops Forest Region" (Lloyd et al. 1990). The data are also being applied in the development of management guidelines for high elevation rangelands in BC
- Collaboration with Mr. D. Williams (UCC, Kamloops) and Dr. Andre Arsenault (MOF, Kamloops) has resulted in a research display for public education at the Wells Gray Park Education and Research Centre
- Part of the results have been presented to forestry workers and government/university researchers in workshops at the University of Northern BC (Bradfield et al. 1998) and the University College of the Cariboo (Zhang and Bradfield 2000)

- Communication and liaison with BC Parks (Wells Gray, Cypress, Tetrahedron) about forest ecology and vegetation responses to natural disturbances at high elevation sites.
- Communication and liaison with government and university researchers at the Mt Cain Biodiversity Project, Vancouver Island.
- Education and training of post-secondary students: Lyn Baldwin (Ph.D. in progress), Shannon Hagerman (1997, 1999a,b), Jeannette Nagel (2000), Kella Sadler (1999, 2000), Patrick Williston (1998).

iii) Summary of research results

Wells Gray Study:

Landscape scale

- Polygon features recognized on aerial photos appear to be only weakly correlated with physical terrain conditions.
- Total length of polygon boundaries provides an estimate of polygon complexity and is the main variable related to physical terrain features.
- The impact of natural disturbances on polygon complexity depends on the extent of disturbance and on landscape conditions prior to disturbance.
- Vegetation heterogeneity within polygons is related to the stage of forest structural development and environmental conditions.
- The scale of polygon mapping is too coarse to depict variation in plant communities.

Community scale

- A vegetation classification using TWINSPAN resulted in eleven plant community-types falling into three main elevation zones. Community-types 1-3 represent the subalpine parkland zone (1850-2150m) characterized by high species richness and ground layer cover. Prominent species include *Cassiope mertensiana, Lupinus arcticus*, *Phyllodoce empetriformis*, and *Arnica latifolia.* Patchy disturbance from lightning strikes and rockfall is common. Types 4-7 represent the main forested zone (1650-1850m), with strong presence of the shrubs, *Rhododendron albiflorum*, *Menziesia ferruginea*, *Vaccinium membranaceum* and *Rubus pedatus*, and herbs, *Arnica latifolia*, *Streptopus roseus* and *Gymnocarpium dryopteris.* A variety of types of natural disturbances occur throughout this zone. Types 8-11 represent the transition zone from ESSF to ICH forests (1350-1500m). Most plots were recovering from fires 40-70 years ago and contained greater amounts of *Pinus contorta*, *Populus tremuloides*, and *Pseudotsuga menziesii.* Common understory species include *Alnus viridis*, *Shepherdia canadensis* and *Spirea betulifolia.*
- Percentages of total vegetation variation accounted for by explanatory variables were: 21-44% (TWINSPAN classification), 17-34% (topography), 41-48% (chemistry of organic and mineral soil horizons), 27-58% (forest structure), and 11-19% (natural disturbances).

Population scale

- Sapling ages varied up to 226 years for *A. lasiocarpa,* and 267 years for *P. engelmannii.*
- *Abies lasiocarpa* showed a bell shaped distribution of sapling ages with a peak in the 60-90 year range indicating that conditions for subalipine fir establishment were more favourable in the early 1900's than at the end of the century. *Picea engelmannii* showed a reverse-J distribution of saplings indicating continuous active recruitment.
- Stand ages (determined from the oldest tree in a plot) varied from 64 to 260 years in the transition zone from upper montane to lower subalpine forest. Stand ages in the main zone of subalpine forest varied from 146 to 398 years.
- The relationship between tree DBH and age was weak. Comparison of predicted and measured tree ages yielded only 65% accuracy within 20 year error class limits.
- *A. lasiocarpa* showed bell-shaped distributions of tree ages, with most trees occurring in the 60 to 120 year age range. *P. engelmannii* exhibited mainly reverse-J age distributions of trees.
- Average width of growth rings in *A. lasiocarpa* was positively correlated with DBH, aspect favourability, and shrub cover, and negatively correlated with elevation and canopy cover. In *P. engelmannii,* average growth ring width was positively correlated with aspect favourablity, fire, canopy height, and shrub cover.

