WHITEBARK PINE FORESTS IN BRITISH COLUMBIA: COMPOSITION, DYNAMICS AND THE EFFECTS OF BLISTER RUST

by

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ABSTRACT

The composition, structure and dynamics of forests containing whitebark pine (*Pinus albicaulis* Engel.) were investigated in 53 stands in British Columbia. Mountain pine beetle (*Dendroctonus ponderosae*) and white pine blister rust (*Cronartium ribicola*) distribution among stands and incidence (percentage of affected trees) within stands were also examined.

Variation in understory composition among stands was analyzed using non-metric multi-dimensional scaling. Compositional changes were strongly correlated with soil moisture, slope, elevation and longitude. UPGMA agglomerative clustering techniques were used to delineate 11 plot groups representing communities with understories dominated by: *Vaccinium membranaceum* (Groups A and B); *Rhododendron albiflorum/Menziesia ferruginea/Vaccinium membranaceum* (Group C); *Vaccinium scoparium* (Groups D, G, and H); *Vaccinium myrtillus* (Group E); *Phyllodoce empetriformis* (Group F); *Xerophyllum tenax* (Group I); and *Juniperus communis* (Groups J and K). Analogous communities are reported in the literature for Alberta and the United States. Whitebark pine was most abundant in *Juniperus communis* communities, in young stands, and at southern latitudes.

White pine blister occurred throughout the geographic range of whitebark pine in British Columbia. It was found in at least 37 of the 53 stands sampled but probably occurred in 52 stands. The incidence of white pine blister rust infections ranged from 0-100% among stands. Only 7 of the 53 stands sampled had mountain pine beetle infestations and incidence of infestation in these stands was low (< 1% of trees). Whitebark pine mortality rates ranged from 0-64% over all stands. ANOVA and simple linear regression were used to elucidate patterns in white pine blister rust incidence and mortality. Variation in white pine blister rust incidence or mortality among stands could not be related to variations in regional climatic conditions or other site characters such as soil moisture, aspect, and elevation. Factors influencing the interception of basidiospores by individual whitebark pine trees appeared more important. Incidence of infection was greatest in young, open stands and mortality was greatest in stands with low total tree density. Stands with *Ribes* present also had a greater incidence of infection. Large trees were more frequently infected than small trees but mortality was greatest among small trees.

Most recent fires in whitebark pine forests were stand-replacing, although some small trees survived fire. Whitebark pine, and sometimes lodgepole pine (*Pinus contorta*), established in abundance shortly after fire. Subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) also frequently colonized stands following fire but took longer to become abundant. The patterns of successional development following fire disturbance were influenced by the life history characteristics of each tree species, availability of seed sources, the nature of the disturbance, characteristics of the pre-disturbance vegetation, and characteristics of vegetation in the surrounding landscape. Forests containing whitebark pine developed along three major successional pathways; differences between the three pathways depended on the relative amounts of lodgepole pine establishing in post-fire stands (i.e., none, some, and abundant lodgepole pine).

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CHAPTER 1

INTRODUCTION

Pinus is the most well-studied and speciose genus of the family Pinaceae. Within the subgenus *Strobus* the section *Strobus* (i.e., white pines) is divided into two subsections: *Cembrae* and *Strobi* (Little and Critchfield 1969). The subsection *Cembrae* is comprised of five high-altitude, high-latitude species called stone pines. The seeds and cones of stone pines are uniquely adapted for dispersal by birds of the genus *Nucifraga*; the cones do not open at maturity and the seeds are large and wingless. These characters are the primary reason for the taxonomic segregation of these five species from other white pines. Whitebark pine (*Pinus albicaulis* Engelm.) is the only stone pine found in North America; all others occur in Europe and Asia. It is distributed over a large portion of western North America growing in subalpine habitats at or near the timberline.

Recent reports indicate a rapid decline in whitebark pine over large areas of the Rocky Mountains in the United States (Arno 1986; Keane and Arno 1993; Kendall and Arno 1990). This decline has been attributed to disease caused by the exotic white pine blister rust fungus (*Cronartium ribicola*); outbreaks of mountain pine beetle (*Dendroctonus ponderosae*); and, in the absence of fire disturbance, successional replacement of whitebark pine by more shade-tolerant subalpine fir (*Abies lasiocarpa*) and Engelmann spruce *(Picea engelmanii*) (Keane *et al.* 1990; Keane and Morgan 1994). White pine blister rust appears to be the most serious cause of the decline; mortality rates due to blister rust are as high as 90% in some areas of Montana (Keane and Arno 1993; Kendall *et al.* 1996).

White pine blister rust is a disease of five needle white pines (Millar and Kinloch 1991). Originating in Asia, it spread throughout Europe by the late 1800's (Wescott 1991). Between 1900 and 1915, white pine blister rust was introduced to eastern North America when infected eastern white pine (*Pinus strobus*) seedlings imported from Europe were widely planted in the northeastern United States. From several points of introduction, the disease spread rapidly throughout the range of eastern white pine (Van

Arsdel 1956). In 1910, white pine blister rust was inadvertently introduced to western North America near Vancouver, British Columbia on a shipment of infected eastern white pine nursery stock imported from France (Hoff and Hagel 1990). Within 25 years of its introduction, white pine blister rust expanded over most of the range of western white pine (*Pinus monticola*), limber pine (*Pinus flexilis*), and sugar pine (*Pinus lambertiana*). The widespread occurrence of blister rust throughout the range of whitebark pine is more recent (Arno 1986; Hoff *et al.* 1994; Keane and Arno 1993; Kendall and Arno 1990). The disease continues to spread throughout the northern range of whitebark pine and has also appeared in arid southern regions of the species range (Kendall and Arno 1990).

Similar to the outcomes of other introduced diseases such as Dutch elm disease on elms and the chestnut blight on the American chestnut tree, white pine blister rust has caused major losses of white pines in North America (Hoff 1990; Keane and Arno 1993; Lavallée 1974; Plourde *et al.* 1991). While diseases that evolve with their hosts are often relatively harmless to the populations they infect, the same diseases may have serious impacts on native species where the pathogen is newly introduced. Because the affected species are often unable to quickly evolve resistance to the disease, host populations can be drastically and rapidly reduced.

Periodic outbreaks of mountain pine beetle have killed many mature whitebark pine in the U.S. in the last century (Ciesla and Furniss 1975). Although mountain pine beetles are a major, natural mortality factor of whitebark pine, there is potential for increased mortality because of interactions with blister rust (Keane *et al.* 1990). Whitebark pine trees infected by blister rust are believed to be more susceptible than uninfected trees to attack by mountain pine beetle (Keane and Arno 1993).

Fire disturbance has a major influence on the structure and composition of forests (Arno 1980; Habeck and Mutch 1973; Romme 1982; Tande 1979). Native peoples used fire to manipulate vegetation for hunting and other purposes for centuries (Pyne 1982); but more recently, however, humans have greatly decreased the occurrence of forest fires by the suppression of both human and naturally caused fires. Fire suppression programs have become increasingly effective in southern British Columbia and Alberta and throughout the United States since the early 1900's (Arno 1980; Hawkes 1990). Fire disturbance plays a key role in the maintenance of whitebark pine populations over the landscape and the fire suppression programs of the last century have contributed to the recent rapid decline of whitebark pine (Keane and Arno 1993). One of the first tree species to establish in abundance following stand-replacing fires, whitebark pine may dominate stands for 225 years or more (Morgan and Bunting 1990; Morgan *et al.* 1994). When disturbance is infrequent, however, relatively shade-intolerant whitebark pine tend to be successionally replaced on moist, subalpine sites by more shade-tolerant and less fire-resistant subalpine fir and Engelmann spruce (Morgan *et al.* 1994). Keane and Arno (1993) indicate that fire suppression programs have caused a dramatic change in the subalpine landscape of Montana.

High-elevation forests are becoming an increasingly important source of wood products and the harvest of whitebark pine trees in subalpine forests of British Columbia has begun only in the last few years. However, whitebark pine is of little commercial value because large trees are infrequent in mature subalpine stands where logging occurs and because trees are often of small size at high elevations where the species is most abundant.

Whitebark pine is of considerable interest and value from an ecological point of view. Keane (1998) has suggested that whitebark pine acts as a "keystone" species in upper subalpine stands where it is abundant and that reduction or loss of this species would have major effects on ecosystem processes, stand characteristics and many wildlife species. Whitebark pine is an important ecosystem component for many reasons. Where it is abundant, the spreading root system of whitebark pine may play an important role in protecting watersheds by stabilizing soil and rock on steep sites. In addition to catching and retaining snow, whitebark pine trees may also buffer other species from extreme weather conditions such as high winds and growing season frosts. It is of great importance to bears, red squirrels, and nutcrackers. The relatively large, wingless seed is an important source of dietary fat for black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos horribilis*) prior to hibernation (Mattson and Jonkel 1990). Good seed crops are positively correlated with cub production and early weaning of young, whereas poor seed crops are associated with increased grizzly bear mortality and conflicts with humans (Mattson and Jonkel 1990). Red squirrels also consume the seeds for their high nutrient content, and they subsist on this food throughout the year by caching and storing seed cones. Annual fluctuations of red squirrel densities are a reflection of yearly whitebark pine cone production in stands with a large whitebark pine component (Reinhart and Mattson 1990). Bears typically obtain seed from squirrel caches and may play a role in regulating red squirrel abundance in whitebark pine stands. There is considerable evidence that Clark's nutcrackers (*Nucifraga columbiana*) and whitebark pines have co-evolved (Lanner 1980, 1982; Mattes 1994; Tomback 1982, 1990, 1994; Tomback and Lindhart 1990; Tomback *et al.* 1990); nutcrackers have both morphological (e.g., sublingual pouch and long pointed bill) and ethological adaptations (e.g., ability to test seed quality by seed colour and resonance) specifically for whitebark pine seed use (Mattes 1994). The large, indehiscent seed promotes animal dispersal and asynchronous cone development improves food supply for the animals. Whitebark pine seed is an important source of food for the Clark's nutcracker, which is the primary disperser of whitebark pine seed (Tomback 1990). The annual life cycle of the Clark's nutcracker (including breeding and moulting time) are adjusted to make best use of the whitebark pine seed source.

There is very little published information about whitebark pine in British Columbia. Thus, the general goal of this research is to accumulate baseline biological data on the structure, composition, and dynamics of whitebark pine communities and to determine the extent to which white pine blister rust and mountain pine beetle have damaged whitebark pine.

The objectives of this project are to:

1. obtain basic information about whitebark pine habitats including data on associated plants and the types of sites where whitebark pine is found;
2. examine how rates of white pine blister rust infection and mortality vary among stands over the geographic range of whitebark pine and relate this variation to site and stand characteristics;

3. document the geographic distribution and incidence of mountain pine beetle infestations in stands and relate variation in infestation rates among stands to site and stand characteristics;

4. examine whitebark pine stand dynamics including, size and age structure of tree populations, tree species recruitment, and successional changes in different whitebark pine habitats.

CHAPTER 2

The composition and structure of whitebark pine forests in British Columbia

Introduction

Understanding how species distributions and interspecific associations vary in space and time is a fundamental concern in community ecology. Regional climatic conditions (e.g., temperature and precipitation), local site characteristics (e.g., aspect, topographic position, soil chemistry), interspecific competition, and natural disturbance (at various temporal and spatial scales) all play an important role in controlling the distribution of individual species and thus the composition and structure of plant communities (Antos and Zobel 1986; Barton 1993; Bernard and Seischab 1995; Cox and Moore 1985; Grime 1977, 1979; Seddon 1971; Shoener 1988; Stohlgren and Bachand 1997; Tilman 1982, Ward *et al.* 1993).

The severity of environmental conditions in temperate, high-elevation ecosystems is the primary factor limiting the kinds of plants that can grow there (Tranquillini 1979; Wardle 1968, 1971). Low temperatures, strong winds, deep snow, and short growing seasons prevent the regeneration and establishment of many species (Allen and Peet 1990; Arno and Habeck 1972; Marchand 1987; Peet 1981; Richards and Bliss 1986; Stohlgren and Bachand 1997; Van Arsdel 1965). Many species of high-elevation habitats, especially those that occur close to or at the timberline, are considered stress-tolerators in the sense of Grime (1974, 1979), in that they possess morphological, physiological, and life history characteristics than enable them to occupy and persist in environments where many other species can not survive (e.g., del Moral 1979). High-elevation tree species such as *Larix lyallii* (Arno and Habeck 1972; Arno and Weaver 1990), *Chamaecyparis nootkatensis* (Antos and Zobel 1986), and *Pinus cembra* (Brzezieki and Keinast 1994) are all good examples of stress-tolerators.

Pinus albicaulis (whitebark pine) is a slow-growing tree of high-elevation habitats (Krajina *et al.* 1982; McCaughey and Schmidt 1990; Ogilvie 1990) and can also be considered a stress-tolerant species. Its distribution can be divided into an eastern and western portion (Critchfield and Little 1966). In the western portion of its range, whitebark pine grows south of 55°N on the leeward side and crests of the British Columbia Coast Mountains and through the Cascade Mountains to the Sierra Nevada of central California. In the eastern portion of its range, it grows on both the leeward and windward sides of the Rocky Mountains from 55°N in British Columbia south to northwestern Wyoming. Whitebark pine is also scattered on isolated peaks on the Interior Plateau of south-central British Columbia and in the mountains of Washington, eastern Oregon and northeastern Nevada (McCaughey and Schmidt 1990; Ogilvie 1990).

The altitudinal range of whitebark pine is related to the timberline, occurring at higher elevations in more continental, drier mountain ranges and in the southern mountain ranges (Ogilvie 1990). In much of the northern portion of its range in British Columbia, Alberta, and Washington, it grows from 1800-2400 m (Arno and Hoff 1989; Ogilvie 1990). It grows between 1700-2800 m in Oregon, between 1500-3000 m in Montana and Idaho, and in California between 2100-3300 m (Arno and Hoff 1989).

The climate where whitebark pine grows can generally be characterized as cold and harsh, often with heavy snowfall, extreme seasonal temperature changes, short growing seasons, and strong winds (Arno and Hoff 1989; Arno and Weaver 1990). Most precipitation comes in the form of snow from October to May (McCaughey and Schmidt 1990). In general, summer precipitation throughout the range of whitebark pine decreases southward (Arno and Weaver 1990; B.C. Ministry of Environment and B.C. Ministry of Forests, unpublished data, 1997, B.C. Min. Environ.Victoria, B.C.). Late summer drought is most common south of 47 °N (Arno and Hoff 1989) but also may occur in mountain ranges of southeastern British Columbia (Braumandl and Curran 1992; Ogilvie 1990) and Montana. Summers are short and cool with the growing season (i.e., number of days > 6°C) lasting about 90 to 100 days (Arno and Hoff 1989). Wind gusts of hurricane velocity (i.e., 117 km/h) occur each year on most whitebark pine sites but particularly on ridgetops (Arno and Hoff 1989).

Whitebark pine occurs over a wide range of site types (Ogilvie 1990; Arno and Hoff 1989; Arno and Weaver 1990). In wet regions (e.g., the Cascade and Coastal Mountains of British Columbia), whitebark pine is generally restricted to dry, southern slopes of upper subalpine and timberline sites (Arno and Weaver 1990), though Pojar (1978) and Yole *et al.* (1989) report that it occurs from valley bottoms to the timberline in the northernmost portions of its range in British Columbia. In the dry, continental mountain ranges of southeastern British Columbia, Montana, Wyoming, and Idaho, whitebark pine is often a major component of both subalpine and timberline forests and occurs over a wide range of local site conditions (Arno and Weaver 1990; Ogilvie 1990; Pfister *et al.* 1977; Steele *et al.* 1981, 1983).

Soils of whitebark pine habitats are often young with little horizon development (e.g., regosols and brunisols) but can also be deeper and more developed humo-ferric podzols (Arno and Hoff 1989; Braumandl and Curran 1992; Ogilvie 1990). Soil parent materials include bedrock at varying stages of weathering, colluvium, glacial-till (Ogilvie 1990) and also glacio-fluvial materials in the valley bottoms of the northern Coastal Mountains (Yole *et al.* 1989). Soil moisture on sites where whitebark pine grows varies from dry to wet and soil nutrient status varies from very rich (e.g., high in calcium and magnesium) to very poor (Angove and Bancroft 1983; Krajina 1969; Krajina *et al.* 1982; Yole *et al.* 1989). Although whitebark pine occurs on productive lower subalpine sites, it is usually competitively displaced by Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) (Arno and Weaver 1990; Keane *et al.* 1990, 1994, Weaver *et al.* 1990).

In accordance with its occurrence on a wide range of habitats, whitebark pine is associated with many subalpine and alpine plant species (Arno and Weaver 1990; Cole 1982; del Moral 1979; Forcella 1978; Franklin and Dyrness 1973; Ogilvie 1990; Pfister *et al.* 1977; Selby and Pitt 1984; Steele *et al.* 1981, 1983; Weaver and Dale 1974). In Idaho and Montana, it occurs in at least half of the forest types described in these states (Pfister *et al.*, 1977; Steele *et al.* 1983). Plant communities containing whitebark pine are best documented for Montana, Idaho, and Wyoming (Arno and Weaver 1990). Published descriptions of communities in other parts of the U.S., however, come from only a few areas (Agee and Curtis 1987; Cole 1982; del Moral 1979; Franklin and Dyrness 1973).

There is very little published data describing plant communities containing whitebark pine in Canada. Descriptions of these communities are included in general studies of high elevation vegetation and are based on data collected from a few locales in: the Rocky Mountains (Achuff 1989; Achuff *et al.* 1984a, b; Corns and Achuff 1982), the east Kootenay Mountains, and the Chilcotin Mountains of southwestern British Columbia

(Selby and Pitt 1984). Plant communities throughout the remainder of the range of whitebark pine in British Columbia have not been described in a quantitative manner, although some qualitative description exists (e.g., Ogilvie 1990).

Recent reports of the rapid decline of whitebark pine due to blister rust *(Cronartium ribicola)* and mountain pine beetle (*Dendroctonus ponderosae*) (Keane and Arno 1993), coupled with recent harvesting in whitebark pine habitats have emphasized the need for basic information about this species and the plant communities in which it occurs. The objectives of this chapter are to:

1. describe the species composition and structure of plant communities throughout the range of whitebark pine in British Columbia;
2. quantify the relationship between species composition of these communities and various environmental factors; and,
3. evaluate the factors controlling the distribution and abundance of whitebark pine in British Columbia.

Materials and Methods

Sampling Methods

During 1995 and 1996, 53 stands, distributed throughout the range of whitebark pine in British Columbia, were sampled (Figure 1). Stands were systematically selected to: (i) cover the geographic range of whitebark pine in British Columbia; and, (ii) include, in a given locale, the most common types of forests and sites where whitebark pine occurs. In general, stands were selected where whitebark pine was a dominant or co-dominant species, but this depended to some degree on the abundance and distribution of the species in a particular geographic area and the age of the stand sampled. Forest cover and topographic maps along with aerial photographs were used to locate stands.

To examine within stand variation in species composition and structure multiple sample plots were placed in most stands sampled during 1995 (i.e., stands #1-29). In these stands, 2-3 400m^2 (20x20m) sample plots were located 50 m apart along an elevational contour. During 1996 only 1 sample plot was placed in most stands sampled (i.e., stands 30-53). Plots were located at or near the center of the stand.

Per cent crown cover of each tree, shrub, and herbaceous species occurring in the sample plot was estimated visually. Also, for each tree species and for all tree species combined, crown cover was estimated by canopy layer. Trees greater than 10 m tall were considered part of the main canopy and trees less than 10 m tall were considered part of the subcanopy. Most plants were identified at the sample site. Those with uncertain identifications were collected and identifications were verified by Brenda Costanzo at the University of Victoria Herbarium. Taxonomic nomenclature follows that of Douglas *et al.* (1989, 1990, 1991, 1994). A soil pit was dug in the center of the plot to the top of the parent material where possible. The depth and texture of the humus and mineral soil horizons were recorded as well as an estimate of the % coarse fragments (i.e., pebbles, rocks, and stones) in each soil horizon. The percentages of the plot covered by humus, decaying wood, mineral soil, rock, and bedrock were estimated visually. Elevation (m), slope inclination (%), and topographic position were also recorded for each plot.

The diameter of all trees in the sample plot was measured at breast height (1.3 m); trees shorter than breast height were also tallied. During 1995, the height and diameter

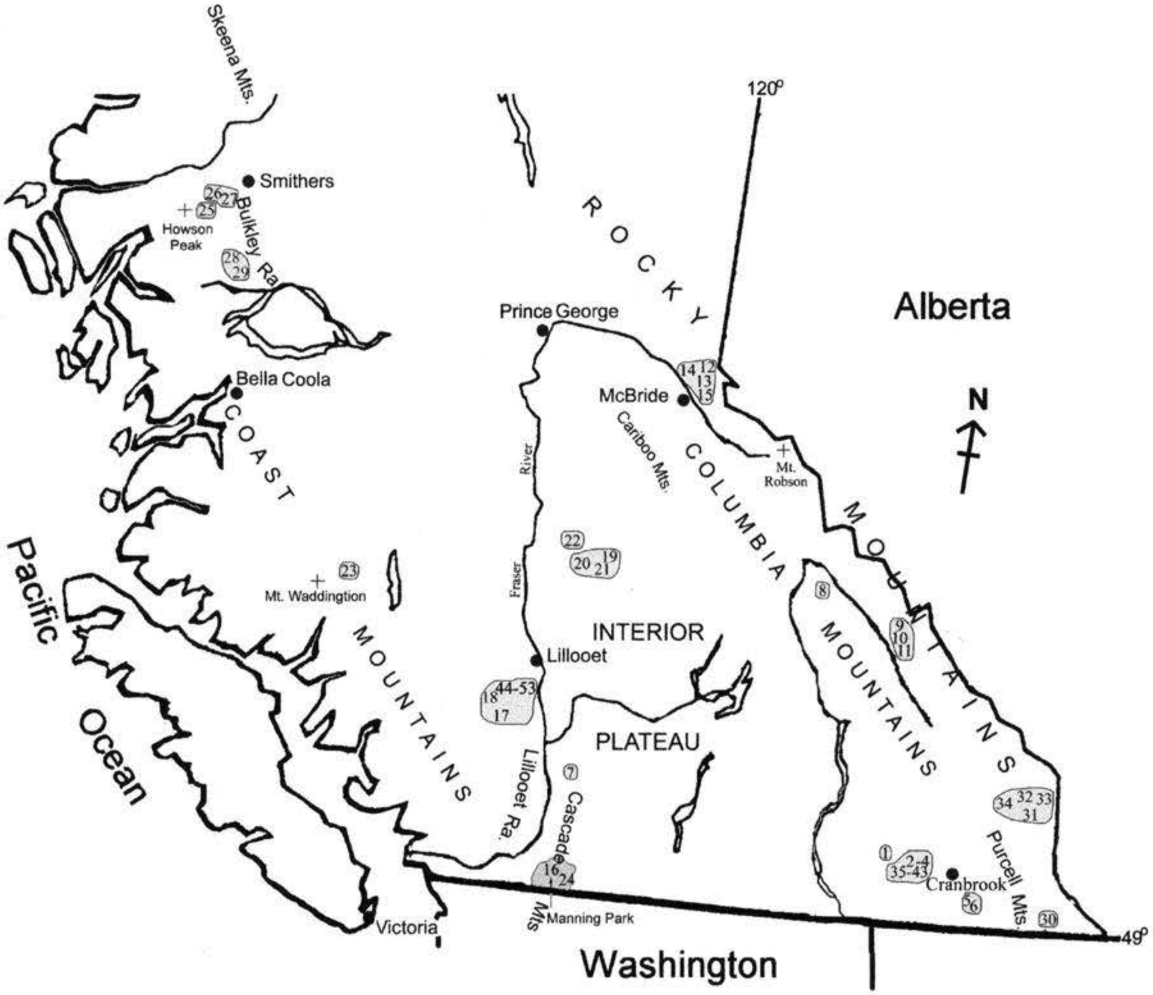


Figure 1. Distribution of 53 stands sampled in British Columbia. Stands sampled in the same locale (i.e., same watershed) are grouped together and indicated by grey shading. Near Cranbrook and Lillooet, where many stands were sampled, mulitple stands are indicated with a hyphen. For example, 35-43 represents stands 35 through 43 near Cranbrook.

were recorded for at least 2 trees of each major canopy species. During more intensive stand studies in 1996, tree heights and diameters were measured for at least 3 trees of each species for each 5 cm diameter class. Increment cores were taken near the base of all trees for which height data were collected. Cores were counted with the aid of a dissecting microscope and the dendrological software WINDENDRO (Regent Instruments 1996). In general, stand age was equated to the age of the oldest tree in the stand (see Chapter 3 for exceptions). Some very old trees, especially old whitebark pine trees, had heartrot, making age determinations impossible. Tree age data were not adjusted for core height because cores were taken near the tree base; thus annual growth ring counts represent minimum tree ages.

Data Analyses

Ordination – Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980) and Canonical Correspondence Analysis (CCA) (ter Braak 1986, 1994) are currently the most widely used ordination techniques for analyzing community data (e.g., Allen and Peet 1990; Bernard and Sieschab 1995; Carelton and MacLellan 1994; Días *et al.* 1994; Sagers and Lyon 1997; Stohlgren and Bachand 1997; Taggart 1994; Velásquez 1994; Xiao-bing 1993; Zhang and Oxley 1994). However, Minchin (1996) indicates that non-metric multidimensional scaling (NMDS) (Kruskal 1964 a, b) ordinations are more robust and effective than DCA and that NMDS should be more widely used to analyse community data. There is considerable controversy over the relative merits of each technique (e.g., Jackson and Somers 1991; McCune 1997; Okland 1996; Palmer 1993; van Groenewoud 1992) and all of these ordination techniques suffer various shortcomings. DCA sometimes performs poorly with skewed species distributions (Palmer 1993) and may occasionally be unstable as a result of detrending (i.e., removal, by segmentation, of a curvilinear second axis [the arch] that is a function of the first axis) in that it will give various solutions depending on the number of segments used (Jackson and Somers 1991). In addition, it may occasionally not handle complex sample designs well and compress one end of a gradient into a "tongue" (Minchin 1987; Okland 1996), and it may also destroy any true arch that actually exists in the data (Palmer 1993; Wartenburg *et al.* 1987). NMDS may not detect discontinuities or may fail to find the best solution (i.e., with minimum stress) (McCune and Mefford 1997). The performance of CCA has not been as well studied but McCune (1997) suggests that it is potentially one of the most misleading multivariate methods for community analysis. CCA is unusual among the ordination methods in that ordination of the community data is constrained by a multiple regression of its relationships with the environmental data. Because of this, the use of even slightly noisy, inaccurate, or irrelevant environmental variables in CCA can distort the representation of gradients in community structure (McCune 1997).

Largely because of the controversy regarding effectiveness of various ordination techniques, confusion over which technique is most appropriate for the analysis of community data seems fairly widespread (Okland 1996). Okland (1996) suggests that constrained ordination (e.g., CCA) and unconstrained ordination techniques (e.g., DCA and NMDS) suit different purposes in ecological analysis. Traditional unconstrained ordination techniques are more appropriate for "general purpose" ecological studies when the objective is to describe community structure, because many ecological studies of community structure suffer from noisy or somewhat irrelevant environmental variables (McCune 1997; Okland 1996). Okland (1996) does indicate, however, that constrained ordination by CCA may be a powerful tool for the hypothesis-testing stage of ecological analysis as the influence of explanatory variables on vegetation composition can be tested using the Monte Carlo approach.

I decided to use NMDS to examine patterns of variation in floristic composition of stands containing whitebark pine, because several comparative analyses have shown a superiority of NMDS compared to DCA (Faith *et al.* 1987; Minchin 1987, 1996). NMDS is a non-parametric multivariate method of analysis and is well suited for data that are non-normal or are on arbitrary, discontinuous or otherwise questionable scales (Mather 1976; McCune and Mefford 1997). I decided to avoid CCA, which is used in most recent community composition studies, because of the potential problems associated with noisy and irrelevant environmental variables and because the primary objective of this section of my research is to describe the structure and composition of stands containing whitebark pine.

Following the general procedures outlined by McCune and Mefford (1997), gradients in species composition were extracted from the samples by species data matrix using NMDS (PCORD Version 3.0; McCune and Mefford 1997) with the Sørenson distance measure. The dimensionality of the data was first determined by conducting a preliminary NMDS run and plotting stress (i.e., a measure of fit) vs. the number of dimensions. Based on this plot, a two dimensional solution was requested for NMDS analyses because additional dimensions provided only a slight improvement in fit. Using random coordinates and 100 iterations, several runs were conducted to ensure stability of the ordination solution and to ensure that the resulting ordination distances represented the best possible fit of the distances in the original n-dimensional space.

The analyses were performed on octave-scale converted species abundance data (essentially a base 2 logarithmic transformation of per cent cover data having 10 values; 0-9 [Gauch 1982]) using PCORD (McCune and Mefford 1997). Only the cover data of understory species (i.e., shrubs and herbs) were used for the ordination. Composition of the understory varied more among stands than did that of the trees, and was also less likely to be related to disturbance; thus, ordination using understory species was likely to reveal more information about environmental gradients in whitebark pine communities. Understory species present in only one plot were eliminated from the sample-species matrix; a resulting 91 shrub and herb species were used in the analyses. An analysis of sample outliers was performed using PCORD Version 3 (McCune and Mefford 1997) with Elucidean distance measures and an outlier cutoff of 3 standard deviations. No outliers were found. Analyses were performed on the 88 individual sample plots rather than averaging the abundance data over multiple sample plots in a stand. This permitted examination of variability in species composition both among and within sampled stands.

Some plants could not be clearly distinguished at the species level due, largely, to the persistent lack of floral parts. Thus, the following groups of plants were grouped together for the data analyses: *Carex concinnoides, Carex rossii,* and *Carex obtusata* = *Carex* spp.; and *Luzula hitchcockii, Luzula parviflora* = *Luzula* spp. All unidentifiable *Poa* were lumped as *Poa* spp.

To examine relationships between changes in understory composition and environmental factors, both Pearson's (r) correlation coefficient and Kendall's (τ) ranked correlation coefficients are presented. The following environmental variables were used:

latitude, longitude, elevation, slope inclination, slope aspect, stand age, and site moisture index. Aspect was rated on a 1 – 5 scale (1 = 180 –225°; 2 = 136 – 180° 3 = 226 – 315°; 4 = 46 – 135° and 316 – 360°; 5 = 271 – 315°). I used a topographic index of soil moisture similar to that of Antos and Zobel (1986). The rated values of aspect and topographic position (1 = crest; 2 = upper slope; 3 = middle slope; 4 = lower slope; and 5 = flat and/or valley bottom) were added to obtain an index of moisture. This index was adjusted by subtracting 1 for sample plots where soils were particularly shallow (<5 cm). Plot positions on the ordination axes were also correlated with the abundance (measured as basal area [m^2] and density [stems/ha]) of subalpine fir, Engelmann spruce, whitebark pine, lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*) and mountain hemlock (*Tsuga mertensiana*). The statistical significance of the correlation coefficients was determined using the appropriate test statistics for each of the Pearson correlation coefficients and the Kendall's ranked correlation coefficients (Devore 1991; Sokal and Rohlf 1995). A significance level of $\alpha = 0.0013$ was used for the tests. Because a two-tailed test was conducted for several variables the α-level 0.05 was divided by 2 (= 0.025 for a two-tailed test) and then Bonferonni corrected (i.e., 0.025/19 = 0.0013) for an overall significance level of 0.025 over the 19 environmental variables tested (see variables above). Single variable and bivariate normality plots were used to determine if ordination scores and environmental variables were normally distributed.

Cluster analysis – Using PCORD (McCune and Mefford 1997), sample plots were classified using a polythetic agglomerative cluster analysis of Sørenson distances linked by the unweighted pair-group method with arithmetic averages (i.e., UPGMA). The same understory species used for the ordination were also used for the cluster analysis (see above). There is always some degree of chaining in cluster analyses, which indicates the degree to which groups are the product of growth by accretion of early groups; low per cent chaining (the desirable outcome) indicates a low probability of growth by accretion (Pielou 1984). Though chaining in cluster analysis is partly due to properties of data, it can be controlled, to some degree, by selection of linkage method (McCune and Mefford 1997). One reason for the selection of the UPGMA linkage method in this cluster analysis was because it showed low per cent chaining (i.e., 3.17%).

The validity of groups defined by cluster analysis was tested using Multi-response Permutation Procedures (MRPP) using the Sørenson distance measure with natural weighting of groups (McCune and Mefford 1997). MRPP is a non-parametric procedure that tests the null hypothesis that clusters correspond to a random allocation of plots to the groupings (McCune and Mefford 1997; Zimmerman *et al.* 1985). Results on the composition and the structure of stands containing whitebark pine are presented within the context of the groups defined by the cluster analysis.

Results

Distribution of whitebark pine

Whitebark pine grows in a diverse array of mountain environments in British Columbia (south of 55°N) including relatively maritime climatic conditions of the Coast and Cascade Mountains, the dry continental climates of the Interior Plateau, Purcell Ranges, and the Rocky Mountains, and the moist continental climate of the Columbia Mountains (Table 1). Climate over the range of whitebark pine in British Columbia varies with latitude (Table 1). In the eastern Cascade Mountains and on the southern most peaks of the Interior Plateau, Columbia and Rocky Mountains, summers are notably dry and most of the growing season water originates from snow melt, whereas in the more northern mountain ranges (e.g., Bulkley Ranges, Pacific Ranges, northern Columbia Mountains) there is little or no summer soil moisture deficit.

The altitudinal range of whitebark pine was fairly consistent with the geographic patterns of the timberline. It occurred at higher elevations in the southern most and driest mountain ranges (Table 1). In general, whitebark pine was most abundant at or near the timberline in dry mountain ranges (e.g., stands 19, 20, 21) with progressively fewer individuals occurring with decreasing elevation. In the colder, northern mountain ranges it was often scattered at the timberline as krummholz and stunted trees but occurred more abundantly in valley bottoms. Whitebark pine was abundant in stands sampled on isolated mountains of the Interior Plateau where the climate is dry and cold (Table 1). Here it was the only tree species on rocky outcrops on all aspects at the timberline and it was particularly abundant on sites near the timberline where soils, though shallow, were not interrupted by rock outcrops. At lower elevations, scattered whitebark pine grew on rocky knolls with lodgepole pine and on moister sites supporting tall, closed-canopy forests of subalpine fir, Engelmann spruce, lodgepole pine, and Douglas-fir.

Whitebark pine was most extensive and common in the dry mountain ranges of southeastern British Columbia (Table 1). In the Purcell Ranges and the southern Rocky Mountains, it occurred as a codominant with subalpine fir, Engelmann spruce and, lodgepole pine in upper subalpine forests and as the dominant or only species at the

Table 1. Distribution and density of whitebark pine by regional climate.

Regional climate[a]	Location[b]	Stand Number[c]	Mean Elevation (m) (range)	Aspect	Mean density[d] (# trees /ha)
Very dry, cold–very cold ($n = 7$)[e]	Chilcotin, Camelsfoot and Lillooet Ranges of the Coast Mountains; Okanagan Range of the Cascade Mountains; Isolated Mountains of Interior Plateau.	19^{*}, 20, 21, 22^{*}, 23^{*}	1972 (1920 – 2070)	all	1210 (725 – 2950)
Dry, cold (n = 29)	Purcell Ranges of the Southeastern Columbia Mountains; Rocky Mountains of southern British Columbia; Coast and Cascade Mountains.	2^{*}, 3^{*}, 4^{*}, 5, 6, 7^{*}, 30, 31, 31, 33, 34, 35, 36^{*}, 37 – 43,	2031 (1775 – 2215)	all	875 (25 – 4600)
Moist, warm ($n = 25$)	lee side of the Coastal and Cascade Mountains in southern British Columbia	16^{*}, 17^{*}, 18^{*}, 24^{*}, 44 – 54	1954 (1650 –2120)	all but predominantly southern	817 (150 – 2900)
Moist, mild ($n = 12$)	Northern Columbia Mountains	12^{*}, 13^{*}, 14^{*}, 15^{*}	1773 (1620 – 1950)	S, SE	392 (25 – 925)
Moist, cold ($n = 6$)	Bulkley Ranges; southern Skeena Mountains and Hazelton Mountains; eastern Kitimat Ranges and Coastal Mountains.	25^{*}, 26, 27, 28, 29	1275 (1050 - 1570)	S, SW, SE	508 (75 – 900)
Wet, mild ($n = 9$)	Southeastern Columbia Mountains; Northern Rocky Mountains.	1^{*}, 8^{*}, 9, 10, 11	1821 (1600-2127)	S, SE, W, N	369 (75 – 1425)

a Climatic regions are based on the British Columbia Biogeoclimatic Ecosystem Classification system (Meidinger *et al.* 1991) and from climate data obtained from Banner *et al.* 1993; Braumandl and Curran 1992; Green and Klinka 1994; Lloyd *et al.* 1990; B.C. Ministry of Environment and B.C. Ministry of Forests, unpublished data, 1997, B.C. Ministry of Enviornment, Victoria, B.C.

b Location represents the geographic distribution of the regional climate; not all mountain ranges presented in the location column were sampled.

c Refer to Figure 1 for illustration of stand location. Stands with an asterisk contain multiple sample plots. Elevation and tree density were averaged over all sample plots in each regional climate.

d Includes only whitebark pine trees greater than 1.3 meters tall.

e. n = total number of sample plots.

timberline and on rocky wind-swept ridges. On north and easterly aspects it grew with scattered alpine larch (*Larix lyallii*) on herb-rich sites.

In the more maritime and relatively warm subalpine climates of the Cascade Ranges and the southern Coast Mountains, whitebark pine occurred predominantly on steep south and southwesterly slopes (Table 1). It was a codominant with subalpine fir and Engelmann spruce in subalpine forests and formed krummholz communities at the timberline with subalpine fir. In parts of the Lillooet Range, whitebark pine occurred on serpentine soils.

There was a notable decrease in the abundance of whitebark pine with increasing latitude and with increasingly wet climatic conditions (Table 1). In the wet Selkirk Mountains it was uncommon and most often scattered on dry rocky sites at the timberline. Northeast of Golden, however, it grew as a canopy tree scattered in forests dominated by mountain hemlock and on raised microsites in boggy areas. The abundance of whitebark pine decreased northward in both the eastern and western portions of its range and it grew primarily on south slopes at its northern limits (Table 1). In the northern Coastal Mountains south of Smithers, whitebark pine grew with mountain hemlock in open-canopied forests near the timberline and was the predominant or only tree species on dry scree slopes of southern exposures. Whitebark pine also occurred in the valley bottoms of northern Coastal Mountains (at approximately 1000 m) where it grew as a co-dominant with subalpine fir and mountain hemlock on deep soils and on dry, rocky knolls.

Ordination patterns

The NMDS ordination had good sample separation (Figure 2). Two major gradients captured most of the variation in the species composition of whitebark pine communities. The first two dimensions of the ordination contained 37.6% and 26.9%, respectively, (cumulative = 64.5%) of the information in the original, unreduced data matrix. Higher dimensions improved the model very little.

Plots sampled in the same stand were generally close together on the ordination (Figure 2). Stand 8 of the interior wet belt was the most homogeneous stand sampled with all plots located very close together in the ordination. All plots of stand 8 contained

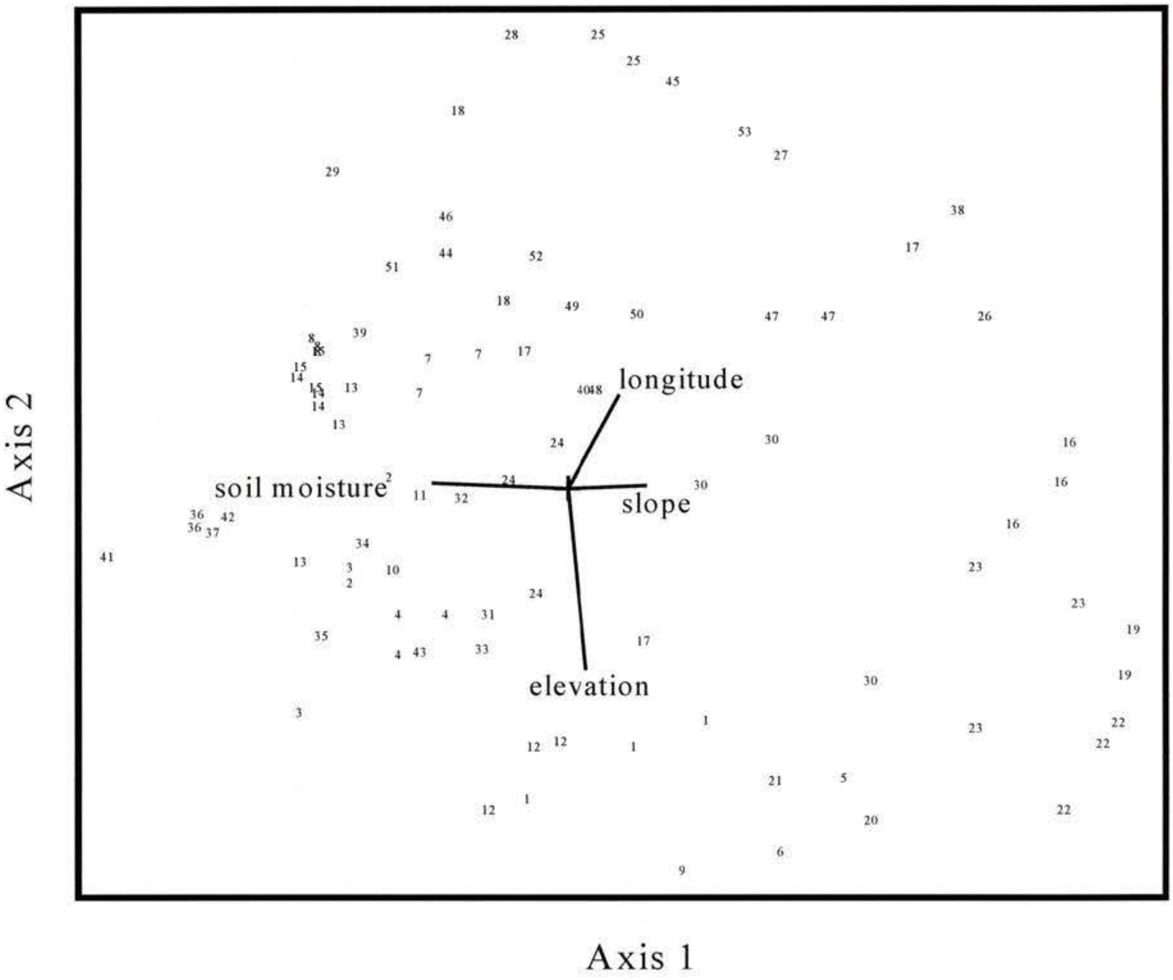


Figure 2. NMDS ordination of sample plots (88 sample plots in 53 stands). The stand in which the plot was sampled is indicated by its number on the ordination diagram. Stand numbers are the same as those presented in Figure 1 and Table 1. Environmental vectors radiate from the centroid of the points. Vector length is proportional to the strength of the correlation of the environmental variable with the ordination axes. Vector direction indicates the direction of increasing values of the environmental variable.

nearly identical per cent crown cover of the dominant shrubs. The understory composition of stands 14 and 15 were very similar to that of stand 8 but the overstory of stands 14 and 15 was dominated by subalpine fir and whitebark pine instead of mountain hemlock and subalpine fir. Stand 17, located in the Coastal Mountains near Lillooet was the most heterogeneous stand sampled. Although only 50 m apart, the plots differed markedly in terms of understory species composition. Located at the timberline, this "stand" of stunted subalpine fir and whitebark pine is a mosaic of dry, elevated microsites with *Juniperus communis* and *Pachistima myrsinites* and moister areas (e.g., snowmelt streams and areas of snow accumulation) with *Vaccinium membranaceum, Rhododendron albiflorum* and many herbaceous species.