- Growth ring evidence for cycles of suppression/release events, and the occurrence of wide and narrow rings indicate that subalpine landscapes are highly variable and dynamic, and that trees show differing sensitivities to environmental conditions.
- *P. engelmannii* exhibited greater variation than *A. lasiocarpa* in size class structure, possibly resulting from greater sensitivity to natural disturbances. Groups of disturbance and topographic variables explained 10-40% of the variation in forest structure. Up to 50% of the structural variation could be explained by differences in site locations.

Coast Study:

Vegetation

- Vegetation variation increased and stand age decreased with increasing distance from the coast.
- 30% of the total variation in species composition could be explained by abiotic (geographic locations, disturbance type, topography, soil) and biotic (forest structure) variables.

Tree growth

- Tree ages varied up to 1047 years, and sapling ages up to 230 years.
- Radial growth rates varied with DBH, species, and type of habitat.
- Forests show a high potential for renewal following natural disturbance.
- *Tsuga mertensiana* and *Abies amabilis* show different regeneration responses to disturbance.

Comparison of Coast vs Interior

- Management of subalpine forests in coastal and interior British Columbia should take into account the important differences in species composition, climate, soils, and natural disturbance regimes.

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Table 1. Percentage of total variance in species composition explained by environmental variables within five main polygon types in Wells Gray Park. Polygon types contain one or more structural stages from young to old forest. Beta diversity denotes degree of vegetation heterogeneity within polygons as measured along the first axis from detrended correspondence analysis (DCA). Percentages of explained variance are shown for the environmental variables analysed separately (underlined values are significant, i.e. $p<0.05$ in Monte Carlo tests), and in three categories (A-C). Total variance explained by all variables in the three categories (A+B+C) was determined using forward selection (asterisks denote which variables were selected).

Polygon types	FA	FR45	FR6	FR7	FV
Number of plots	14	15	23	23	17
Number of structural stages	4	2	1	1	2
Beta diversity (s.d. units)	4.34	4.03	3.75	3.10	3.88
Total var. expl. (A+B+C)	46	55	44	19	40
A) Disturbances (%)	50	31	28	26	21
Windthrow	14*	12	5	6	6
Scree	5	0	0	3	0
Avalanche	14*	0	10*	6	0
Fire	13	12*	5	4	13*
Fire-degree	18	10	7	5	6
B) Topography (%)	28	32	34	31	23
Slope	10	9*	9	12	5
Heat-Index	12	10*	10*	10	4
Elevation	7	14*	15*	13*	12*
C) Soil and Surface features (%)	42	30	34	32	31
Boulders	15*	8*	8*	6	4*
Mineral Soil	5	9	9*	9	5
Surface H_2O	9	0	6	11*	13*
Outcrop	14*	7*	3	9	4
Depth of forest floor	7	9	8	3	7

Table 2. Percentage of total variance in species composition explained by forest structure variables within 5 main polygon types in Wells Gray Park. Underlined values are significant percentages of variation explained ($p<0.05$ from Monte Carlo permutation tests of the separate variables). Total variance explained was determined by forward selection across all variables (asterisks denote significant variables selected).

Polygon types	FA	FR45	FR6	FR7	FV
Total variance explained (%)	29	29	22	27	12
Canopy-height	14	15	6*	5	12*
Epiphyte abundance	11	12*	5	5	5
Canopy cover	7	10	5	6	7
Int–tree cover	4	9	5	7*	8
Saplings cover	7	10	6	7	6
Shrubs cover	15	16	16*	20*	7
Herbs cover	17*	16*	11	10	8
Moss	12*	11	4	6	8
Litter	9	8	5	5	6
Logs	5	4	5	4	5

Table 3. Percentage of total variance (inertia) in species data from Wells Gray Park and coastal study areas explained by categories of abiotic and biotic variables. Numbers of explanatory variables used in the different categories are shown in brackets beside the percentage values. Minimum data set refers to those variables chosen by forward selection as explaining significant levels ($p < 0.05$) of variation in the species data. Significance was determined by Monte Carlo permutation tests.