Axis 1 of the ordination was significantly correlated with the environmental characteristics, slope inclination, soil moisture, and longitude (Table 2). Though longitude was significantly correlated with Axis 1, the correlation of longitude with Axis 2 was stronger. Plots sampled on steep, dry sites were located on the right side of the ordination graph and moist plots on more level ground were located on the left (Figure 2). Plots sampled in the Coastal and Cascade Mountain Ranges were generally located in the upper right corner of the ordination graph and those sampled on the continental mountain ranges of central and eastern British Columbia were located on the bottom left. Axis 2 was significantly correlated with longitude and elevation (Table 2); higher elevation and more easterly sample plots were closer to the bottom of the ordination graph (Figure 2).

In most instances, correlations of tree basal area and density with either Axis 1 or Axis 2 give different results depending on whether the Pearson's correlation coefficient or the Kendall's ranked correlation coefficient was used (Table 2). Unlike the environmental variables examined above, axis scores and tree basal areas and densities do not have bivariate normal distribution, which was entirely due to the strongly skewed distribution of basal areas and densities for all tree species. Therefore, I interpreted only the non-parametric Kendall's correlation coefficients. Using Kendall's correlation coefficient, Engelmann spruce basal area and density was significantly, negatively correlated with Axis 1 (Table 2) which generally reflects greater size and abundance of Engelmann spruce trees in moister sample plots. Basal area and density of both

Table 2. Pearson (r) and Kendall (τ) correlations between plot attributes and NMDS ordination axes (see Figure 2). Test statistic (i.e., t and t_s) for the Pearsons correlation coefficient and the Kendall's correlation coefficient, respectively, are presented with corresponding *p*-values. Statistically significant correlations (i.e., $p \leq 0.0019$) are highlighted in bold print. Correlations are based on all 88 sample plots.

	Axis 1						Axis 2					
Variable	r	t	*p*	τ	t_s	*p*	r	t	*p*	τ	t_s	*p*
Latitude	0.098	0.91	0.3658	0.033	0.45	0.3264	0.253	2.42	0.0176	0.200	2.77	0.0056
Longitude	**0.345**	**3.41**	**0.0010**	**0.256**	**3.56**	**0.0006**	**0.488**	**5.18**	**0.0000**	**0.343**	**4.76**	**0.0002**
Elevation (m)	0.197	1.86	0.0658	0.167	2.32	0.2040	**– 0.678**	**8.54**	**0.0000**	**– 0.463**	**6.43**	**0.0000**
Slope inclination (°)	**0.427**	**4.00**	**0.0002**	**0.324**	**4.50**	**0.0000**	0.092	0.86	0.3919	0.088	0.11	0.2224
Aspect[a]	– 0.214	2.03	0.0450	– 0.148	2.06	0.0394	– 0.209	1.98	0.0562	– 0.165	2.29	0.0220
Soil moisture index[b]	**– 0.557**	**6.22**	**0.0000**	**– 0.368**	**5.11**	**0.0000**	0.101	0.94	0.3469	0.069	0.96	0.1711
Stand age (years)	– 0.067	0.46	0.5328	0.034	0.47	0.3192	0.220	2.09	0.0391	0.179	2.49	0.0132
Basal area (m^2/ha):												
Abies lasiocarpa	– 0.268	2.58	0.0116	– 0.179	2.48	0.0132	0.373	**3.73**	**0.0003**	**0.285**	**3.95**	**0.0002**
Picea engelmannii	– 0.223	2.13	0.0364	– **0.339**	**4.71**	**0.0002**	0.101	0.94	0.3468	0.110	1.52	0.1260
Pinus contorta	– 0.054	0.49	0.6191	– 0.228	3.17	0.0016	– 0.143	1.33	0.1849	– 0.153	1.81	0.0170
Pinus albicaulis	– 0.087	0.81	0.4184	– 0.030	0.42	0.6674	0.289	2.79	0.0064	0.166	2.30	0.0214
Pseudotsuga menziesii	– 0.045	0.41	0.6796	– 0.047	0.65	0.5156	– 0.060	0.56	0.5774	– 0.053	0.74	0.2266
Tsuga mertensiana	– 0.071	0.65	0.5132	– 0.125	1.74	0.0818	0.298	2.89	0.0048	**0.303**	**4.21**	**0.0002**
Density (stems/ha)[c]												
Abies lasiocarpa	-0.270	2.60	0.0109	-0.204	2.83	0.0046	0.319	3.12	0.0024	**0.273**	**3.79**	**0.0002**
Picea engelmannii	-0.312	3.04	0.0031	**-0.379**	**5.26**	**0.0000**	-0.049	0.45	0.6486	-0.140	1.94	0.0524
Pinus contorta	-0.023	0.22	0.8281	-0.194	2.69	0.0072	-0.153	1.43	0.1560	-0.197	2.74	0.0062
Pinus albicaulis	0.132	1.24	0.2190	0.161	2.24	0.0250	-0.039	0.36	0.7187	-0.029	0.40	0.6892
Pseudotsuga menziesii	0.169	1.59	0.1145	0.119	1.65	0.0990	-0.217	2.05	0.0427	-0.205	2.85	0.0044
Tsuga mertensiana	-0.133	1.24	0.2182	-0.155	2.15	0.0316	0.305	2.96	0.0038	**0.257**	**3.57**	**0.0004**

a Aspect was rated on a 1 – 5 scale (1 = 180 –225°; 2 = 136 – 180° 3 = 226 – 315°; 4 = 46 – 135° and 316 – 360°; 5 = 0 – 45°).

b The soil moisture index is derived by adding rated topographic position (1 = ridge top, 2 = upper slope, 3 = middle slope, 4 = lower slope, 5 = flat) to aspect ratings and subtracting 1 for sites with shallow soils. Low moisture index values represent dry sites and high values moist sites.

c Includes only trees greater than 1.3 meters tall.

subalpine fir and mountain hemlock were significantly positively correlated with Axis 2 (Table 2). The increase in basal area and density of subalpine fir and mountain hemlock along Axis 2 largely reflect the negative effects of cold temperatures on the distribution of these species.

Plot group characteristics

The ordination results indicated no obvious discontinuities among sample plots with respect to species composition (Figure 2). Cluster analysis was used to group sample plots based on dominant understory species to facilitate the description of different forest types. Eleven plot groups (A – K) were delineated (Figure 3). MRPP analysis supported these groupings; the null hypothesis that clusters correspond to a random allocation of plots to the groups was rejected (p <0.0001).

Plots of groups A and B represent mesic, subalpine communities dominated by an understory of *Vaccinium membranaceum*. Group A plots were sampled in upper subalpine forests of the southern Coast and Cascade Mountains. Located in a relatively moist, warm subalpine climate, these forests occurred on the steep, southerly slopes of colluvial sites with considerable exposed mineral soil and rock (Table 3). The forested sites sampled in these mountains were generally located between avalanche tracks. Whitebark pine was a codominant canopy species with subalpine fir and Engelmann spruce (Table 4). Though *Vaccinium membranaceum* was the dominant understory shrub in these forests, *Pachistima myrsinites* and *Rhododendron albiflorum* were also common with the former occurring on drier sites and the latter on moister sites. *Pyrola secunda*, *Lupinus arcticus*, *Arnica latifolia*, and *Viola orbiculata* were common herb species. *Valeriana sitchensis* was most common on moister sites. Group B plots were sampled in stands located largely in the moist, cold climate of the Bulkley Ranges near the northern limit of whitebark pine's range (stand 24 was sampled in the Cascade Mountains). These forests were located at lower elevations than Group A plots and were found on all slope aspects (Table 3). Group B plots had less whitebark pine than Group A plots (Table 3), and were dominated by subalpine fir with lesser amounts of Engelmann spruce and whitebark pine. Unlike the stands of Group A, Group B stands contained some mountain hemlock in the understory. *Vaccinium membranaceum* was less abundant in Group B

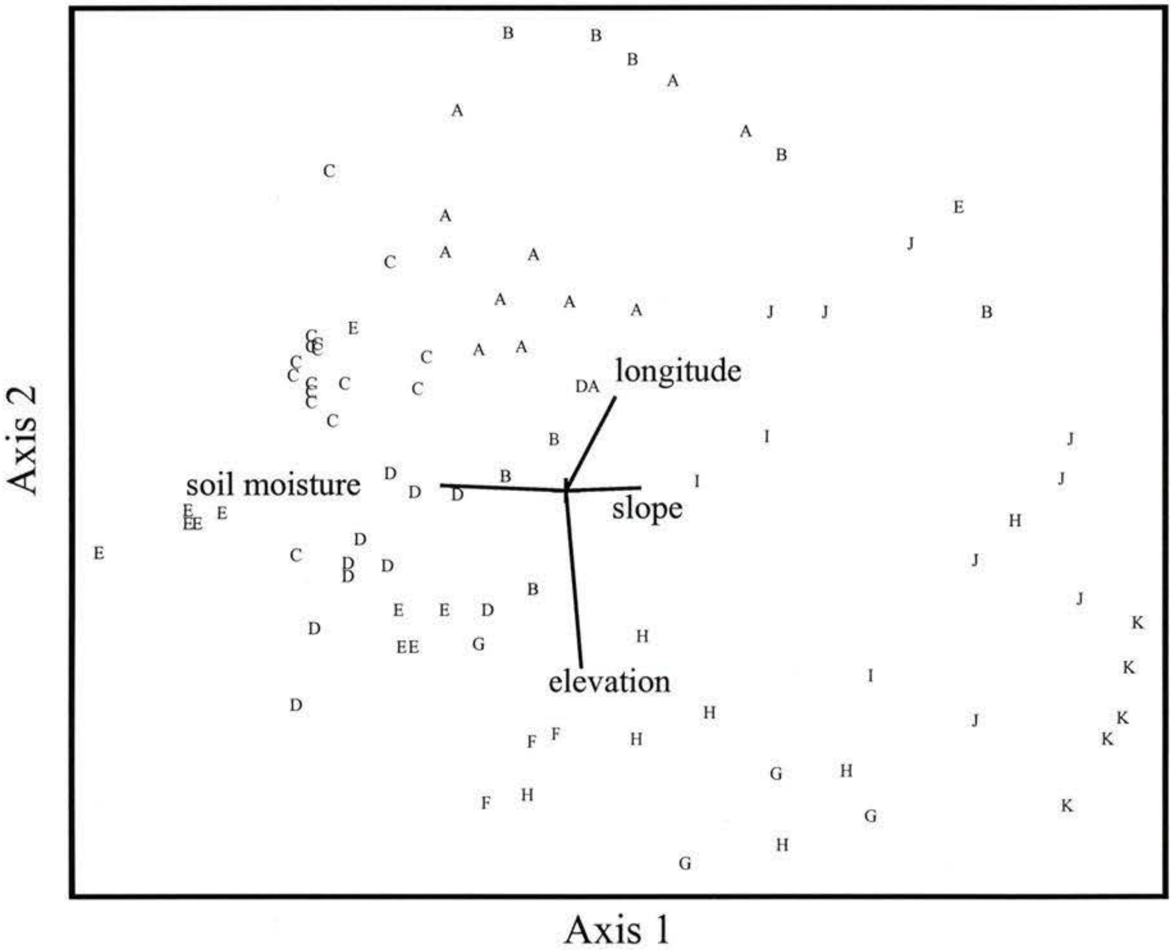


Figure 3. Overlay of cluster analysis results on the NMDS ordination diagram. Eleven plot groups are indicated by alphabetical symbols A – K.

Table 3. Characteristics of plot groups. Characters are averaged over all plots in a group except for aspect and stand age, for which the range is given.

	Plot group										
	A	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**
Aspect (°)	S ,SE	all	all	all	N, NE, NW	S	N, E, W, SW	E, SE, SW	S, SE	S, SE	S, SE
Elevation (m)	1 847	1 503	1 655	1 921	2 072	1 937	2 021	2 237	1 808	1 945	1 978
Slope inclination (%)	51	52	33	31	24	43	37	41	45	54	46
No. of shrub spp. / plot	4	5	4	4	4	4	3	3	7	4	3
No. of herbaceous spp. / plot	5	5	2	2	2	9	14	11	10	11	14
% cover surface mineral soil	22	8	9	10	14	23	8	41	5	48	30
% cover surface rock	14	19	6	3	15	12	2	28	3	20	4
Litter depth (cm)	2.7	2.0	2.4	3.5	3.7	1.4	2.5	0.5	5.3	0.1	0.5
% cover overstory[a]	29	24	30	44	22	0	30	4	28	2	4
Maximum canopy height	20.8	19.0	19.7	19.7	14.8	5.4	18.2	10.8	24.2	11.6	10.0
Total tree density[b] (stems/ha)	3 563	3 100	2 318	3 639	3 777	1 425	3 031	1 290	2 591	2 338	1 980
Density whitebark pine[c] (stems/ha)	1 037	344	258	541	1 673	800	750	275	250	821	1 755
Total tree basal area (m^2/ha)	49	36	32	34	29	7	32	11	22	16	16
Basal of area whitebark pine	17	12	7	12	10	5	11	2	5	4	13
Stand age range[d] (years)	105-378	195-385	68-462	40-505	37-339	68	93-323	46-216	323	112-216	94, 318

a % cover overstory = cover of all trees over 10 m in height.

b density of trees greater than 1.3 m tall

c density of whitebark pine trees greater than 1.3 m tall

d The range of stand ages is given when greater than 3 stands were sampled in a group; when only 1 or 2 stands were sampled in a group the ages of the stands are given.

Table 4. Average per cent with standard deviation (in parentheses) of cover by plot group for species that occurred in 3 or more of the 88 plots sampled and had an average cover of > 1% in at least 1 group. Overstory = % crown cover of all trees greater than 10 m in height. Understory = % crown cover of all trees less than 10m in height. The number in brackets under the plot group indicates the number of sample plots in that group; species cover data was averaged over sample plots.

Plot Group	A (*n* =12)	B (*n* = 8)	C (*n* = 16)	D (*n* = 11)	E (*n* = 11)	F (*n* = 3)	G (*n* = 4)	H (*n* = 7)	I (*n* = 3)	J (*n* = 8)	K (*n* = 5)
Stand No. (see Figure 1)	7, 17, 18, 44, 45 46, 48, 49, 52, 53	24, 25, 26, 27, 28	7, 8, 13, 14, 15, 29, 51	2, 3, 10, 11, 31, 32, 34, 35, 40	4, 36, 37, 38, 39, 41, 42, 43	12	9, 20, 21, 33	1, 5, 6, 16, 17	30	16, 17, 23, 47	19, 22
Trees											
Abies lasiocarpa											
Overstory	11 (16)	15 (20)	11 (14)	19 (17)	2 (3)	0 (0)	8 (12)	4 (6)	14 (8)	0.4 (0.7)	0 (0)
Understory	20 (22)	33 (21)	19 (11)	16 (19)	9 (5)	6 (18)	7 (12)	6 (6)	9 (3)	10 (15)	0 (0)
Picea engelmanii											
Overstory	17 (23)	6 (8)	3 (3)	5 (3)	3 (4)	0 (0)	2 (3)	0.3 (0.7)	6 (9)	0 (0)	0 (0)
Understory	0 (0)	5 (6)	3 (4)	8 (11)	5 (4)	3 (2)	2 (3)	1 (2)	0.3 (0.5)	0.1 (0.6)	0.3 (0.4)
Pinus albicaulis											
Overstory	16 (13)	7 (11)	5 (5)	18 (9)	5 (7)	0 (0)	10 (8)	0.5 (1)	7 (4)	2 (4)	3 (8)
Understory	8 (11)	4 (8)	3 (3)	9 (15)	16 (15)	9 (6)	5 (5)	5 (5)	2 (3)	15 (10)	24 (21)
Pinus contorta											
Overstory	2 (3)	3 (5)	7 (9)	6 (9)	14 (13)	0 (0)	11 (15)	0 (0)	5 (4)	1 (2)	1 (2)
Understory	0 (0)	1 (2)	4 (7)	0.9 (0.3)	6 (8)	0 (0)	8 (10)	5 (13)	0 (0)	11 (19)	10 (9)
Pseudotsuga menziesii											
Overstory	0 (0)	0.5 (0.9)	0.2 (0.5)	0.5 (1)	0 (0)	0 (0)	0.3 (0.5)	0 (0)	1 (2)	0 (0)	0 (0)
Understory	0 (0)	0.4 (0.7)	0.1 (0.3)	0 (0)	0 (0)	0 (0)	0.8 (0.9)	0 (0)	0.7 (0.5)	0 (0)	1 (1)
Tsuga mertensiana											
Overstory	0 (0)	0 (0)	3 (7)	0.2 (0.6)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Understory	0 (0)	1 (2)	3 (7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Table 4.
(continued)

Plot Group	A (*n* =12)	B (*n* = 8)	C (*n* = 16)	D (*n* = 11)	E (*n* = 11)	F (*n* = 3)	G (*n* = 4)	H (*n* = 7)	I (*n* = 3)	J (*n* = 8)	K (*n* = 5)
Shrubs											
Alnus crispa	0 (0)	0.3 (0.7)	0 (0)	1 (3)	0 (0)	0 (0)	0 (0)	0 (0)	1 (2)	0 (0)	0 (0)
Arctostaphylos uva-ursi	0 (0)	0.3 (0.7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (4)	14 (9)
Juniperus communis	0 (0)	1 (4)	0 (0)	0 (0)	0.1 (0.3)	1 (0)	0 (0)	0.3 (0.4)	2 (3)	6 (6)	16 (9)
Lonicera utahensis.	0 (0)	0.1 (0.4)	0 (0)	0 (0)	0 (0)	0 (0)	12 (8)	0 (0)	0 (0)	0 (0)	4 (5)
Menziesia ferruginea	0 (0)	0 (0)	14 (13)	20 (15)	8 (11)	0 (0)	13 (25)	0 (0)	3 (3)	0 (0)	0 (0)
Pachistima myrsinites	9 (2)	5 (7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)	3 (4)	0 (0)
Phyllodoce empetriformis	0 (0)	0 (0)	8 (11)	0 (0)	5 (6)	27 (26)	0 (0)	2 (4)	0 (0)	0 (0)	0 (0)
Rhododendron albiflorum	5 (7)	9 (13)	15 (10)	5 (4)	12 (8)	2 (1)	8 (15)	1 (3)	0 (0)	3 (7)	0 (0)
Shepherdia canadensis	0 (0)	0.1 (0.4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4 (1)	0 (0)	0 (0)
Sorbus sitchensis	0 (0)	0.3 (0.3)	3 (4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Spiraea betulifolia	0 (0)	0 (0)	0 (0)	0 (0)	0.1 (0.2)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)
Vaccinium caespitosum	3 (4)	0 (0)	1 (2)	0 (0)	0 (0)	7 (6)	0 (0)	0 (0)	0 (0)	4 (9)	0 (0)
Vaccinium membranaceum	38 (39)	16 (18)	15 (13)	9 (21)	5 (15)	0 (0)	0 (0)	0.6 (0.7)	2 (2)	7 (10)	0 (0)
Vaccinium myrtillus	0 (0)	0.1 (0.2)	0 (0)	0 (0)	42 (23)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Vaccinium scoparium	0 (0)	6 (8)	0.2 (0.5)	27 (16)	10 (15)	5 (0)	33 (27)	30 (18)	8 (10)	4 (5)	0 (0)
Herbs											
Achillea millefolium	0 (0)	0.1 (0.1)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0.4 (1)	0 (0)	1 (0.9)	2 (3)
Anaphalis margaritacea	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.7)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Anemone occidentalis	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.4 (0.5)	4 (6)	0 (0)	0.8 (1)	0.6 (1)
Anemone multifida	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (3)	0 (0)	0 (0)	0 (0)	0 (0)	1 (2)
Antennaria racemosa	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.5)	0.1 (0.2)	0 (0)	0 (0)	0 (0)
Aquilegia formosa	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0.7)	0 (0)	0 (0)	0 (0)	0 (0)
Arenaria capillaris	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.6 (1)	0 (0)	3 (3)	0.4 (0.5)
Arnica latifolia	4 (5)	0 (0)	0.6 (2)	2 (3)	0 (0)	4 (2)	18 (21)	0.1 (0.4)	6 (4)	0 (0)	0.5 (0.9)

Table 4 (continued)

Plot Group	A (*n* =12)	B (*n* = 8)	C (*n* = 16)	D (*n* = 11)	E (*n* = 11)	F (*n* = 3)	G (*n* = 4)	H (*n* = 7)	I (*n* = 3)	J (*n* = 8)	K (*n* = 5)
Aster spp.	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (4)	0 (0)	0 (0)	0.1 (0.4)	0 (0)
Aster subspicatus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.7 (1)	0 (0)	4 (2)
Calamagrostis purpurascens	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.1 (0.2)	0 (0)	10 (15)
Carex spp.	0 (0)	0.1 (0.4)	0 (0)	0 (0)	0 (0)	2 (1)	5 (4)	16 (30)	1 (0.9)	0 (0)	11 (6)
Cornus canadensis	0 (0)	0 (0)	2 (2)	0.3 (0.9)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Castilleja miniata	0 (0)	0.1 (0.2)	0 (0)	0 (0)	0 (0)	0 (0)	1 (2)	0 (0)	0 (0)	0.4 (1)	0 (0)
Epilobium angustifolium	0 (0)	0.6 (0.1)	0.1 (0.3)	0.7 (0.3)	0.2 (0.3)	0 (0)	2 (2)	0.1 (0.2)	0 (0)	0.3 (0.5)	0 (0)
Erythronium grandiflorum	0 (0)	0 (0)	0 (0)	0.2 (0.6)	0 (0)	0 (0)	0.5 (0.5)	9 (6)	0.7 (0.6)	0.1 (0.4)	0 (0)
Fragaria virginiana	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.8 (0.5)	0 (0)	0.7 (1)	0 (0)	1 (2)
Hieracium gracile	0 (0)	0 (0)	0 (0)	0 (0)	0.2 (0.2)	0.3 (0.3)	0 (0)	2 (2)	0 (0)	0.3 (0.5)	0.8 (1)
Linnaea borealis	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	6 (7)	0 (0)	0 (0)	0 (0)	1 (2)
Lupinus arcticus	8 (11)	0 (0)	0 (0)	0.9 (3)	1 (3)	0 (0)	0 (0)	5 (7)	0.2 (0.3)	5 (4)	0 (0)
Luzula spp.	0 (0)	0 (0)	0 (0)	0.2 (0.6)	0.1 (0.2)	1 (2)	0 (0)	4 (7)	0 (0)	1 (3)	0 (0)
Moneses uniflora	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0 (0)	0 (0)	0 (0)
Pedicularis bracteosa	0 (0)	0 (0)	0.1 (0.5)	0.2 (0.6)	0.3 (0.4)	2 (2)	2 (0.9)	0 (0)	0 (0)	0 (0)	0.2 (0.4)
Pedicularis contorta	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (3)	0 (0)	0 (0)	0 (0)
Pedicularis racemosa	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (4)	0 (0)	2 (4)	0 (0)
Phlox diffusa	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.4 (0.8)	0 (0)	2 (2)	0 (0)
Poa cusickii	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	5 (7)	0 (0)	0.3 (0.4)	0 (0)
Poa secunda	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.5)	0 (0)	0 (0)	0 (0)	18 (35)
Poa spp.	0 (0)	0.6 (0.4)	0 (0)	0 (0)	0 (0)	2 (0.6)	0.1 (0.3)	2 (6)	0 (0)	0 (0)	0.6 (1)
Pyrola secunda	2 (2)	0.4 (0.6)	0.1 (0.5)	0.1 (0.3)	0 (0)	0 (0)	4 (8)	0 (0)	0 (0)	0.1 (0.3)	0.3 (0.4)
Rubus pedatus	0.3 (0.9)	1 (4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Saxifraga bronchialis	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.1 (0.4)	0 (0)	2 (3)	0 (0)
Sedum lanceolatum	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0.1 (0.2)
Silene douglasii	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (2)	0 (0)	0.4 (1)	0 (0)	0.3 (0.7)	0 (0)
Solidago multiradiata	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (3)	0 (0)	0 (0)	0.3 (0.4)	0.6 (1)
Thalictrum occidentale	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (4)	0 (0)	0 (0)
Trisetum spicatum	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.8 (0.9)	0.1 (0.2)	0 (0)	0.3 (0.7)	0.4 (0.9)

Table 4 (continued)

Plot Group	A (*n* =12)	B (*n* = 8)	C (*n* = 16)	D (*n* = 11)	E (*n* = 11)	F (*n* = 3)	G (*n* = 4)	H (*n* = 7)	I (*n* = 3)	J (*n* = 8)	K (*n* = 5)
Valeriana sitchensis	4 (5)	0 (0)	0 (0)	0.1 (0.5)	0 (0)	0.2 (0.3)	2 (3)	0 (0)	2 (3)	0 (0)	0 (0)
Viola adunca	0 (0)	2 (4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.2 (0.3)	0 (0)	0 (0)	0 (0)
Viola glabella	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (3)	0 (0)	0 (0)	0 (0)	0 (0)
Viola orbiculata	5 (7)	0 (0)	0.3 (0.5)	0.3 (0.9)	0 (0)	0 (0)	0 (0)	0 (0)	0.8 (0.6)	0 (0)	0 (0)
Xerophyllum tenax	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	65 (9)	0 (0)	0 (0)
Zygadenus elegans	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.3 (0.5)	0 (0)	1 (2)	0 (0)	0 (0)

than in Group A stands but *Pachistima myrsinites* and *Rhododendron albiflorum* were common in stands of both groups. *Vaccinium scoparium*, absent in Group A stands, occurred commonly in Group B stands. *Rubus pedatus* and *Antennaria racemosa* were the most abundant herbs; however, total herb cover was generally low.

Group C plots occurred in mesic to moist subalpine forests with an understory dominated by *Menziesia ferruginea*, *Rhododendron albiflorum*, and *Vaccinium membranaceum* (Table 4). These forests occurred throughout a large portion of the range of whitebark pine in British Columbia, and were sampled on all aspects of moderately steep slopes in the Coastal Mountains and the northern Columbia and Rocky Mountains (Table 3). Subalpine fir was the dominant tree species with lower crown cover of whitebark pine, lodgepole pine, and mountain hemlock (Table 4). Herb cover in these forests was low.

Group E plots represent mesic to moist upper subalpine communities on gentle, northerly slopes of the Purcell Mountains (Table 3). Lodgepole pine had the highest average overstory cover (Table 4) although subalpine fir had the greatest cover in older stands. Whitebark pine and sometimes lodgepole pine were abundant in young fire initiated stands (see Chapter 4). Cover of ericaceous shrubs in these forests was very high, with *Vaccinium myrtillus* the dominant species (Table 4); however, the herbaceous layer was sparse. Overall, the density of whitebark pine in these forests was very high and was exceeded only in forests sampled on the Interior Plateau (Table 3).

Plots of group F represent one, young, open stand located at the timberline in the Northern Rocky Mountains. Whitebark pine cover was low but greater than that of subalpine fir or Engelmann spruce, the only other trees present (Table 4). The high cover of *Phyllodoce empetriformis* in the understory was the reason for the segregation of this stand in the cluster analysis. Herbaceous species were common in this open-canopied stand; *Arnica latifolia* and *Anemone multifida* had the highest cover.

Groups D, G, and H represent a series of mesic upper subalpine to timberline communities with an understory dominated by *Vaccinium scoparium* (Table 4). These plots were sampled largely in the Columbia Mountains but also in the Cascades and Coastal Mountains and on isolated peaks in the Interior Plateau. Located on moderately steep (>30° inclination) aspects both Group D and G plots had high cover of *Menziesia ferruginea* but are distinguished from one another by the presence of *Lonicera utahensis* and high herbaceous cover in Group G plots. Of all forests sampled, *Arnica latifolia* had the highest cover in Group G plots where it dominated the herb layer (Table 4). Several other species indicative of moist, nitrogen rich soils occurred in these stands (e.g., *Aquilegia Formosa, Linnaea borealis, and Valeriana sitchensis*). Group D plots were located on predominantly northerly slopes, whereas Group G plots occurred on all slope aspects. Group H plots were amongst the highest elevation sites sampled; they occurred on warm aspects of the Coastal and Cascade Mountains, and in moist areas of the Columbia Mountains. Soils of these timberline sites were shallow and rocks were abundant (Table 3). Subalpine fir, which often formed tree skirts, and whitebark pine occurred as scattered trees of generally stunted growth. Subalpine larch (*Larix lyallii*) occurred in some stands in the southern Columbia Mountains but had low cover (<1%). *Vaccinium scoparium* was the dominant shrub (Table 4). Several characteristic high-elevation herbaceous species occurred on these sites (Table 4); *Carex* spp. and *Erythronium grandiflorum* had the highest cover. Total herbaceous cover was relatively high and diverse.

Group I plots were sampled in a single, closed canopy stand in the southeastern Purcell Mountains near the British Columbia/Montana border (Table 3). On a steep south slope, this stand had deep soil with a silty-clay texture and a thick humus layer (Table 3). Of all plot groups, this one had the greatest diversity of shrub species (Tables 3 and 4), although none of these shrubs had very high canopy cover. The most distinctive feature of this stand was the very high cover of *Xerophyllum tenax*, a species that is absent from all other plot groups (Table 3). Several good indicators of moist/rich soils were scattered in this stand (e.g., *Arnica latifolia, Thalictrum occidentale, Valeriana sitchensis, Zigadensis elegans*, and *Parnassia fimbriata*).

Groups J and K represent a series of communities sampled on dry sites. Group K plots were the driest sites sampled; they occurred in the dry continental climate of the Interior Plateau, on limestone ridge tops where soils were very shallow and exposed bedrock was common. Whitebark pine was abundant on these sites; among all groups it had the highest crown cover and density in Group K plots (Tables 3 and 4). Lodgepole pine was also common but subalpine fir and Engelmann spruce were virtually absent, presumably because these sites were so dry. The mat-forming shrubs *Arctostaphylos uva-ursi* and *Juniper communis* were the dominant shrubs; *Lonicera utahensis* was the only additional shrub on these sites, but it had considerably lower cover. The herb layer was dominated by drought-tolerant grasses (*Calamagrostis purpurascens* and *Poa secunda*) and sedges (*Carex* spp.). Plots in Group K had the highest cover of grasses and *Carex* spp. of any plot group. Group J plots represent stands of steep, dry, rocky ridges and upper slopes in the moister climates of the Cascade and Coastal Mountains (Table 4). Whitebark pine had considerably lower densities in Group J than in Group K plots but trees were small in plots of both groups (Table 4). The greater cover of subalpine fir probably reflects the moister climate of these mountain ranges. Shrub diversity in Group J plots was greater than in Group K plots but cover of all shrub species was relatively low (Table 3); *Vaccinium membranaceum* and *Juniperus communis* were the dominant shrubs. Various herbaceous species characteristic of dry rocky outcrops and high-elevations (e.g., *Lupinus arcticus*, *Phlox diffusa*, *Saxifraga bronchialis*, *Arenaria capillaris*) occurred in these plots (Table 3) but group J plots did not have the high cover of grasses found in the drier Group K plots.

Stand structure of closed forests

Plot groups A, B, C, D, E, G, and I occurred on sites that can support closed-canopy subalpine forests with large trees. Because stand age has a significant effect on the abundance of individual tree species in these forests (Table 5), it is best to examine stand structure and composition for these groups within this context.

Most young stands sampled (i.e., 37-125 years old) contained the four major species of these forests: subalpine fir, Engelmann spruce, whitebark pine and lodgepole pine (Table 6). Whitebark pine was most abundant in young stands of Groups E and G. Both lodgepole pine and whitebark pine established abundantly in stand 38 (Table 6), however, lodgepole pine had a greater density than did whitebark pine in the larger diameter classes (Table 6). Because lodgepole pine was abundant and grew faster, it formed a dense pole stand with whitebark pine in the understory. The presence of whitebark pine, but not small lodgepole pine in this stand suggests that whitebark pine is

Table 5. Kendall's correlations of tree species basal area (m^2/ha) and density (stems/ha) with stand age. The test statistic (t_s) and corresponding p-values are presented. Correlations are statistically significant at $p \leq 0.0021$ (i.e., [0.025/12]).

Species	τ	t_s	p
Basal area (m^2/ha):			
Abies lasiocarpa	0.261	3.63	0.0002
Picea engelmannii	0.023	0.32	0.7490
Pinus contorta	0.251	-3.45	0.0006
Pinus albicaulis	0.213	-2.96	0.0030
Pseudotsuga menziesii	0.074	3.58	0.0002
Tsuga mertensiana	0.258	1.03	0.3030
Density (stems/ha)[a]			
Abies lasiocarpa	0.319	4.43	0.0002
Picea engelmannii	0.130	1.81	0.0702
Pinus contorta	0.218	-3.02	0.0026
Pinus albicaulis	0.308	-4.28	0.0002
Pseudotsuga menziesii	0.122	1.69	0.0910
Tsuga mertensiana	0.238	3.30	0.0010

[a] Includes only trees greater than 1.3 meters tall.

Table 6. Tree density (stems/ha) by size-class (cm) for selected stands. Stand numbers correspond to those shown on Figure 1 and plot group letters to those shown in Tables 3 and 4. For stands with multiple sample plots, densities were averaged over size classes. Trees less than 1.3 m tall are indicated as < d.b.h. Stands are listed in order of increasing age within each age category

Stand No.	Plot group	Species	<d.b.h.	0–10	11–20	21–30	31–40	41–50	51–60	>60
						Stands 37–125 years old				
39	E	*Abies lasiocarpa*	2 725	725	0	0	0	0	0	0
		Picea engelmannii	1 000	550	0	0	0	0	0	0
		Pinus albicaulis	4 800	400	0	0	0	0	0	0
		Pinus contorta	100	125	0	0	0	0	0	0
31	D	*A. lasiocarpa*	5 200	1 950	25	0	0	0	0	0
		P. engelmannii	525	200	50	0	0	0	0	0
		P. albicaulis	200	75	0	0	0	0	0	0
15	C	*A. lasiocarpa*	4 767	333	33	17	8	0	0	0
		P. engelmannii	17	26	25	0	0	0	0	0
		P. albicaulis	975	83	42	0	0	8	0	0
		P. contorta	217	483	308	133	33	0	0	0
12	F	*A. lasiocarpa*	3 108	575	17	0	0	0	0	0
		P. engelmannii	25	8	25	0	0	0	0	0
		P. albicaulis	842	608	158	33	0	0	0	0
		P. contorta	17	0	0	0	0	0	0	0
38	E	*A. lasiocarpa*	2 550	1 000	75	0	0	0	0	0
		P. engelmannii	225	350	100	0	0	0	0	0
		P. albicaulis	1 525	1 825	25	0	0	0	0	0
		P. contorta	0	1 400	1 525	0	0	0	0	0
21	G	*A. lasiocarpa*	125	100	0	0	0	0	0	0
		P. engelmannii	25	25	0	0	0	0	0	0
		P. albicaulis	2 150	525	25	25	0	0	0	0
		P. contorta	375	250	150	200	25	0	0	0
		Pseudotsuga menziesii	125	150	150	50	0	0	0	0

Table 6 (continued)

Stand No.	Plot group	Species	<d.b.h.	0–10	11–20	21–30	31–40	41–50	51–60	>60
1	H	*A. lasiocarpa*	525	317	75	42	0	0	0	0
		P. albicaulis	658	117	17	8	0	0	0	0
		Larix lyallii	25	0	0	0	0	0	0	0
53	A	*A. lasiocarpa*	3 725	100	0	0	0	0	0	0
		P. engelmannii	0	25	0	0	0	0	0	0
		P. albicaulis	775	1 375	850	250	0	0	0	0
9	G	*A. lasiocarpa*	3 300	700	350	25	0	0	0	0
		P. engelmannii	50	100	175	50	100	0	0	0
		P. albicaulis	350	325	1 025	75	0	0	0	0
		P. menziesii	0	25	0	0	0	0	0	0
22	K	*P. albicaulis*	1 392	1 317	92	17	0	0	0	
		P. engelmannii	8	0	0	0	0	0	0	0
		P. contorta	58	158	133	17	8	0	0	0
		P. menziesii	8	25	0	0	0	0	0	0
Stands 126-250 years old										
11	D	*A. lasiocarpa*	1 500	1 000	225	50	0	0	0	0
		P. engelmannii	125	1 575	800	125	0	25	0	0
		P. albicaulis	125	125	175	25	75	25	0	0
		P. contorta	0	0	25	50	0	25	0	0
40	D	*A. lasiocarpa*	3450	75	125	75	0	0	0	0
		P. engelmannii	50	25	0	25	25	0	0	0
		P. albicaulis	950	925	450	325	25	0	0	0
		P. contorta	0	0	25	25	0	0	0	0
23	J	*P. engelmannii*	8	0	0	0	0	0	0	0
		P. albicaulis	392	425	225	25	0	0	0	0
		P. contorta	350	842	550	167	25	8	0	0

Table 6 (continued)

Stand No.	Plot group	Species	<d.b.h.	0–10	11–20	21–30	31–40	41–50	51–60	>60
2	D	*A. lasiocarpa*	1 988	1 213	138	0	0	0	0	0
		P. engelmannii	413	1063	50	0	0	0	0	0
		P. albicaulis	1 100	863	88	38	25	0	0	0
		P. contorta	0	588	525	63	0	0	0	0
		Larix lyallii	0	38	38	0	0	0	0	0
46	A	*A. lasiocarpa*	1 450	3 025	625	100	0	0	0	0
		P. engelmannii	0	50	25	0	0	0	0	0
		P. albicaulis	0	825	850	275	50	0	0	0
28	B	*A. lasiocarpa*	3 150	1 575	225	125	50	0	0	0
		P. albicaulis	650	0	0	25	75	50	50	0
		Tsuga mertensiana	25	50	25	0	0	0	0	0
24	B	*A. lasiocarpa*	6 075	3 550	600	125	17	8	0	0
		P. engelmannii	175	175	50	42	17	0	0	0
		P. albicaulis	133	108	17	17	50	8	0	0
		P. contorta	8	8	17	25	33	0	8	0
		P. menziesii	0	17	8	8	0	8	0	0
30	I	*A. lasiocarpa*	2 150	1 800	308	17	17	0	0	0
		P. engelmannii	75	50	0	8	17	0	0	0
		P. albicaulis	817	158	17	33	42	0	0	0
		P. contorta	42	17	25	42	25	8	0	0
		P. menziesii	25	0	0	0	0	8	0	0
8	C	*A. lasiocarpa*	650	1 025	83	25	0	0	0	0
		P. engelmannii	17	208	117	58	0	0	0	0
		P. albicaulis	0	8	8	75	33	8	0	0
		P. contorta	0	0	25	108	92	0	8	0
		T. mertensiana	467	817	267	92	17	0	0	0
		P. menziesii	0	12.5	0	0	0	13	13	0

Table 6 (continued)

Stand No.	Plot group	Species	<d.b.h.	0–10	11–20	21–30	31–40	41–50	51–60	>60
						Stands > 250 years old				
35	D	*A. lasiocarpa*	2 500	2 525	200	50	0	0	0	0
		P. engelmannii	75	1 175	125	25	0	0	0	0
		P. albicaulis	675	100	25	25	25	50	0	0
		Pinus contorta	0	150	150	25	0	0	0	0
		P. menziesii	50	0	0	0	25	0	0	0
		T. mertensiana	0	50	25	0	0	0	0	0
19	K	*P. albicaulis*	550	1013	1100	138	0	0	0	0
		P. menziesii	63	50	0	0	0	0	0	0
52	A	*A. lasiocarpa*	1 850	2 300	225	75	125	25	0	0
		P. engelmannii	0	0	0	25	0	25	100	100
		P. albicaulis	0	0	0	50	50	25	25	0
33	G	*A. lasiocarpa*	5 775	2 800	275	50	50	0	0	0
		P. engelmannii	1 975	1 600	200	75	25	0	0	0
		P. albicaulis	375	200	0	0	25	50	0	0
36	E	*A. lasiocarpa*	1 350	1 225	475	50	13	0	0	0
		P. engelmannii	113	75	0	0	0	0	0	0
		P. albicaulis	1 850	988	0	0	0	13	0	25
		Pinus contorta	25	188	238	13	0	0	0	0
25	B	*Abies amabilis*	75	50	50	0	0	0	0	0
		A. lasiocarpa	383	533	208	42	42	0	0	0
		T. mertensiana	163	563	488	150	13	0	0	0
		P. albicaulis	25	0	25	88	88	13	0	0
51	C	*A. lasiocarpa*	7 075	6 800	475	125	25	0	0	0
		P. engelmannii	125	225	0	25	25	0	0	0
		P. albicaulis	775	100	0	25	75	50	0	0
3	D	*A. lasiocarpa*	3 613	2 500	625	100	38	0	0	0
		P. engelmannii	138	38	25	0	0	0	0	0
		P. albicaulis	25	0	0	25	63	25	0	25
		Pinus contorta	0	0	0	0	13	0	0	0

considerably more tolerant of shade than lodgepole pine. When lodgepole pine was uncommon or absent in post-fire stands (e.g., stands 39, 31, 53, 9) whitebark pine was the major seral species. Whitebark pine did not grow markedly faster than its shade-tolerant associates subalpine fir and Engelmann spruce and thus larger whitebark pine trees in young stands were generally the result of earlier establishment (e.g., stand 21). Because the Clark's nutcracker caches whitebark pine seed in clumps, whitebark pine does not form dense young pole stands like lodgepole pine.

In intermediate-aged stands (i.e., 126-250 years old), lodgepole pine was less dense than in younger stands and occurred predominantly in larger size classes; few lodgepole pine successfully established in the understory (Table 6). Though the density of whitebark pine was lower in these stands than in younger stands, it continued to establish in the understory on most sites (Table 6). Subalpine fir was the most abundant tree in intermediate-aged stands; it was present in most diameter classes and constituted most of the multi-layered canopy that began to form in these stands (Table 6). Engelmann spruce was not as dense as subalpine fir in these stands and established less well in the understory than subalpine fir (e.g., stands 11, 40, 2, 46, 30).

With the exception of stand 52, whitebark pine was the largest tree found in stands greater than 250 years old (Table 6). The largest trees (up to 87 cm diameter at breast height) occurred in old, moist forests of the southern Coastal and Columbia Mountains (e.g., stands 52, 36, 3) (Table 6). In some old stands, whitebark pine had a bimodal size-class distribution, that is, trees in middle size classes were absent (Table 6). Although whitebark pine continued to establish in old stands (e.g., stands 51, 3, 35) (Table 6), few apparently survived to maturity. When the tree canopy was particularly dense (e.g., stand 36) fewer whitebark pine appeared to survive and the bimodal size class distribution was more pronounced (Table 6). Subalpine fir was the dominant canopy species in almost all old stands and the density of small individuals was very high (Table 6). On steep to moderately steep slopes of intermediate-aged and old stands, subalpine fir often spread through layering, which produced a very dense carpet of fir. Except on nutrient rich sites (e.g., stand 33 Group G) Engelmann spruce was a minor canopy component in most old stands (Table 6).

Structure of open forests

Plot groups F, H, J, and K were timberline or dry sites that supported only open stands. In young and old dry forests (e.g., stands 22 and 19) whitebark pine had the highest density (Table 6). Trees were small with no whitebark pine exceeding 30 cm d.b.h. Most whitebark pine grew in clumps in both stands. In stand 22, lodgepole pine occurred in all size classes and, though less dense, grew faster than whitebark pine on these sites. Small Douglas-fir (i.e., < d.b.h. and 0-10 cm) occurred on these sites but the absence of larger trees in the old stand suggests that they are unable to grow large at these elevations.

Whitebark pine was less dense on moister timberline sites (e.g., stands 1 and 12) (Table 6) and often grew in clumps. Subalpine fir was abundant in these stands; it often had tree skirts and formed tree islands.