	Wells Gray Park			Coast
	All plots (n=134)	Mid-elevation (n=59)	Soil plots (n=43)	All plots (n=143)
Total inertia (s. d. units)	7.76	3.36	4.42	7.68
Abiotic variables	28 (22)	41 (22)	100 (42)	35 (26)
Locations				8 (3)
Habitats/ Disturbances	11 (6)	12 (6)	19 (6)	7 (6)
Topographic Features	17 (12)	26 (12)	34 (11)	8 (4)
Surface Features	6 (4)	7 (4)	16 (4)	3 (3)
Soil Conditions			73 (21)	7 (10)
Minimum Data Set	21 (10)	12 (4)	55 (12)	25 (15)
Biotic variables	29 (21)	48 (21)	58 (21)	29 (25)
Minimum Data Set	22 (11)	31 (8)	33 (6)	16 (7)

Table 4. Pearson correlations of average ring width on selected environmental variables for three size classes of *Abies lasiocarpa* (fir) and *Picea engelmanii* (spruce) in Wells Gray Park. Asterisks denote significant correlations (* p<0.05; ** p< 0.01). The three disturbance factors (fire, windthrow, and rockslide) were analyzed as binary variables.

Species		Fir			Spruce	
Size class (DBH cm)	< 10	10-29	≥30	< 10	10-29	≥30
DBH	0.32**	0.21**	0.16	0.40	0.26	-0.04
Elevation	-0.16**	-.19**	-0.03	-0.15	-.30**	-0.07
Aspect favourability	0.30**	0.27**	-0.02	0.41**	0.62**	-0.23*
Fire	0.11	0.04	-0.02	0.24**	0.31**	-0.24*
Windthrow	-0.08	-0.21**	-0.14	-0.16*	-.24*	0.04
Rockslide	-0.02	0.09	-0.02	-0.08	-0.08	0.12
Canopy height	-0.01	0.11	-0.16	-0.05	0.36**	0.07
Canopy cover	-0.24**	-.20**	0.05	-0.33**	-0.10	-0.09
Intermed. tree cover	-0.05	0.02	-0.22*	-0.11	-0.09	-0.06
Shrub cover	0.01	0.27**	-0.02	0.16*	0.25*	0.21*
Total no. observations	544	300	106	154	89	104

Table 5. Percentage of total variance (inertia) in tree densities within size classes explained by eight categories of environmental variables (A-H) for different data sets in Wells Gray Park. Densities within three size classes (i.e. DBH between 1-10 cm, 10-30 cm, and > 30 cm) were used as explanatory variables in groups F, G, and H. Explanatory variable types are indicated in brackets as b (binary), n (numeric). Total variance explained was determined by forward selection across all variables.

	All plots			High-elevation			Mid-elevation			Transition zone		
	All species	Fir	Spruce	All species	Fir	Spruce	All species	Fir	Spruce	All species	Fir	Spruce
No. plots	134	134	120	50	50	40	59	59	55	25.	25	25
Total inertia (s.d.)	0.434	0.437	3.34	0.326	0.354	3.049	0.433	0.356	2.67	0.338	0.439	1.318
A. Disturbances (b)	9	7	12	14	20	18	14	11	19	35	32	45
B. Topographic factors (n)	7	10	7	12	11	14	21	22	16	38	25	22
C. Surface features (n)	5	2	4	9	6	9	5	6	8	30	9	39
D. Site locations, 21 variables (b)	25	27	26	28	8	34	48	17	49	27	16	33
E. Community types,11 variables (b)	21	18	13	12	8	10	16	14	12	30	46	8
F. Snags density, 3 variables (n)	5	5	6	6	10	6	9	6	11	18	17	25
G. Fir density, 3 variables (n)			9			12			14			31
H. Spruce density, 3 variables (n)		9			14			17			18	
Total var. expl. (%)	13.8 (6 var.)	9.15 (4 var.)	15.3 (6 var.)	18.4 (4 var.)	25.4 (6 var.)	22.9 (6 var.)	24.4 (4 var.)	24.7 (4 var.)	25.0 (4 var.)	43.5 (4 var.)	30.5 (2 var.)	37.3 (3 var.)