Discussion

Compositional correlation among forest layers

The degree to which there are relationships among the composition of different vegetation layers has significant implications for several applications in forest ecology (e.g., ecosystem classification; models of community dynamics). It may also affect interpretations regarding the factors that influence compositional patterns in vegetation. The strength of correlations between the composition of different layers has long been questioned (Bratton 1975; Cain 1936; del Moral and Watson 1978; Gagnon and Bradfield 1986; Gleason 1926, 1939; Hoffman and Kazmierski 1969; Whittaker 1960) and direct quantitative tests have shown weak correlations between the composition of forest layers (McCune and Antos 1981; Sagers and Lyon 1997). Compositional correlation among forest layers also appears weak in this study.

The differing responses of the tree and understory layers to the moisture and stand age gradients, provides indirect evidence of weak relationships among forest layers in communities containing whitebark pine. While both the understory and tree layer composition showed significant relationships along a soil moisture gradient, only the composition of the tree layer varied significantly along a gradient of stand age (i.e., time since disturbance). Moreover, while moisture is the most important environmental factor influencing the composition of the understory it appears secondary to stand age in its influence on the composition of the tree layer.

Other studies have noted differences in response of forest layers to environmental gradients such as soil moisture (McCune and Antos 1981; Sagers and Lyon 1996). Differences in response to environmental gradients may largely be a matter of scale, that is, the same environmental gradient may not be perceived equally by all vegetation layers (McCune and Antos 1981). In forest communities containing whitebark pine, the understory layer was considerably more sensitive to changes in soil moisture (defined mostly by topographic position and aspect) than the tree layer. Sagers and Lyon (1997) found similar relationships between forest layers and soil moisture availability in riparian habitats. The tree layer likely experiences a much narrower range in soil moisture conditions because deep and extensive root systems make possible access to deeper soil moisture. In contrast, the shallow roots of many understory plants (especially herbaceous species) can make access to soil moisture more difficult. Thus, understory plants that can tolerate lower surface soil moisture levels will be found more frequently in dry environments, which relates to greater changes in composition along the soil moisture gradient than for trees.

Differences in rates of change of forest layers with respect to stand age has also been observed in other studies (Gilliam *et al.*, 1995; McCune and Antos 1981); among forest layers, the rate of recovery from disturbance may differ significantly (McCune and Antos 1981; Sagers and Lyon 1997). In this study, middle aged stands (approximately 80 to 160 years) generally supported an understory similar to that found in older forests (i.e., > 200 years). In contrast, the composition of the tree layer changes considerably within this time frame with a significant decrease in abundance of whitebark pine and lodgepole pine and increase in subalpine fir, Engelmann spruce, and mountain hemlock with stand age. The understory of very young stands containing whitebark pine is often considerably more species rich (particularly in herbaceous species) than middle-aged or old stands while the composition of the tree layer resembles middle-aged stands but greatly differs from old stands. Response to disturbance is influenced by a variety of life history traits (Grime 1979); compared to trees, understory shrubs and herbs recover more quickly in disturbed areas because of faster rates of colonization and maturation (Achuff and La Roi 1977; McCune and Antos 1981; Sagers 1993).

General community patterns

In British Columbia, compositional variation among types of forest communities containing whitebark pine can largely be attributed to soil moisture and elevation. Variation in vegetation composition and structure in mountainous habitats is often interpreted within the context of these gradients (Allen and Peet 1990; Antos and Zobel 1986; del Moral 1979; Peet 1981; Reigel *et al.* 1990; Stohlgren and Bachand 1997; Whittaker 1967). Compositional variation along the moisture axis generally reflects differences in soil moisture due to aspect, local topography (e.g., ridge top, upper slope, concave, etc.,), exposure, and patterns of snow accumulation and snowmelt. Increases in elevation are often associated with decreases in temperature and evapotranspiration, and increases in precipitation and snow depth (Barry 1981; Tranquillini 1979).

The changes in community composition that occur along the soil moisture and elevation gradients largely reflect plant responses to harsh environmental conditions on dry sites and on sites at the timberline. Communities on dry, rocky sites are dominated by species that are likely able to tolerate late summer drought (e.g., *Juniperus communis*, and various grasses). Communities dominated by species intolerant of summer drought are frequently restricted to areas where snow accumulates. As in this study, ericaceous communities dominated by *V. myrtillus* or *Phyllodoce empetriformis* are frequently associated with snow accumulation sites (Arno and Habeck 1972; del Moral 1979; Ogilvie 1990). Several researchers have indicated that patterns of snow accumulation and snowmelt strongly influence vegetation patterns (del Moral 1979; Douglas and Bliss 1977; Reigel *et al.* 1990). Though accumulation of snow on protected sites (e.g., depressions, northerly aspects) delays growth relative to more exposed sites (e.g., ridge crests, southerly aspects), snow melt provides soil moisture that may alleviate late-summer drought. Snow cover also provides insulation that reduces damage caused by winter desiccation. The shortened growing season at high elevations may retard leaf cuticle development in many species (Tranquillini 1979), which decreases resistance to water loss from strong winds and exposure to sun on ridges or southerly slopes. Species unable to tolerate the wind and radiation of exposed sites are more frequent where snow cover provides some protection.

There was also significant east/west variation in community composition. This correlation with longitude reflects, to a large degree, the distribution of *Vaccinium* spp. but is probably also a sampling artifact. The distribution of *V. myrtillus* and *V. scoparium* are largely restricted to the southeast portions of British Columbia; neither of these species occur in the Coastal Mountains of British Columbia (Douglas *et al.* 1990). While communities with abundant *V. membranaceum* occur in the Coastal Mountains, Rocky Mountains and Selkirk Mountains in British Columbia (Achuff *et al.* 1984b; Ogilvie 1990) I only sampled these communities in the Coastal Mountains. The correlation with longitude would likely not have been as strong if more *V. membranaceum* dominated sites were sampled in eastern British Columbia.

Time since fire disturbance has a significant effect on community composition through its effects on the composition of the tree layer; young stands are generally dominated by lodgepole pine and whitebark pine, and older stands by subalpine fir and Engelmann spruce. The frequency of fire disturbance and the subsequent rates of vegetation recovery have important influences on community composition and may vary significantly along major environmental gradients (Harmon *et al.* 1984; Peet 1981). For example, fires are often less frequent on moist sites (e.g., sheltered ravines, valley bottoms) compared to dry sites (Arno 1980; Romme and Knight 1981). Allen and Peet (1990) on the other hand, found fires to be more frequent on moist, north facing montane slopes in Colorado, which explained the presence of lodgepole pine-dominated communities on these sites. Frequent fires may partly explain the dominance of lodgepole pine or whitebark pine on dry sites, but ordination results provide little evidence in support of this; stands of varying ages are found in most communities sampled. However, Arno (1986) has indicated that moist, north slope communities containing whitebark pine burn less frequently than those on drier slopes and that this is an important reason for the greater amounts of subalpine fir on moist sites. Relationships between fire disturbance and moisture or elevational gradients and their effects on the species composition of whitebark pine communities is still not well understood.

Community comparisons with other localities

Communities similar to all of those described in this study are found in other localities. The *Vaccinium membranaceum* dominated communities (i.e., plot groups A and B) were sampled in the Coastal Mountains of British Columbia. A community similar to *Vaccinium membranaceum* communities of southwestern British Columbia (Group A plots) occurred on steep, mesic sites between 1850-2200 m in the Rocky Mountains of eastern British Columbia, Alberta, and northern Idaho and Montana (Achuff *et al*. 1984 a, b; Habeck 1969; Tomback *et al.*1995). Although I found *Vaccinium membranaceum* dominated communities mostly on southerly slopes, in the Rocky Mountains they occurred on various aspects. In Rocky Mountain stands 175-300 years old, Engelmann spruce and subalpine fir were the dominant tree species with *Vaccinium membranaceum* and *Rhododendron albiflorum* the dominant shrubs. The understory had few herbs with *Valeriana sitchensis* and *Viola orbiculata* the most common species, which is consistent with my results. Crown cover of whitebark pine in the Rocky Mountains was only about 5%, considerably less than on sites that I sampled in British Columbia. Agee and Kertis (1986) also described a *V. membranaceum* dominated community that contained whitebark pine; it occurred on steep upper slopes, between 1219-1896 m, in northern Washington. Aside from the dominance of *V. membranaceum* in the shrub layer, these communities differed markedly from the ones sampled in this study because *R. albiflorum* was absent and *Vaccinium deliciosum* and *Phyllodoce empetriformis* were common.

Rhododendron albiflorum/Menziesia ferruginea/Vaccinium membranaceum communities containing whitebark pine (i.e., Group C plots) in this study were sampled in moist, upper subalpine forests in the northern Rocky Mountains and the southern Coastal Mountains in British Columbia. A similar community occurred between 1770 and 2130 m on cool slopes of the Cascade Mountains in northern Washington (Arno and Habeck 1972) where whitebark pine grew with alpine larch (*Larix lyallii*), subalpine fir and Engelmann spruce. Whitebark pine density was about half that of the communities I sampled in British Columbia (i.e., 120 trees/ha) but this is probably because whitebark pine is often less abundant on cooler aspects in the Cascade Ranges (Arno and Habeck 1972; Arno and Hoff 1989). Similar vegetation was also documented for northern

Montana (Achuff *et al.* 1984 a,b; Habeck 1969)

The *Vaccinium scoparium* phase of the *Abies lasiocarpa*/*Vaccinium scoparium* habitat type described by Pfister *et al.* (1977) most closely resembles the upper subalpine *Vaccinium myrtillus* communities (i.e., Group E plots) sampled in southeastern British Columbia. This community is widespread in southern Montana occurring on well-drained soils, broad ridges, and gentle slopes at higher average elevations (i.e., 2100-2400 m) than *Vaccinium myrtillus* communities sampled in British Columbia. In southern Montana stands, *Vaccinium myrtillus* only occasionally dominated the understory; *Vaccinium scoparium* was generally the most abundant species. While older stands in Montana were dominated by lodgepole pine and subalpine fir, mature stands in British Columbia were predominantly of subalpine fir; young stands in British Columbia contained abundant lodgepole pine and whitebark pine. British Columbia stands also contained greater cover of shrubs indicative of moister environmental conditions (e.g., *Rhododendron albiflorum* and *Menziesia ferruginea*). *Carex geyeri*, an indicator of dry conditions (Arno and Weaver 1990; Pfister *et al.* 1977), was a prominent understory herb in Montana stands; the herb layer in British Columbia stands was depauperate. Higher summer precipitation in the Cranbrook study area probably accounts for the greater frequency of *Vaccinium myrtillus* dominated communities in British Columbia than in Montana. Several other upper subalpine communities in northwestern Montana had high *Vaccinium myrtillus* cover but low constancy; they also had considerably greater cover of *Xerophyllum tenax* and *Luzula hitchcockii* (Pfister *et al.* 1977). Timberline communities dominated by *Vaccinium myrtillus* occur on north and west aspects of the Cascade Mountains and occasionally in western Montana (Pfister *et al.* 1977; del Moral 1979). Krummholz subalpine fir and whitebark pine always occurred in these communities but the cold, windy conditions limited the occurrence of lodgepole pine. While the cover of whitebark pine in the Cascade Mountains was similar to that in the *Vaccinium myrtillus* communities I sampled in southeastern British Columbia, cover of whitebark pine in western Montana was considerably higher (i.e., 32 %). The undergrowth was more diverse than in lower elevational stands I sampled (because of more herbaceous species) but dominant species were the same. Lower elevation shrubs such as *Rhododendron albiflorum* and *Menziesia ferruginea*, which occurred in subalpine British Columbia communities, were absent in timberline stands in both the Cascade Mountains and in western Montana.

Only one stand containing whitebark pine with an understory dominated by *Phyllodoce empetriformis* was sampled in this study but similar communities also occur in upper subalpine to timberline habitats of the Rocky Mountains in British Columbia, Alberta, and Montana (Arno and Habeck 1972; Forcella 1978; Ogilvie 1990), the Columbia Mountains in British Columbia (B.C. Ministry of Environment, unpublished data, 1995, B.C. Ministry of Environment, Victoria, BC.) and in the Cascade Mountains of southern British Columbia and northern Washington (Agee and Kertis 1987; Arno and Habeck 1972; Arno and Hoff 1989; del Moral 1979; Franklin and Dyrness 1973). Whitebark pine occurred with a dominant understory of *Phyllodoce empetriformis* on south or east facing slopes in the Cascades and the Rocky Mountains of southern Montana (Arno and Habeck 1972; del Moral 1979). Alpine larch was dominant in some of these stands and whitebark pine occurred as krummholz on windswept ridges in these areas (del Moral 1979). The stand sampled in this study was considerably north of the range of alpine larch and was also considerably north of any other documented *P. empetriformis* communities containing whitebark pine. However, upper subalpine whitebark pine communities sampled on south and eastern aspects of the northern Rockies had a dominant understory of *Phyllodoce glanduliflora* (Achuff *et al.* 1984a), a species that frequently occurs and hybridizes with *P. empetriformis*.

Communities containing whitebark pine with an understory dominated by *Vaccinium scoparium* are widespread in British Columbia and also occur in Alberta (Achuff *et al.* 1984 a, b; Forcella 1978), Washington and northeastern Oregon (Arno and Habeck 1972; Daubenmire and Daubenmire 1968; Franklin and Dyrness 1973) and in Montana, Idaho and Wyoming (Forcella 1978; Pfister *et al.* 1977; Steele *et al.*, 1981, 1983). *Vaccinium scoparium* communities occur over a fairly wide habitat range from mesic, subalpine sites to dry, timberline sites. However, they appear to be restricted to dry, rocky southerly slopes near the timberline in coastal mountain ranges (Arno and Habeck 1972; Franklin and Dyrness 1973). In more continental regions, they extend to lower elevations (Pfister *et al.* 1977, Steele *et al.* 1981, 1983). Because *Vaccinium scoparium* communities occur over a wide range of habitats, understory species composition varies considerably. The *Abies lasiocarpa*/*Vaccinium scoparium* habitat types described for Montana, Idaho and Wyoming resemble the subalpine *Vaccinium scoparium* communities sampled in British Columbia (i.e., plot groups D and G). They occur on various aspects between 2100 and 2800 m in elevation. As in British Columbia stands, subalpine fir is the dominant climax species and both lodgepole pine and whitebark pine are important seral species. *Arnica latifolia, Carex spp.* and *Valeriana sitchensis* are reported to usually be present in the understory (Forcella 1978; Pfister *et al.* 1977; Steele *et al.* 1981, 1983). In contrast, *Erythronium grandiflorum*, which is distinctive species in British Columbia stands, is absent or has low cover and constancy in forests further south. In drier parts of Montana, and in Idaho and Wyoming, *Abies lasiocarpa*/*Vaccinium scoparium* communities grade into stands of almost pure and abundant whitebark pine (with an understory of *Vaccinium scoparium*) at the timberline. This type of transition was not apparent in British Columbia; whitebark pine seems to occur with subalpine fir to the timberline on sites dominated by *Vaccinium scoparium*. In addition to *Vaccinium scoparium, Phyllodoce empetriformis*, *Erythronium grandiflorum*, *Carex spp*. and *Anemone occidentalis* were common in British Columbia timberline stands. The composition of timberline communities in the northern Rocky Mountains of British Columbia (Achuff *et al.* 1983a, b) was similar to those I sampled in other parts of British Columbia. In contrast, timberline sites in Montana, Idaho, and Wyoming had considerably greater cover of grasses and *Carex geyeri* (Pfister *et al.* 1977; Steele *et al.* 1981, 1983). Differences in precipitation patterns probably account for the differences in species composition among *Vaccinium scoparium* communities. Forcella (1978) also noted clinal changes in the species composition of whitebark pine/*Vaccinium scoparium* communities with latitude. He suggested, however, that this variation could not entirely be attributed to habitat differences and that the floristic composition of these communities was also a function of the available flora.

Communities that contain whitebark pine and have an understory dominated by *Xerophyllum tenax* are restricted to southeastern British Columbia, but are extensive in Montana and occur south to central Idaho (Pfister *et al.* 1977; Steele *et al.* 1981). The eastern limits of these communities are generally associated with the edges of the maritime climate influence (Pfister *et al.* 1977). *Xerophyllum tenax* sites with whitebark pine occupy the mid-to upper elevations of the subalpine zone (i.e., ca. 1800-2200 m) occurring on predominantly dry, southerly aspects in British Columbia and Montana but on various aspects in Idaho (B.C. Ministry of Environment, unpublished data, 1995, B.C. Min. Environ., Victoria, BC; Pfister *et al.* 1977; Steele *et al.* 1981). The stand sampled in this study is quite similar to the *X. tenax* communities identified by Pfister *et al.* (1977) and Steele *et al.* (1981) in Idaho and Montana. The British Columbia stand, however, had considerably more *X. tenax*, but markedly less *Vaccinium* spp. than more southern stands. Tree composition closely resembles Idaho communities with dominant subalpine fir, and lesser amounts of Engelmann spruce, lodgepole pine and whitebark pine. In Montana, subalpine fir co-dominates stands with lodgepole pine and Douglas-fir at lower elevations; Pfister *et al.* (1977) suggested that frequent fires maintained seral species as dominants in these stands. Crown cover of whitebark pine in the British Columbia stand was similar to that in Montana and Idaho stands, about 7%.

Whitebark pine communities with an understory dominated by *Juniperus communis* are widespread. In this study, these communities were sampled in the eastern Coastal and Cascade Mountain Ranges and on isolated peaks in the Interior Plateau, but they also occur in the Rocky Mountains and the southern Columbia Mountains in British Columbia (Achuff *et al.* 1984; Ogilvie 1990) and are very common in Alberta (Ogilvie 1990; Forcella 1978). Whitebark pine/*Juniperus communis* communities are also common in the eastern Cascades of Washington (Agee and Kertis 1987; Daubenmire and Daubenmire 1968; del Moral 1979; Franklin and Dyrness 1973) and the Rocky Mountains of Montana, Idaho, and Wyoming (Pfister *et al.* 1977; Steele *et al.* 1981, 1983). The moist climate variant of the *Juniperus communis* communities sampled in this study (i.e., Group J plots) closely resembled whitebark pine/*Juniperus communis* communities in Washington, Oregon, and the northern Rocky Mountains of British Columbia, Alberta and northwest Montana (B.C. Ministry of Environment, unpublished data, 1995, B.C. Min. Environ. Victoria, BC.; Pfister *et al.* 1977), which occurred predominantly on southern slopes and dry, exposed high ridges and rocky knolls or scree slopes at or near the timberline. They also resembled whitebark pine/*Juniperus communis* communities in Wyoming and Idaho that occur at lower topographic positions on gentle slopes, in cold air drainages and other protected areas (Agee and Kertis 1987;

del Moral 1979; Steele *et al.* 1981, 1983). Whitebark pine is the dominant tree in these communities with lesser amounts of subalpine fir and alpine larch (Agee and Kertis 1987). As in the stands sampled in British Columbia, diverse understories that vary considerably among regions have also been noted in other areas (Steele *et al.* 1981; Pfister *et al.* 1977). The dry climate variant of the whitebark pine/*J. communis* community (i.e., Group K plots), sampled in the Interior Plateau of British Columbia, resembles whitebark pine/ *J. communis* communities in similarly warm and dry areas of eastern Idaho and western Wyoming. Like the British Columbia stands, these communities occurred on upper slopes and ridges. Whitebark pine was often the sole dominant in these communities on wind exposed sites in both Idaho and Wyoming; in more protected areas, both whitebark and lodgepole pine dominated stands. Subalpine fir and Engelmann spruce were usually absent because of the harsh environmental conditions (Steele *et al.* 1983) but *Pinus flexilis* was often a minor component of stands in Idaho and Wyoming. These dry climate whitebark pine/*Juniperus communis* communities had a considerably less diverse understory than the moist climate variant; *Juniperus communis* and *Arctostaphylos uva-ursi* were the most common shrubs in both British Columbia stands and Idaho and Wyoming stands. However, while the understory of Idaho and Wyoming stands had low herb cover, herb cover (predominantly graminoids) in British Columbia stands was quite high. This is probably because the stands are more open due to stunted tree growth but may also be due to differences in soils or substrate (i.e., surface geologic type); British Columbia stands were sampled on calcareous substrates (i.e., limestone) and one stand had moderately deep soils with no exposed bedrock. In whitebark pine/*Juniperus communis* communities whitebark pine ranges from a scattered tree on rocky sites and talus slopes to an abundant tree on upper slopes with greater soil development (Agee and Kertis 1987; Steele *et al.* 1983).

While the most commonly occurring communities containing whitebark pine were sampled in this study, several others occur in British Columbia. Sites dominated by *Festuca scabrella* occurred on south and west-facing upper-subalpine/timberline slopes of the Rocky Mountains (B.C. Ministry of Environment, unpublished data, 1995, B.C. Min. Environ., Victoria, B.C.; Ogilvie 1990). Whitebark pine occurred as small stunted trees but was often abundant with considerably lesser amounts of subalpine fir.

Communities dominated by *Cassiope mertensiana* occurred on more mesic, upper subalpine to timberline sites in the northern Rocky Mountains, the Selkirk Mountains of southeastern British Columbia, and in the Cascade Mountain Ranges in Washington (Achuff *et al.* 1984a, b; B.C. Ministry of Environment, unpublished data, 1995, B.C. Min, Environ., Victoria, BC; del Moral 1979; Ogilvie 1990). In the northern Rocky and Selkirk Mountains, communities dominated by *C. mertensiana* occurred on moderate slopes with southerly and easterly aspects (Achuff *et al.* 1984a, b). In the Cascade Mountains, this community occurred on wind protected sites of various aspects at about 2200 m (del Moral 1979). A distinctive lichen dominated community occurred on the upper, eastern slopes of the northern Coastal Mountains (Banner *et al.* 1993; Yole *et al.* 1989). *Cladina rangiferina* and *Cladonia* spp. formed the main ground cover with a sparse shrub cover of *Vaccinium membranaceum* and *Cassiope mertensiana*. Whitebark pine was the most prominent tree species on these sites. In the southern Rocky Mountains of British Columbia, *Dryas octopetala* dominated the understory on wind exposed sites where relatively little snow accumulated (Ogilvie 1990). A tall willow-forb (i.e., *Salix* spp. – *Valeriana*) community occurred on steep, easterly aspects between 1580-1960 m in the Rocky Mountains of Alberta and southeastern British Columbia (Achuff *et al.* 1984 a, b; Ogilvie 1990). A similar community occurred between 2012 and 2713 m on northerly aspects in eastern Idaho and northwestern Wyoming (Steele *et al.* 1983). Whitebark pine had 15 % crown cover in these communities and *Pachistima myrsinites*, *Shepherdia canadensis*, and *Viola canadensis* were other common understory species. No *Salix-Valeriana* dominated communities containing whitebark pine have been documented for Montana (Pfister *et al.* 1977).

Factors limiting the distribution and abundance of whitebark pine

Winter desiccation of foliage is an important factor that defines the northern and elevational limits of whitebark pine (Arno and Weaver 1990). For most trees at high latitudes and altitudes, shortened growing seasons often result in incomplete leaf cuticle development; thus, foliage exposed to the wind above the snowpack is more prone to desiccation (Tranquillini 1979; Wardle 1971). Sowell *et al.* (1982) have shown that cuticular resistance of whitebark pine foliage to desiccation drops significantly with increasing elevation in the Sierra Nevada. Low resistance to foliar desiccation also delineates the northern and elevation limits of subalpine fir, Engelmann spruce, lodgepole pine and alpine larch (Wardle 1971; Richards and Bliss 1986). However, the fact that whitebark pine is more abundant and often the only species on exposed timberline sites, suggests that it is much more tolerant of winter desiccation than are other subalpine species. In this study, subalpine fir was usually most abundant in timberline areas where snow probably covered whole trees and could protect the foliage from exposure. Lodgepole pine, which commonly occurred with whitebark pine at lower elevations, was distinctly absent from most near-timberline stands and from exposed sites. Kronfuss (1994) found that *Pinus cembra*, a close relative of whitebark pine, is very sensitive to small fluctuations in temperature and begins the initial phases of height growth two months earlier than larch or spruce in high-elevation habitats of the Alps. Weaver (1990) indicated that the climatic conditions under which *Pinus cembra* grows are similar to those where whitebark pine grows. Thus, it is possible that early growth initiation also occurs in whitebark pine, which would increase the time available for maturation of the leaf cuticle and this could explain why whitebark pine can occur at higher elevations and on more exposed sites compared to other subalpine species.

Moisture stress caused by summer drought (i.e., soil moisture deficits) may also have an important influence on the distribution of whitebark pine. The effect of soil moisture stress is particularly evident in comparisons of vegetation on calcareous substrates versus vegetation on non-calcareous substrates. Limestone often weathers to produce excessively well-drained soils that limit the growth of many conifers (Pfister *et al.* 1977). In especially dry climates such as northern Nevada and eastern California, whitebark pine is largely confined to non-calcareous substrates (Weaver and Dale 1974). In contrast, whitebark pine grows on both calcareous and non-calcareous substrates in most northern regions of its range in the U.S. (Arno and Weaver 1990; Steele *et al.* 1981, 1983; Pfister *et al.* 1977; Weaver and Dale 1974) and also in British Columbia. However, the communities on limestone substrates in British Columbia (e.g., stand 19 in the Interior Plateau) were composed of drought tolerant species including *Juniperus communis* and many grasses. Pfister *et al.* (1977) found similar communities on limestone derived soils in Montana. Results of my study showed that whitebark pine was most abundant (and virtually the only species) on high elevation sites where other trees would likely experience summer soil moisture stress. Whitebark pine may have more efficient stomatal control or may be better able to tolerate low soil water potentials compared to its common associates.

Competition with subalpine fir and the prominence of fungal diseases associated with prolonged snow cover probably contribute to the lower abundance of whitebark pine on northerly (and sheltered) timberline slopes. Competition with subalpine fir may be more intense on northerly timberline sites because subalpine fir grows more vigorously and is more abundant on these sites (Pfister *et al.* 1973). I observed mortality of whitebark pine seedlings from snow mold on several timberline sites. Hoff and Hagel (1990) have reported high whitebark pine seedling mortality from brown felt blight (*Herpotricha coultrei* Peck.) after prolonged snow coverage. The importance of fungal infections associated with areas of snow accumulation has long been recognized for its importance in controlling species distributions in high elevation habitats. For example, Van Arsdel (1965) reported that prolonged snow coverage facilitated the snow molds that killed most young *Pinus cembra* and *Pinus mugo* occurring at the timberline. More recently, Senn *et al.* (1994) reported lower mortality rates of *Pinus cembra* seedlings planted on early snow-free sites compared to those planted on sites with long-lasting snow cover.

Low temperatures that produce growing season frosts may also limit the upward extension of whitebark pine. This hypothesis is supported by the absence of whitebark pine in frost pockets (Weaver 1990). However, Tranquillini (1979) has suggested that the direct effects of summer frosts on trees are limited and that the low temperatures have an indirect effect by interfering with cuticle development, which leads to winter desiccation. Arno and Habeck (1972) suggested that the absence of alpine larch at low elevations and lack of success in cultivating this species is because higher temperatures at lower elevations might cause damage. Whitebark pine, in contrast, may grow to very low elevations; it has been found on frequently disturbed sites in valleys of the Bitterroot Mountains (Arno and Habeck 1972). Also, increased seedling photosynthesis and survival of cultivated trees at low elevations suggests that temperatures of low elevation sites may not significantly limit whitebark pine (Jacobs and Weaver 1990; Weaver 1990). Competition with sympatric species at lower elevations is more likely to limit the occurrence of whitebark pine at lower elevations.

The reduced abundance of both whitebark pine and lodgepole pine with stand age reflects poor competitive ability. Both whitebark pine and lodgepole pine quickly and often abundantly colonize subalpine sites following fire. But, because both species are relatively intolerant of shade, lodgepole pine and whitebark pine may be successionally replaced by shade-tolerant subalpine fir and, to some degree, Engelmann spruce. Though the abundance of whitebark pine decreases considerably with stand age, it may persist in the understory considerably longer than lodgepole pine suggesting that it is, at least, able to tolerate shade better than lodgepole pine. The occurrence of whitebark pine on frequently disturbed sites in the canyon bottoms of the Bitterroot Mountains in Montana (Arno and Habeck 1972) emphasizes the important effect of disturbance on the maintenance of whitebark pine at low elevations. Natural disturbance is vital to the maintenance of substantial whitebark pine populations in subalpine stands where subalpine fir and Engelmann spruce are abundant. Arno and Weaver (1990) indicate that the suppression of natural fire disturbance has resulted in decreased establishment of new whitebark pine communities.

Seed dispersal and caching habits of Clark's nutcracker (*Nucifraga columbiana*) also play an important role in the distribution and abundance of whitebark pine. Part of the reason why whitebark pine is more abundant on southern slopes and other exposed sites (e.g., ridges, roadside cuts, burned sites) is because of the seed caching behavior of Clark's nutcracker. Clark's nutcracker preferentially caches seed on south-slopes and other exposed sites because these sites are subject to lower seed predation and because they usually have less snow, which makes seed retrieval easier (Hutchins 1990; Hutchins and Lanner 1982; Tomback 1986; Tomback 1994). This, combined with the prominence of fungal diseases on sites with prolonged snow cover and competition with subalpine fir, probably accounts for the lesser abundance of whitebark pine on north exposures and other protected sites near the timberline.

Grime (1974, 1979) has argued strongly that the occurrence of a plant in a particular habitat is the result of evolved adaptations to disturbance and stress. Accordingly, he classified plants based on three primary life-history strategies: competitive species, which are adapted to productive, undisturbed habitats; ruderal species, which are adapted to productive and frequently disturbed habitats; and stress-tolerant species, which are adapted to both unproductive and undisturbed habitats. While these strategies represent extremes in evolutionary specialization varying intermediate "secondary" strategies occur (e.g., Bzreziecki and Kienast 1994; del Moral 1983; Grime 1979). Like its close relative *Pinus cembra*, whitebark pine represents a classic example of a stress-tolerant species (Brzeziecki and Keinast 1994). Relative to other conifers, whitebark pine is inherently slow-growing; even in newly disturbed habitats with ample light, it grows considerably slower than co-occuring lodgepole pine. Whitebark pine is tolerant of severe environmental conditions; for example, adaptations such as early initial shoot growth may account for its greater tolerance to winter desiccation compared to other sympatric conifers. Earlier initial shoot growth and, presumably, earlier cone initiation, however, is contrary to del Moral's (1983) suggestion that stress tolerant species are "late bloomers". The competitive ability of whitebark pine is low; though it occurs over a wide range of habitat types, from productive to very non-productive, its relatively slow growth causes it to be successionally replaced by faster growing species on productive sites. On unproductive sites such a rock outcrops, talus slopes, and xeric sites, whitebark pine is considerably more abundant and persistent mostly because the species that it competes with on more productive sites (e.g., subalpine fir) are rare or absent due to the extreme environmental conditions.

Chapter 3

The distribution and incidence of blister rust and mountain pine beetle in whitebark pine stands in British Columbia

Introduction

Abiotic disturbances such as wind, fire, and landslides have long been recognized for their important influence on the composition, structure, and dynamics of forest ecosystems (Ahlgren and Ahlgren 1960; Arno 1980; Day 1972; Hemstrom and Franklin 1982; Pickett and White 1985; Rowe and Scotter 1973; Tande 1979). Until recently, the effect of biotic disturbances, especially the role of pathogens, has received considerably less attention (Burdon 1987; Dickman and Cook 1988; Gilbert *et al.* 1994).

Existing at endemic levels, pests and pathogens play an important role in forests as they eliminate less vigorous individuals (compromised by overcrowding, drought, etc.) and create canopy openings in which new seedlings can establish or small trees in the seedling bank can increase in growth (Mattson and Addy 1975). However, both native and exotic pests and pathogens can reach epidemic levels at which they often kill even vigorous trees, and in some cases they have destroyed most individuals of a species over large areas (Hudak *et al.*1992; Keane and Arno 1993; Lavallée 1986; Morin and Bergeron 1995; Ziller 1975). These organisms can have a profound impact on the structure and dynamics of the forests they affect (Dickman and Cook 1988; Burdon 1987; Gilbert *et al.* 1994; Keane and Morgan 1994; Keane *et al.* 1990; Kneeshaw and Bergeron 1996; Schuman 1991) and they are also of great economic importance because they may destroy large amounts of merchantable timber.

Epidemics of spruce budworm (*Choristoneura fumiferana*), Canada's most destructive forest pest, have caused enormous losses of *Abies balsamea* in Ontario and Quebec, and mountain pine beetle (*Dendroctonus ponderosae*) continues to be the most destructive pest of lodgepole pine forests in western North America, causing considerable commercial timber loss and large changes in stand structure (Hudak *et al.* 1992). Once a major hardwood timber and horticultural species of the eastern United States, the American chestnut (*Castenea dentata*) has been virtually eliminated by chestnut blight, a disease caused by the introduced fungus *Endothia parasitica* (Anagnostakis 1987;

Bingham et *al.* 1971). Similarly, Dutch elm disease, caused by the introduced fungus *Ceratocystis ulmi*, has resulted in extensive mortality of North American elms (Bingham et *al.* 1971; Hudak *et al.* 1992). Since its introduction to North America in the early 1900's, white pine blister rust (*Cronartium ribicola*) has contributed to major losses of timber species like *Pinus strobus* and *Pinus monticola* (Lavallée 1974, 1986; MacDonald and Hoff 1991; Plourde *et al.* 1991). Within 25 years of its introduction, white pine blister rust also spread throughout the ranges of *Pinus flexilis* and *Pinus lambertiana* (Hoff 1992).

Recently, white pine blister rust and epidemics of mountain pine beetle were found responsible for the rapid decline of whitebark pine in Montana between 1971 and 1992 (Keane and Arno 1993). Though numerous insects and diseases are reported to cause damage to whitebark pine (Arno and Hoff 1989; Bartos and Gibson 1990; Hagel *et al.* 1987; Hepting 1971; Hiratsuka and Funk 1976; Hoff and Hagel 1990; Smith 1978), the introduced white pine blister rust and native mountain pine beetle are considered the most widespread and damaging (Finck *et al.*1988; Hoff and Hagel 1990; Keane and Arno 1993).

White pine blister rust infects trees through leaf stomata (Patton and Johnson 1970). The fungus grows through the leaf to the main stem producing cankers on branches and the main stem within 12 to 18 months of infection (Hunt 1983; Hunt and Meagher 1992). Three to four years later, blister rust cankers begin to fruit (Hunt 1983). Because it disrupts the transport of material in the phloem, repeated annual fruiting causes progressive branch and stem die-back above the site of the canker and, eventually, the death of the tree. Blister rust appears to be especially detrimental to young trees that are likely to be killed by a single canker on the main stem; larger trees are more commonly killed through progressive branch die-back.

The life-cycle of white pine blister rust requires two hosts; two spore producing stages occur on whitebark pine and three other spore producing stages occur on the alternate hosts, *Ribes* spp. (gooseberries and currants) (Callan and Funk 1994; Hunt and Meagher 1992). In late summer, teliospores are produced on the underside of *Ribes* leaves. In the fall, teliospores germinate to produce basidiospores that are transported, by wind, to pine foliage where they germinate and infect the tree through the leaf stomata.

Successful infection is visible as a needle spot within about 30 days (Tomback *et al.* 1995). The range of basidiospore dispersal is about 2 km (aeciospores from infected pines may travel up to 150 km to re-infect *Ribes* bushes) (Wescott 1990). However, because fungal spores generally require high humidity or liquid water for development and germination (Harrison *et al.* 1994), dry environments may significantly limit the spread of white pine blister rust (Arno and Hoff 1989; Hoff and Hagel 1990; Van Ardsel 1965; Wescott 1990).

Like most bark beetles, endemic populations of mountain pine beetle are secondary in their attack in that they infest trees that are already of poor health (Hudak *et al.* 1992). Under epidemic population levels, however, mountain pine beetles also attack healthy trees (Knight and Heikkenen 1980). In the U.S., a large proportion of mature whitebark pine trees in the Rocky Mountains were killed by epidemics of mountain pine beetle between 1909 and 1940 (Ciesla and Furniss 1975; Furniss and Carolin 1977). Beetle infestations evidently spread upward into whitebark pine forests after having become established in the lodgepole pine forests below. Similar situations were documented during mountain pine beetle epidemics of the 1970's and 1980's in the Pacific Northwest (Arno and Hoff 1989; Bartos and Gibson 1990). Although bark beetles are a major, natural mortality factor in whitebark pine forests, there is potential for increased effects because of interaction with blister rust. Whitebark pine trees infected by blister rust are thought to be most susceptible to attack by mountain pine beetle. Keane and Arno (1993) found evidence of mountain pine beetle attack present only on rust infected trees sampled in Montana during 1992.

Mountain pine beetles attack trees in mid- to late summer and excavate galleries, parallel to the grain of the wood, in which females lay their eggs. The resulting larvae feed on the phloem, excavating a further network of galleries in the inner bark. Because the phloem provides food for the developing larvae, phloem thickness is a critical determinant of which trees will be attacked and is the reason why larger and older trees are preferred (Baker *et al.* 1971). Infested trees generally die from a combination of damage caused by the larvae and by blue stain fungus, which is carried by the beetles (Hudak *et al.* 1992). The foliage of infested trees turns red-brown in the spring following the attack, and death of the tree soon follows.

Populations of mountain pine beetle have decreased from the epidemic levels observed in western North America during the 1970's and 1980's, and while these epidemics may have had an important effect on stands containing whitebark pine, the effects of blister rust on this species are believed to be of more immediate importance (Arno 1986; Keane and Arno 1993; Kendall and Arno 1990). White pine blister rust appears to be the most serious cause of the recent decline in whitebark pine; mortality from blister rust is as high as 90-100% in some areas of the U.S. (Keane and Arno 1993; Kendall *et al.* 1996; Smith and Hoffman 1996). Furthermore, an epidemiological study of white pine blister rust on various North American white pines, indicates that, in contrast to many insect infestations, the severity of white pine blister rust is not cyclical over a period of years but rather that population growth is logistic and thus, rates of infection and mortality will continue to increase (Merrill 1991). Blister rust also poses a particularly difficult problem because whitebark pine has very low levels of natural resistance to this disease (Arno and Hoff 1989; Hoff *et al.* 1980).

Neither the range nor the degree of damage to whitebark pine caused by white pine blister rust infections and mountain pine beetle infestations in British Columbia have been documented. The objectives for this chapter, therefore, were to:

1. determine amounts of mortality of whitebark pine and incidence of white pine blister rust infection in stands throughout the geographic range of whitebark pine in British Columbia, and identify environmental conditions and stand characteristics associated with greater amounts of mortality and disease;
2. document the geographic distribution and severity of mountain pine beetle infestations on whitebark pine.

Materials and Methods

Sampling Methods

During 1995 and 1996, 53 stands distributed throughout the range of whitebark pine in British Columbia were sampled (see methods on stand selection and plot placement in Chapter 2). In each stand, 1–3 400m^2 (20x20m) plots were placed at least 50 m apart. All whitebark pine trees in a plot were examined for evidence of white pine blister rust infection and for past or present mountain pine beetle infestation. The following information was recorded for all whitebark pines: diameter at breast height (trees shorter than breast height were recorded as < 1.3 m tall); the number of blister rust cankers on the tree and their location (i.e., main stem or branch); the presence of crown damage (i.e., the percentage of the tree crown killed and whether or not branch flagging and dead tops were present); the presence or absence of mountain pine beetle infestation (instances of infestation were recorded for each tree if the characteristic "J"-shaped galleries mined by these beetles were present); and whether the tree was standing dead (i.e., a snag) or alive. When it could be determined, the cause of death was noted. Because rodents feed on bark at the site of blister rust cankers (Hoff 1992), the presence of such damage was also noted. Binoculars were used to check for cankers on the trunk and branches of large trees.

Vegetation composition and structure data as well as site data were collected in each sample plot as described in Chapter 2. Stand age was determined from annual ring counts of increment cores taken from the largest trees in the sample plots.

Data Analyses

Very little evidence of mountain pine beetle infestation was found on whitebark pine and no whitebark pine deaths could be attributed solely to the beetle. Consequently, only a tabular summary of these findings is presented; the data are too limited to permit analysis of factors related to beetle infestation. Data analyses in this chapter examine how the total amounts of whitebark pine mortality and the rates of blister rust infection vary among stands.

White pine blister rust in stands is described by 3 dependent variables: (i) the percentage of dead whitebark pine trees per plot (% mortality); (ii) the percentage of living whitebark pine trees with obvious blister rust cankers in a plot ($\text{infection}_{\text{min}}$); and (iii) the percentage of living whitebark pine trees in a plot with any evidence of blister rust infection (including trees with dead tops, flagged branches, and rodent gnawing) ($\text{infection}_{\text{max}}$). Cankers can be difficult to detect on some trees because rodents often eat them, and because the height of large trees makes cankers difficult to see (even with binoculars); $\text{infection}_{\text{min}}$ is thus likely to underestimate the actual infection level. In contrast, $\text{infection}_{\text{max}}$ is likely to overestimate the actual infection rate because not all branch flagging is due to blister rust cankers and because not all sites of rodent herbivory are at the site of a canker. These same measures of mortality and infection are being used in extensive surveys of whitebark pine in the U.S. (e.g., Kendall *et al.* 1996; Smith and Hoffman 1996) and thus should permit useful comparisons of mortality and blister rust incidence among studies. They are also the only practical way to assess blister rust infection.

Because there are several potential causes of seedling mortality other than blister rust (e.g., drought, insulation, herbivory, frost heaving, damping off fungi and poor root development [McCaughey 1994; McCaughey and Schmidt 1990; Tomack *et al.* 1995]) and because infection on seedlings can be difficult to detect, whitebark pine trees less than 1.3 m tall were eliminated from calculations of mortality and infection. Deaths determined to be the result of intense suppression were eliminated from calculations of mortality rates; these accounted for less than 1% of whitebark pine mortality. Small, dead understory trees with suppressed growth and no sign of blister rust (old cankers are easily seen on small trees) were determined to have died as the result of suppression. Because mortality and infection rates of whitebark pine could be quite unreliable when calculated from very small numbers of trees, only stands with ≥ 10 trees (45 of the 53 stands) were included in the analyses. For stands with multiple plots, percentage mortality and percentage infection were averaged over the plots to give a value for the stand (see Sit 1995). Percent mortality and percent infection data were normalized using an arcsine transformation prior to analysis (Sokal and Rolf 1995).

Variables that may explain variation in mortality and blister rust infection rates among stands can be divided into two groups. The first group (abiotic variables) includes: latitude, mean summer precipitation (mm), elevation (m), a soil moisture class, and slope aspect. Mean summer precipitation data for the Engelmann Spruce-Subalpine Fir vegetation zone (i.e., the uppermost forested zone in southern British Columbia) were obtained from a database of long-term climate records (B.C. Ministry of Environment and B.C. Ministry of Forests, unpublished data, 1997, B.C. Ministry of Environment, Victoria, B.C.). Data were available from 76 meteorological stations in the Engelmann Spruce-Subalpine Fir vegetation zone. For each stand sampled, mean summer precipitation data from the closest meteorological station were used; distances of sample stands from meteorological stations ranged 0.5 to 297 km (mean = 133 km). The elevational range of meteorological stations used was 1021 to 1920 m. Soil moisture classes were derived from the soil moisture index developed in Chapter 2. Plots with a soil moisture index of 1, 2, or 3 were grouped as very dry sites; those with an index of 4 or 5 as dry sites; and those with 6 or 7 as moist sites. Aspect was divided into 5 categories (1 = 180 –225°; 2 = 136 – 180° 3 = 226 – 315°; 4 = 46 – 135° and 316 – 360°; 5 = 0 – 45 °). The second group of variables describes structural and compositional characteristics of a stand. These include the percentage crown cover of all main canopy trees (i.e., trees taller than 10 m); the understory plant community type (see Chapter 2); the density (stems/ha) and basal area (m^2/ha) of whitebark pine and of all trees in the plot greater than 1.3 m tall; stand age; and the presence/absence of *Ribes* spp. in the plot. Normalization of density data was achieved by a log-transformation, whereas a square root transformation was used for basal area data. The density, basal area, and canopy cover data for replicate plots were averaged to get a value for the stand sampled. Total main canopy cover was normalized using a square root transformation prior to analysis. Understory plant community type and the presence/absence of *Ribes* spp. are categorical variables and did not require transformation.