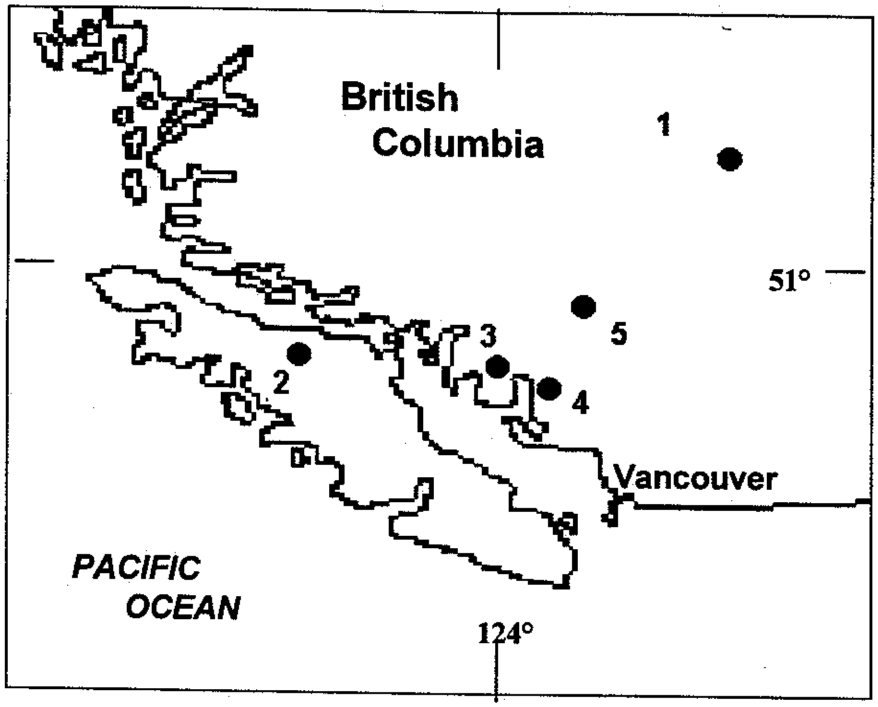

Fig. 1. Study area locations for subalpine forest research in southern British Columbia: Wells Gray Park (1); Mt. Cain Recreation Area (2); Tetrahedron Park (3); Cypress Provincial Park (4); Lizzie lake / Cerise Creek (5).

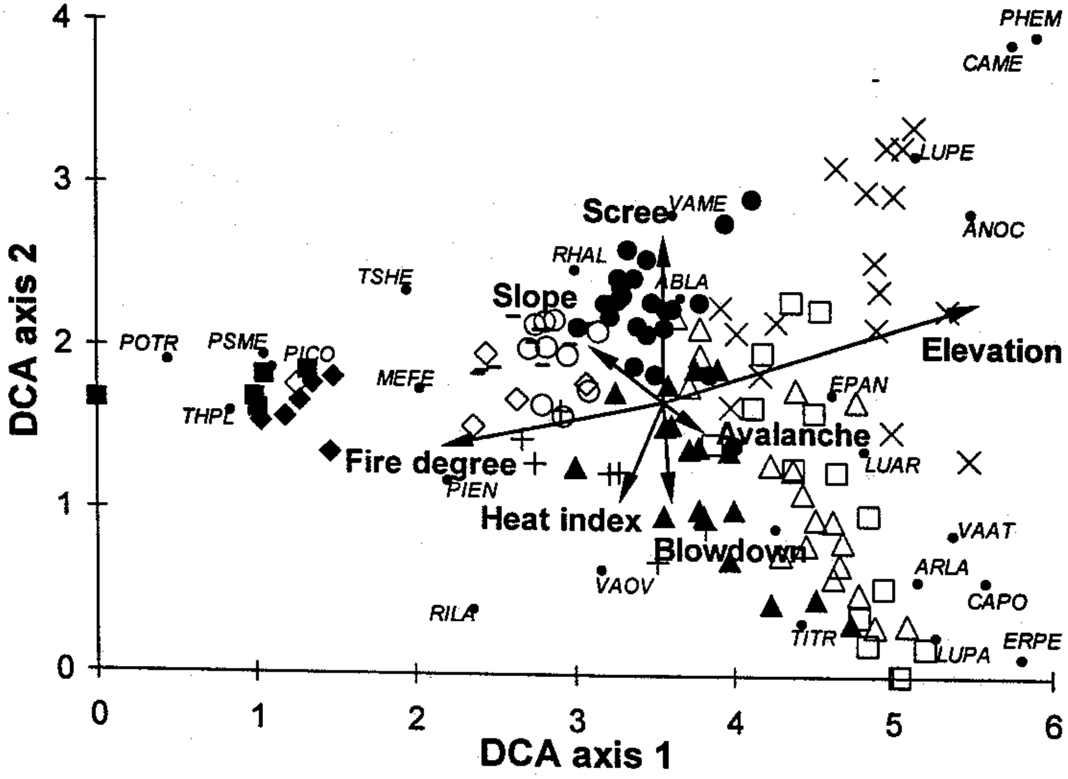

Fig. 2. DCA triplot showing relationships between eleven plant community-types from TWINSPAN and the major environmental and disturbance gradients in Wells Gray Park. Selected species are indicated by four letter code names (full species names are listed in file WellsGray\spcodlst.doc). Plots are denoted by symbols representing plant community-types: 1=×, 2=□, 3=Δ, 4=●, 5=O, 6=▲, 7=+, 8=–, 9=◇, 10=◆, 11=■. Selected environmental variables are indicated with arrows showing direction and strength of regression with the DCA ordination axes.

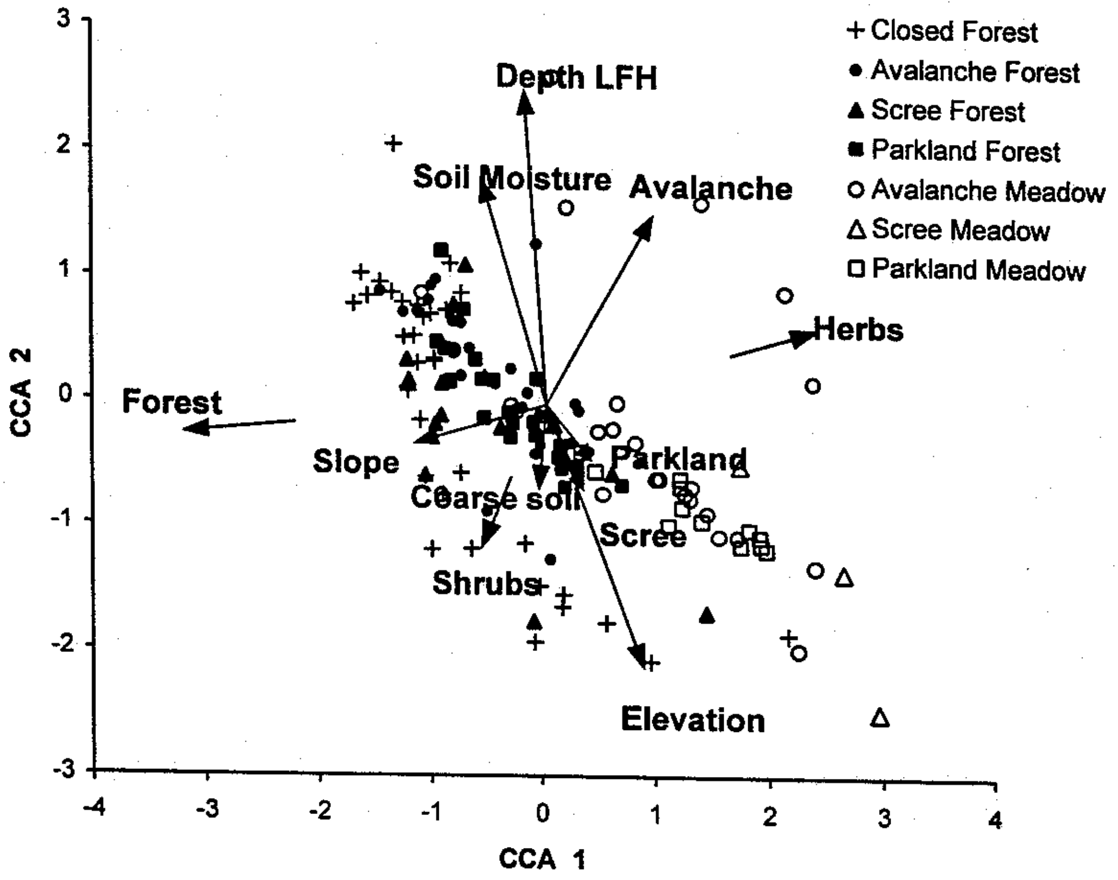

Fig. 3. Canonical Correspondence Analysis (CCA) of 143 plots for the coastal study area. Geographic locations were used as covariables in the analysis. Symbols denote different types of habitat recognized. Long vectors represent abiotic environmental variables included "actively" in the CCA. Short vectors denote biotic variables included "passively" by regression on the CCA axes