Potential relationships between the independent variables and whitebark pine mortality or blister rust infection rates in stands were assessed with one-way analysis of variance for categorical variables and by simple linear regression for continuous variables using the ANOVA and Regression procedures in SAS (SAS Institute Inc 1994).

Results

Distribution of blister rust and mountain pine beetle

Infestation of whitebark pine by mountain pine beetle was rare. Only 7 of the 53 stands sampled contained signs of mountain pine beetle infestation, and the number of beetle infested whitebark pine trees within stands was very low (Table 7). Over all stands, only 17 of 3594 whitebark pine trees greater than 1.3 m tall had mountain pine beetle galleries. Furthermore, galleries were not extensive and the sparseness of horizontal larval galleries on many trees (which extend outward from the "J" shaped maternal gallery where eggs are laid) suggests that larvae often did not survive the winter. All but one of the infested trees observed was dead but none of the deaths could be attributed solely to mountain pine beetle (Table 7). Many trees infested by beetle had sign of blister rust infection (e.g., old cankers) (Table 7). Past and present infestations of mountain pine beetle were restricted to stands in the southern and drier portions of the range of whitebark pine in British Columbia (see Table 1 and Figure 1 in Chapter 2). Infested trees were observed over a wide elevational range (Table 7). Almost all infested trees were greater than 10 cm in diameter (Table 7).

In contrast to damage by bark beetles, whitebark pine was infected by white pine blister rust throughout its geographic range in British Columbia (Figures 4 and 5). Blister rust was found in at least 37 of the 53 stands sampled (i.e., using $\text{infection}_{\text{min}}$; trees with obvious cankers) but probably occurred in 52 of the 53 stands (i.e., using $\text{infection}_{\text{max}}$; which includes trees with other signs of rust infection besides cankers). Incidence of blister rust infection in stands ranged from 0 to 100 %, with an average $\text{infection}_{\text{min}}$ rate of 19 % among stands. $\text{Infection}_{\text{max}}$ averaged 36% over all stands. Differences between the two measures of blister rust incidence in a stand (i.e., $\text{infection}_{\text{min}}$ and $\text{infection}_{\text{max}}$) were most pronounced for older stands (e.g., stands of the Lillooet sample area [see Figures 4 and 5]). Mortality of whitebark pine ranged from 0 to 64% with an average of 21 % over all stands.

Table 7. Summary of mountain pine beetle infestations on whitebark pine.

Stand Number[a]	Elevation (m)	N[b]	Number trees infested	Average tree diameter[c] (cm)	Number infested trees that were dead	Number beetle infested trees with blister rust infection
4	2170	319	1	7.2	1	1
5	2320	6	3	10.0	2	2
7	1750	27	2	52.1	2	0
16	2103	147	1	11.3	1	0
17	1885	116	6	13.7	6	4
23	1950	89	1	15.0	1	1
48	1775	33	3	20.9	2	1

a See Figure 1, in Chapter 2 for location of stands.

b N = total number of whitebark pine trees per stand. Includes living and dead trees > 1.3 m tall.

c When more than 1 tree was infested the average diameter at breast height is given; otherwise the diameter of the tree is given.

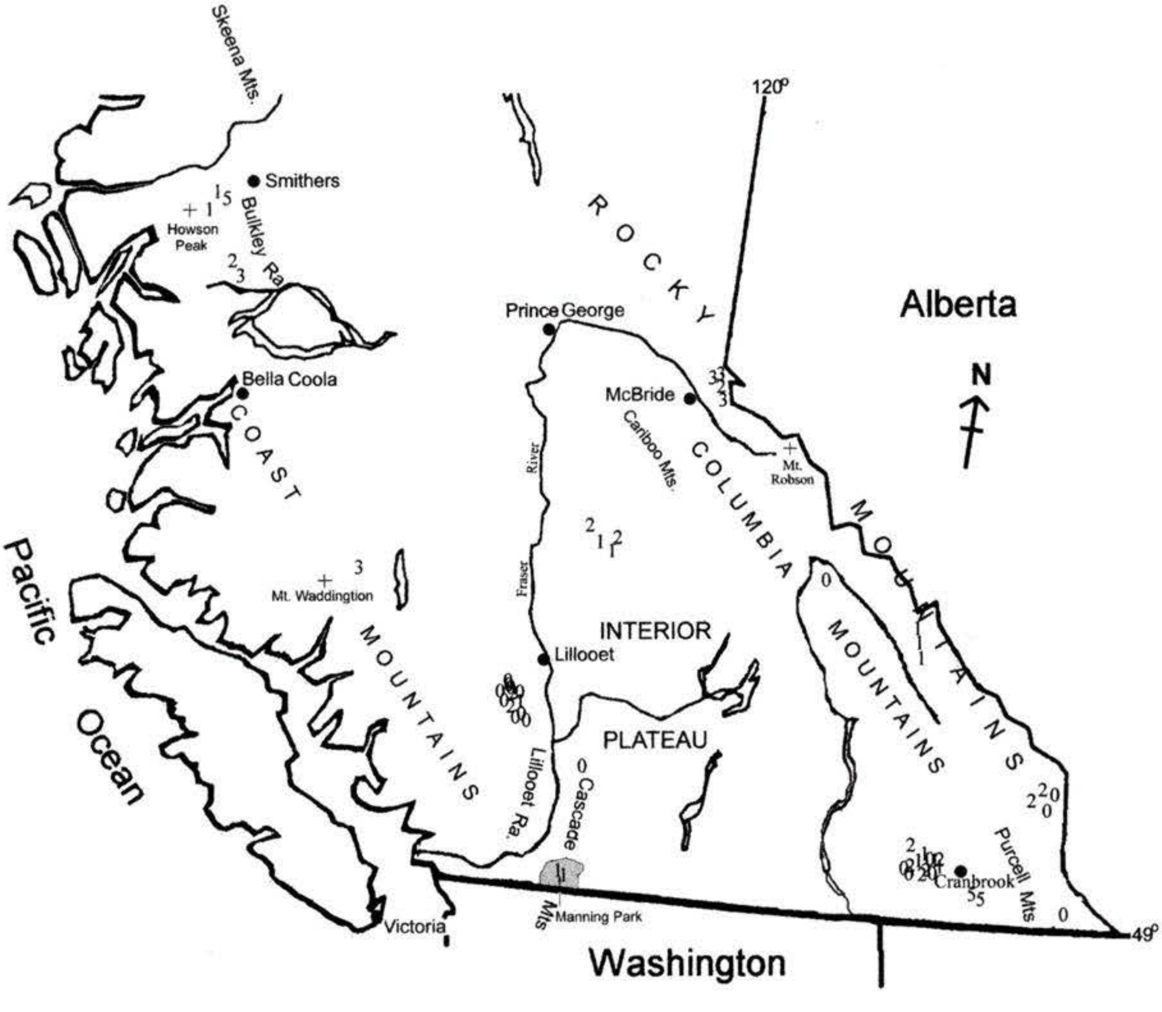


Figure 4. Distribution and incidence (i.e., infection$_{\min}$) of white pine blister rust in 53 stands sampled in British Columbia. Blister rust incidence (i.e., percentage of infected trees in a stand) is coded as: 0= none infected; 1= 1-20%; 2= 21-40%; 3= 41-60%; 4= 61-80%; 5= 81-100%.

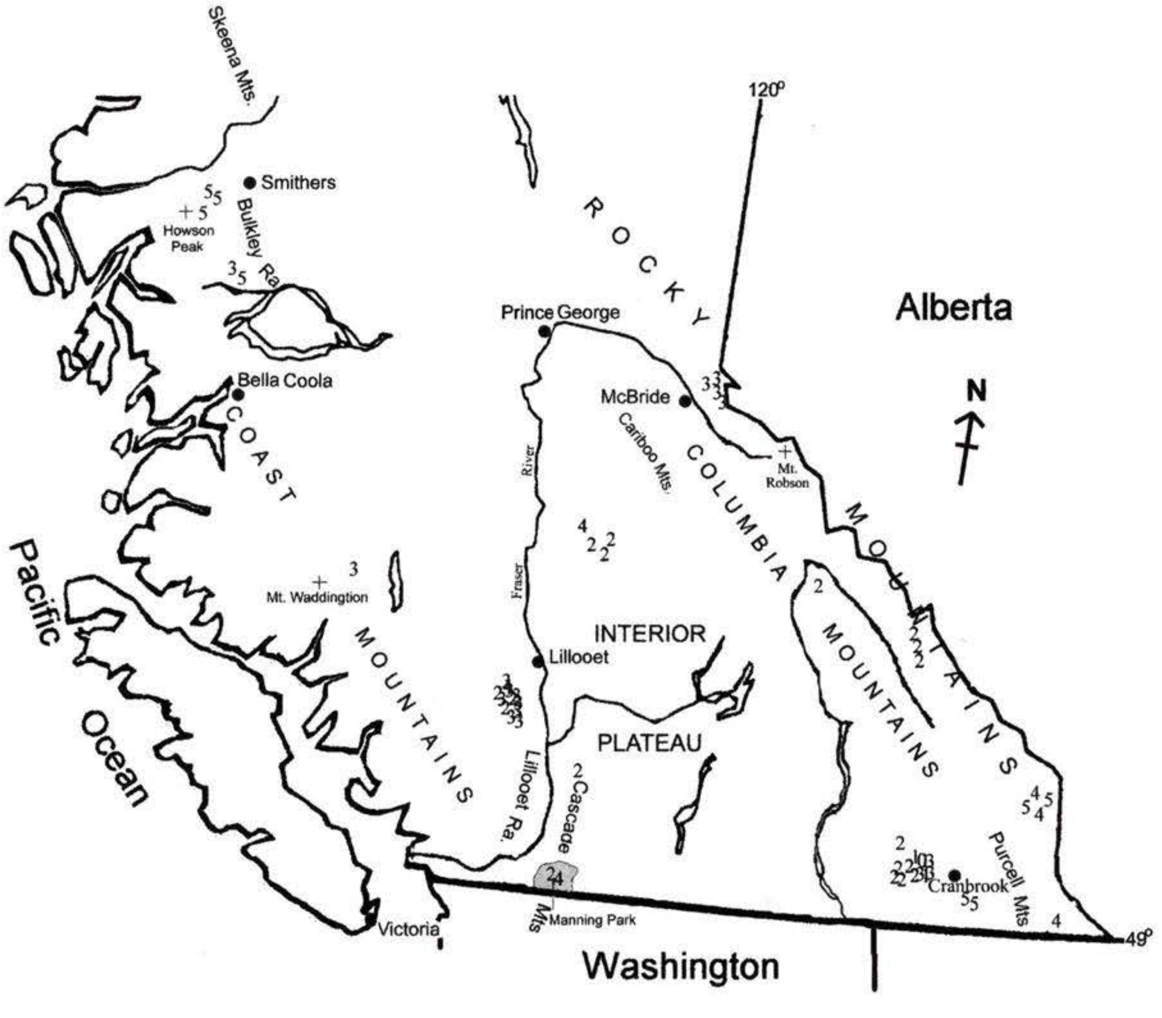


Figure 5. Distribution and incidence (i.e., infection$_{max}$) of white pine blister rust in 53 stands sampled in British Columbia. Blister rust incidence (i.e., percentage of infected trees in a stand) is coded as: 0=none infected; 1=1-20%; 2= 21-40%; 3=41-60%; 4=61-80%; 5=81-100%.

Individual tree mortality and infection

When examined by tree size class, whitebark pine mortality was more frequent among trees 0.1 to 10 cm and 10.1 to 20 cm in d.b.h. than among large trees (Table 8). The same pattern occurred for infection$_{\text{min}}$ (rates of live trees based on the presence of cankers as means of assessing infection) (Table 9). Large trees appeared half as likely to be infected, but this may be largely due to difficulties in observing cankers in the crowns of large trees. In contrast, when all signs of blister rust infection were used (i.e., infection$_{\text{max}}$), trees of the smallest diameter class (i.e., 0.1-10 cm) had lower rates of infection (Table 9).

Predicting mortality and infection in stands

Table 10 shows the relationships of abiotic conditions and stand characteristics to rates of mortality and blister rust infection in stands. Total tree density had a significant relationship with the rate of mortality observed in stands. Stands with a higher total tree density had significantly lower whitebark pine mortality rates (Figure 6). No other abiotic or stand characters had a significant effect on the rate of mortality observed in a stand.

Abiotic conditions had no significant effect on infection$_{\text{min}}$ rates observed in stands (Table 10). However, total tree canopy cover, whitebark pine basal area, total tree basal area, and stand age had a significant negative relationship with infection$_{\text{min}}$ rates (Table 10; Figure 7). For the stands sampled in this study, total tree canopy cover, whitebark pine basal area, and total tree basal area gave significant positive correlations with stand age; $r = 0.4030$, 0.3581 and 0.3209, respectively. Thus, young stands with sparse canopies, and low basal area of whitebark pine and low total tree basal area had higher infection$_{\text{min}}$ rates (Figure 7).

The only significant relationship with infection$_{\text{max}}$ rates was the presence of *Ribes* spp. in the stand. Stands containing *Ribes* bushes had significantly greater infection$_{\text{max}}$ rates than stands without *Ribes* (Figure 8). Abiotic conditions and other compositional and structural stand characteristics did not influence the infection$_{\text{max}}$ rates.

Table 8. Mortality of whitebark pine in relation to stem diameter at breast height (cm).

Diameter class	N	Mortality (% dead trees)
0.1–10	2 597	21.9
10.1–20.0	690	22.3
> 20.0	307	13.6
Total	3 594	

Note: Pearsons χ^2 test for goodness of fit was used to test for differences in mortality between diameter classes; $\chi^2 = 18.15$ (3 df; $p = 0.0001$)

Table 9. Infection of whitebark pine in relation to stem diameter at breast height (cm).

Diameter class	N	$\text{Infection}_{\text{min}}$[a] (% of trees)	$\text{Infection}_{\text{max}}$[b] (% of trees)
0.1–10	2 020	22.6	40.3
10.1–20.0	535	18.9	51.7
> 20.0	264	9.8	52.6
Total	2 819		

Note: Pearsons χ^2 test for goodness of fit was used to test for differences in rates of infection between diameter classes. Chi-squared values for $\text{infection}_{\text{min}}$ and $\text{infection}_{\text{max}}$ are: $\chi^2 = 24.25$ (3 df; $p<0.0001$); and $\chi^2 = 28.95$ (3 df; $p<0.0001$).

a Includes living trees that are infected with obvious cankers.

b Includes living trees that are infected with obvious cankers and also trees showing other evidence of blister rust infection such as flagged branches, dead tops, and rodent gnawing but no definite cankers.

Table 10. List of investigated variables and their individual relationships with mortality and infection rates in stands.

			Mortality				% Infection$_{min}$				% Infection$_{max}$		
		R^2	F	p	Effect	R^2	F	p	Effect	R^2	F	p	Effect
Abiotic conditions:													
Latitude	Regression	0.0127	0.53	0.4721	ns	0.0410	1.78	0.1899	ns	0.1228	5.74	0.0212	ns
MSP (mm)[a]	Regression	0.0009	0.37	0.5430	ns	0.0488	2.10	0.1543	ns	0.0428	1.83	0.1834	ns
Elevation (m)	Regression	0.0043	0.18	0.6737	ns	0.0000	0.00	0.9543	ns	0.0583	2.53	0.1189	ns
Soil moisture [b]	ANOVA	0.0828	1.76	0.1852	ns	0.0186	0.37	0.6939	ns	0.0031	0.06	0.9420	ns
Aspect[c]	ANOVA	0.1021	1.05	0.3936	ns	0.1641	1.82	0.1463	ns	0.1092	1.13	0.3554	ns
Stand characteristics:													
Plant community [d]	ANOVA	0.4220	2.26	0.0400	ns	0.4232	2.27	0.0391	ns	0.3294	1.52	0.1782	ns
Tree canopy cover	Regression	0.0076	0.31	0.5801	ns	0.1927	9.78	0.0032	–	0.0565	2.45	0.1249	ns
Density													
Pinus albicaulis	Regression	0.0950	4.32	0.0440	ns	0.0248	1.04	0.3133	ns	0.0123	0.51	0.4784	ns
All trees	Regression	0.2494	13.62	0.0004	–	0.0002	0.01	0.9277	ns	0.0003	0.13	0.9096	ns
Basal area													
Pinus albicaulis	Regression	0.0183	0.76	0.3871	ns	0.2581	14.26	0.0005	–	0.0002	0.10	0.7521	ns
All trees	Regression	0.0290	1.22	0.2750	ns	0.1865	9.39	0.0038	–	0.0036	0.15	0.7039	ns
Stand age	Regression	0.1001	4.55	0.0387	ns	0.2116	11.00	0.0019	–	0.0000	0.00	0.9979	ns
Presence of *Ribes*	Regression	0.0114	0.97	0.4956	ns	0.0057	0.66	0.4230	ns	0.3794	25.06	0.0000	+

Note: a probability level of (0.05/13 = 0.0038) has been Bonferroni corrected, for an overall significance level of 0.05 over 13 variables

a MSP = Mean summer precipitation (mm).

b Three soil moisture classes are derived from soil moisture index values described in chapter 1. Moisture class 1(very dry) = stands with index values 1–3; moisture class 2 (dry) = stands with index values 4 and 5; moisture class 3 (moist) = stands with index values 6 and 7.

c Aspect classes are derived in the same manner as described in Chapter 1.

d Corresponds to the eleven plot groups delineated in Chapter 1.

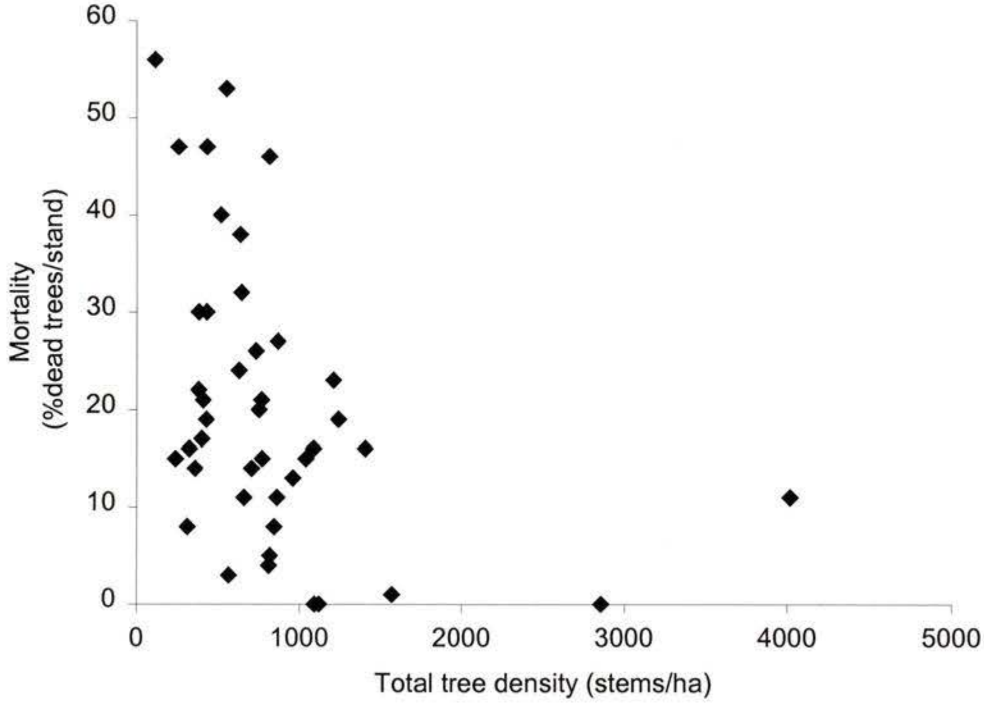


Figure 6. Untransformed whitebark pine mortality rates versus total tree density (trees > 1.3 m tall).

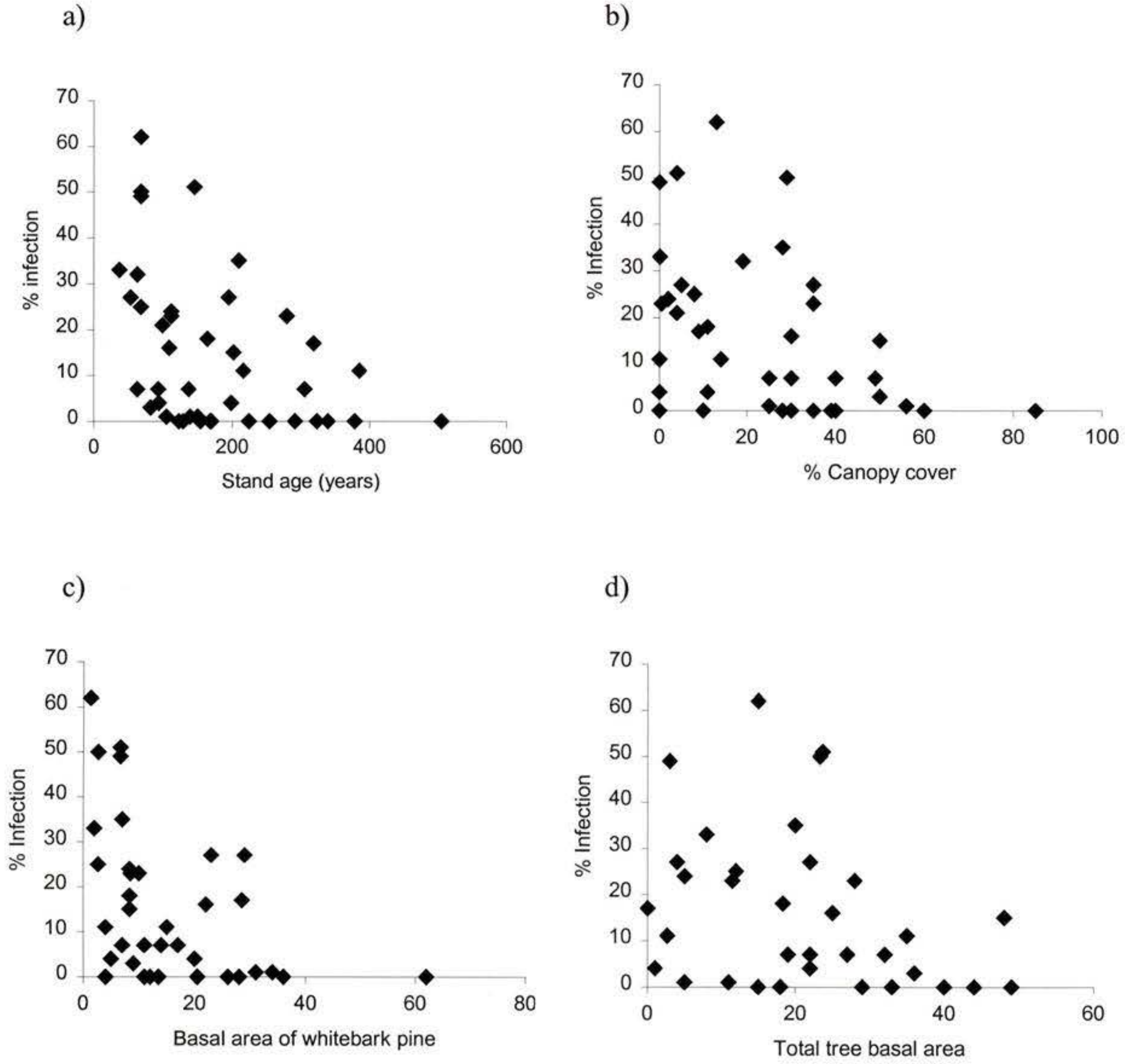


Figure 7. Untransformed infection$_{min}$ rates in relation to a) stand age; b) total tree canopy cover (%); c) whitebark pine basal area (m^2/ha); and, d) total tree basal area (m^2/ha).

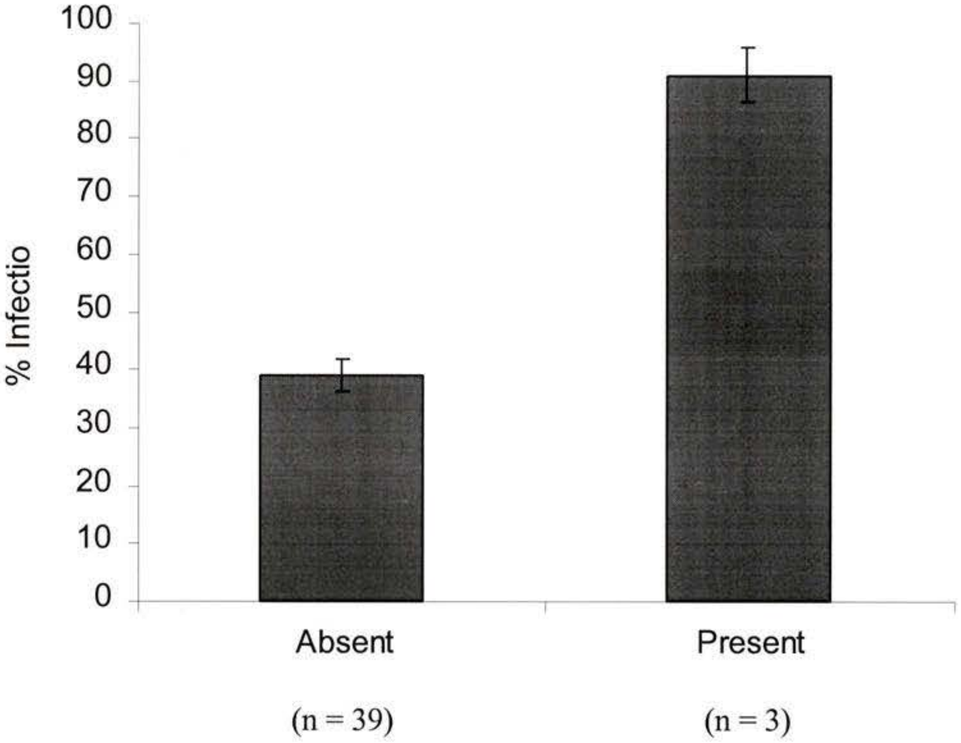


Figure 8. Average untransformed $\text{infection}_{\text{max}}$ rates in stands with and without *Ribes* spp. present.

Discussion

Factors influencing the distribution and incidence of white pine blister rust

The patterns of disease in natural plant populations are determined by complex interactions between the host, the pathogen, and the environment (Alexander 1992; Burdon 1987; Ingvarsson and Ericson 1998). The incidence and severity of disease in a given population depends, in large part, on the characters of the host (e.g., size, age, density, genotype) the location of the host relative to sources of infection, and occupation of specific climatic areas or microhabitats that confer increased susceptibility (Burdon 1987).

Climate (i.e., gross patterns in precipitation and temperature) has important effects on the distribution, incidence, and severity of many fungal diseases (Burdon 1987; Gilbert *et al.* 1994; Harrison *et al.* 1994; Jarosz and Burdon 1988; Smalley and Guries 1993; Van Arsdel 1965; Yang *et al.* 1997). Diseases caused by most pathogenic fungi are most severe and spread most rapidly under humid climatic conditions (Harrison *et al.* 1994; Van Arsdel *et al.* 1956). For example, the incidence of western gall rust on lodgepole pine is greatest in moist climatic regions of western Alberta and at high elevations where the temperatures are cooler (Yang *et al.* 1997). Climatic variation, however, has not had a significant influence on the development of epidemics of the introduced Dutch elm disease (Gibbs 1978; Smalley and Guries 1993; Sutherland *et al.* 1997). I also found no significant relationships between climate and white pine blister rust infection or mortality rates of whitebark pine in British Columbia. Though the amounts of blister rust infection and whitebark pine mortality rates in stands varied considerably within British Columbia, this variation could not be attributed to climate. This finding suggests that climatic conditions throughout the range of whitebark pine in British Columbia are quite suitable for blister rust to complete its life cycle and infect trees. This result was somewhat surprising; the expectation was that blister rust incidence and mortality would decrease with decreasing temperatures (i.e., northward and with increasing elevation) and in drier regional climates (e.g., the Interior Plateau). Though Hoff and Hagel (1990) suggested that low temperatures limit blister rust distribution, mean temperatures in whitebark pine habitats throughout British Columbia are well within the limits reportedly conducive to basidiospore germination (B.C. Ministry of Environment and B.C. Ministry of Forests, unpublished data, 1997, Victoria, B.C.; Van Arsdel 1956). Furthermore, I found no significant relationships between infection or mortality rates and the temperature gradient described by latitude. Because prolonged dry conditions inhibit basidiospore germination (Van Arsdel *et al.* 1956, 1965), significantly lower infection rates and mortality were expected in populations sampled in the Interior Plateau. Mean summer rainfall (May to September) in this area is low (288 mm) compared to other parts of British Columbia where whitebark pine occurs. However, the absence of a relationship between mean summer precipitation and blister rust infection rates or mortality in the study suggests that blister rust infections are not limited in dry regional climates of British Columbia. Because both teliospores and basidiospores germinate within a period of hours under favourable moisture conditions (Van Arsdel *et al.* 1956), a single late afternoon or evening rainfall in dry regions may be sufficient for spore germination and infection of whitebark pine (e.g., Snow *et al.* 1968). Occasional fog or low-lying cloudbanks in whitebark pine habitats may also provide sufficient leaf moisture for infection. The absence of a relationship between mean summer precipitation and blister rust infection and mortality may also reflect inaccuracies in the climate data used; meteorological stations were frequently located sufficient distances from my sample stands.

When considered in a broader context, however, the relationship between climate conditions and the levels of blister rust observed in stands is more obvious. Based on this study, and several others (Hoff and Hagel 1990; Keane and Arno 1993; Kendall *et al.* 1996; Smith and Hoffman 1996), there appears to be a distinct southward reduction in blister rust incidence and mortality over the entire range of whitebark pine (Hoff *et a*l. 1994). Blister rust incidence and mortality is relatively high throughout British Columbia and in northern Idaho, northwestern Montana (Keane and Arno 1993; Hoff and Hagel 1990; Kendall *et al.* 1996) and in Washington and Oregon (Hoff and Hagel 1990; Hoff *et al.* 1994) compared to southwestern Montana, central Idaho, and northwestern Wyoming (Keane and Arno 1993; Hoff *et al.* 1994; Kendall *et al.* 1996; Smith and Hoffman 1996). Little or no infection or mortality occurs in central California or Nevada. This generalized climatic pattern throughout the geographic range of whitebark pine is consistent with disease epidemiology studies of white pine blister rust on *Pinus strobus* in eastern North America, which indicated that blister rust was most widespread and severe in the cool and moist northern portions of the species range (Van Arsdel 1965). Kinloch and Dulitz (1991) also report a southward trend in the spread of blister rust on *Pinus lambertiana*; stands in moist areas of western Oregon are more severely affected than those in drier areas of central and southern California. Clearly, the scale at which climatic effects are investigated is important.

Local and microclimatic conditions such as, topography, aspect, cold air drainage and shading may also have an important influence on the distribution, incidence and severity of fungal diseases (Jarosz and Burdon 1988; Van Arsdel 1965). The incidence of damping-off disease on tropical tree seedlings, for example, is higher on shaded individuals (Augspurger 1984). The occurrence of white pine blister rust on *Pinus flexilis* (limber pine) in central Wyoming was restricted to cool eastern slopes (Brown 1978). Similarly, in relatively dry regions of southwestern Wisconsin, incidence of blister rust infections on *Pinus strobus* were greater on cool aspects and in cold air drainages; in moister northern climates local and microclimatic conditions had little effect (Van Arsdel 1965). While Keane and Morgan (1994) found no relationship between blister rust incidence and elevation in Montana, stands located at higher elevations in central and western Wyoming had greater blister rust infection rates than lower elevation stands (J.J. Smith, pers. com., Feb. 1998). The lack of significant variation in blister rust infection rates with aspect, elevation, and the topographically derived soil moisture index in British Columbia suggests that the local and microclimatic conditions are not important factors influencing the level of blister rust in British Columbia. These findings also support the above assertion that the climatic conditions (i.e., precipitation and temperature) throughout the range of whitebark pine in British Columbia may be suitable for blister rust to complete its life cycle. However, the effects of aspect, elevation and soil moisture were tested over all the stands sampled over a range of regional climates in British Columbia, and as such, it is possible that the effects of microclimatic conditions may have been obscured. Examination of these effects could be better evaluated in dry regional climates (e.g., the Interior Plateau) where local and microclimatic conditions may have a more pronounced effect on the distribution and severity of blister rust.

Many forest declines caused by disease are triggered by predisposing stress factors such as extremes of moisture and light (Houston 1984; Paul 1990). The high incidence of chestnut blight in chestnut plantations (Bazzigher and Miller 1991) and the high incidence of a canker disease on a tropical tree in Panama (Gilbert *et al.* 1994) have been attributed, in part, to periods of severe drought. Shade-tolerant plants frequently acclimate to low light conditions by lowering respiration rates. Pathogens that infect these individuals pose a serious threat; with similarly low rates of respiration they may consume a considerable amount of the photosynthate that the host produces (Paul 1990). Whitebark pine often grows in high stress environments where other tree species are unable to survive (e.g., on dry, rocky sites and at timberlines). One might therefore expect to observe higher levels of blister rust incidence and mortality where the trees are growing under stress. In this study, however, there was no greater incidence of disease or mortality in high stress environments (e.g., timberline habitats, dry soils). Moreover, high levels of blister rust were found even on vigorously growing whitebark pine trees that occurred at lower elevations. Light stress is an unlikely factor contributing to increased susceptibility of whitebark pine to blister rust because suppressed trees in the understory of stands with a dense main canopy were often free of blister rust while those located in open stands were frequently infected.

Whether the occurrence of disease varies among habitats of differing nutrient availability is not well known. On the basis of only a few studies in natural plant populations, disease incidence on nutrient rich sites appears considerably greater (Paul 1990). The incidence of blister rust on whitebark pine on the richest sites sampled (i.e., Group G stands, see Chapter 1) did not vary significantly from blister rust incidence on nutrient-poor sites.

It is often assumed that the spread of introduced diseases like white pine blister rust is associated with habitat disturbance by humans (Gilbert *et al.* 1994). While human activities have led to the establishment of new infection centers of Dutch elm disease (Gibbs 1978) and fusiform rust on hard pines (Bingham *et al.* 1971), the spread of blister rust appears independent of human activities. Blister rust on whitebark pine was found in very isolated areas of the species range in British Columbia, and high levels of blister rust have also been found in several protected areas such as wilderness areas and National

Parks in Canada and the U.S. (Keane and Arno 1990; Kendall *et al.* 1996).

Although environmental conditions and human disturbance appear to have little effect on the distribution, incidence, and severity of blister rust on whitebark pine in British Columbia, factors influencing the interception of basidiospores by individual whitebark pine trees may be considerably more important. The significant effect of tree diameter on blister rust infection$_{max}$ rates is likely related to the ability of trees to intercept airborne basidiospores. Large trees have more foliage and thus the chance of intercepting spores is greater. Similar positive correlations of tree size (and age) with the incidence of blister rust infection were also found in post-fire stands in northern Idaho (Tomback *et al.* 1995) and in central Idaho and western Wyoming (J.J. Smith, pers. comm., Feb. 1998). The effect of tree size on the infection$_{min}$ rates (i.e., infection rates determined using only visible cankers), however, yielded the opposite results; small trees had significantly greater infection rates than larger trees. Some studies have reported a decrease in disease incidence with increasing tree age and size (e.g., Patton 1960; Sutherland *et al.* 1997) and attributed this to age-related physiological or morphological characters that confer some level of resistance. In this study, however, it is likely that the effect of tree size on infection$_{min}$ rates is related more to problems associated with detecting cankers on large trees (see section below on evaluating blister rust in the field) than to characters associated with tree size.

The lower mortality rates of large trees is also unlikely to be the result of size or age related resistance; it is more likely that large trees simply die more slowly. A single canker that girdles the main stem often quickly kills small trees. Blister rust often directly infects the main stem of small trees through epicormic needle fascicles, or often has only a short distance to travel down a branch to the main stem. On large whitebark pine trees, cankers are restricted to branches and the main stem at the top of the tree; no cankers were found low on the main stem of large trees. Most large trees appear to be killed branch by branch until too little foliage is left to support the tree. Thus, it takes considerably more time to kill a large whitebark pine tree. A 20 year study of blister rust in a natural eastern white pine stand illustrates the relationship between tree size and mortality rates; after 20 years, seedlings and saplings were virtually eliminated from the stand whereas only half of the largest trees were dead or dying at the end of the study (Powers and Stegall 1971).

Spore movement may explain the significant effect of total tree density on whitebark pine mortality rates. Forests with high tree densities may act as screens to airborne spores decreasing the chance that any whitebark pine will be infected. Lower incidence of blister rust infection was also related to high total tree densities in Idaho and western Wyoming (J. J. Smith, pers. comm., Feb. 1998). In a recently burned area in northern Idaho, Tomback *et al.* (1994) found that the incidence of blister rust infection on whitebark pine increased significantly with distance from the whitebark pine seed source (i.e., the mature, unburned forest) and suggested that the mature forest may have slowed air-borne spore dissemination giving some protection to whitebark pine regeneration located closer to the seed source. It is not readily apparent why mortality rates but not infection rates have a significant association with total tree density in this study. While susceptibility of whitebark pine to infection appears independent of total tree density, perhaps infected trees in dense stands are more stressed and die more easily.

The negative relationships of $\text{infection}_{\text{min}}$ with tree canopy cover, whitebark pine basal area, total tree basal area, and stand age may also be associated, in part, with the probability of a whitebark pine tree intercepting basidiospores. Young stands without a well-developed canopy to protect whitebark pine trees probably have a greater chance of high blister rust incidence. The significant relationships between $\text{infection}_{\text{min},}$ total tree basal area and whitebark pine basal area may result from the positive association of these factors with stand age. $\text{Infection}_{\text{max}}$ rates showed no relationship with these stand characters, which emphasizes the differences between these measures of blister rust incidence (see below). Keane and Morgan (1994) found no effect of stand age on the incidence of blister rust infection on whitebark pine in western Montana.

Host density is an important factor influencing disease incidence (Burdon and Chilvers 1982). The abundance and proximity of *Ribes* to western white pine (*Pinus monticola*) has long been recognized as a important factor contributing to the rates of blister rust infection observed in stands (Lachmund 1934) and seven decades of eradicating *Ribes* in eastern North America significantly reduced blister rust infection rates on eastern white pines (Ostroesky *et al.* 1988). In this study, the presence of *Ribes* in stands was related to high rates of blister rust infection on whitebark pine. However, in regions where environmental conditions are more likely to limit spore development and production on *Ribes* leaves (e.g., dry mountain ranges such as the Sierra Nevada), the abundance and proximity of *Ribes* to whitebark pine is unlikely to be as important. Because infections are not transmitted between whitebark pine trees, the role of whitebark pine densities in stands is less clear. This study revealed no significant relationship between the incidence of infection in stands and whitebark pine density; however, density may indirectly affect disease incidence through its role in spreading the disease. When both whitebark pine density and blister rust infection are high, there is a greater chance that the rust will reach distant uninfected stands because more aeciospores are released from more infected trees and because aeciospores released from blister rust cankers on whitebark pine trees may travel several hundred kilometers to re-infect *Ribes* bushes.

Measures of blister rust incidence

The two measures of blister incidence used in this study (i.e., infection$_{\text{min}}$ and infection$_{\text{max}}$) gave contradictory results regarding the factors affecting disease incidence. These differences are largely associated with the problems in assessing whether or not a tree is infected in the field. Evaluating blister rust infection on white pines is relatively straightforward under controlled experimental conditions, in seed orchards, plantations, and in young natural or open stands because the individuals are small enough to permit examination of the foliage for leaf spots (i.e., the necrotic tissue surrounding the area where the fungus entered the leaf) and because blister rust cankers can be easily seen on both the main stem and on branches. In its natural habitat, however, determining the presence of blister rust cankers can be problematic. Cankers are often difficult to see on very large trees even with the use of binoculars, and thus many cankers may be missed. Because cankers are easily seen on small trees, calculated infection rates for young stands are fairly accurate. However, for old stands with many large whitebark pine trees, infection rates calculated based on the presence of cankers may be considerably lower than actual infection levels, which could account for the significant associations between infection$_{\text{min}}$ and factors related to stand age. The error introduced by this method of assessing infection may obscure real relationships between disease incidence and the independent variables. Using additional symptoms, (e.g., branch flagging, rodent gnawing) to determine whether or not a tree is infected is a reasonable way to compensate for the inability to see cankers on large trees. However, both blister rust cankers and squirrel herbivory cause branch flagging. Approximately 80% of squirrel feeding sites occur at a canker (J.J. Smith, pers. comm., Feb. 1998); the remaining 20% of squirrel feeding sites appear less discriminating. Therefore, an assessment including branch flagging may introduce over-estimates of infection. However, the error should be spread relatively evenly over all trees as squirrel damage occurs on trees of all sizes (Finck *et al.* 1988), which makes this source of error unlikely to obscure relationships between disease incidence and independent variables. Determination of blister rust infection rates in stands with large trees is likely to be more accurate when all signs of blister rust are used to assess individual trees.

Few researchers acknowledge the problems associated with evaluating blister rust infection in natural stands. Also, few indicate how they determined whether or not a tree was infected (i.e., by using only blister rust cankers, or other symptoms of the rust) and how infection rates were calculated. Reported rates of blister rust infection vary considerably within and among studies. While substantial variation is a common phenomenon in plant pathogen studies and has sound biological basis (Burdon 1987), some of the variation in the reported blister rust infection rates may be attributed to the methods used to determine tree infection. For surveys of blister rust infection on trees in their natural habitat, the methods used to determine whether or not a tree was infected and how blister rust infection rates were calculated should be clearly presented so that comparisons among studies can be made with greater confidence.

Prospects for stand structure, dynamics, and the future of the species.

In light of its effects on eastern and western white pines, Klinkowski (1970) ranked the white pine blister rust as one of the most catastrophic plant disease epidemics in history. The seriousness of the effect of blister rust on whitebark pine has only been recognized more recently (Arno 1986; Keane and Arno 1993). Blister rust has spread throughout the range of whitebark pine in British Columbia. Though mortality rates are not as high as those reported in Montana my results suggest that the disease may be more severe in British Columbia than in Wyoming, Idaho, California and Nevada. The lack of habitat specificity associated with blister rust incidence in British Columbia is reminiscent of the introduced Dutch elm disease and chestnut blight epidemics, which progressed to eliminate most elms and chestnuts in North America. The white pine blister rust epidemic on whitebark pine will probably have serious implications for stand structure and dynamics where whitebark pine is an important component of natural forests.

Regeneration of whitebark pine following disturbance is likely to be greatly delayed in areas where infection rates are high because seed sources are diminished and because most young regenerating trees are quickly killed by blister rust. Simulation models of stand dynamics predict major reductions in whitebark pine densities within 40 to 50 years of blister rust introduction into a stand (Keane and Morgan 1994). Keane and Morgan (1994) suggest that most subalpine stands will be converted to dense subalpine fir and spruce with minor components of whitebark pine, and that timberline and dry sites currently dominated by whitebark pine will be converted to herbaceous and shrub dominated communities through the elimination of whitebark pine.

Mortality factors that cause a build up of fuel in stands may make them more susceptible to fire. Brown (1974) found that beetles created ground fuels by killing trees and increased drying by opening up stands. Dickman and Cook (1988) suggested that disease related mortality in mountain hemlock forests of central Oregon increased the susceptibility of these forests to stand-destroying fires. Keane and Morgan (1994) have alluded to the fact that high levels of whitebark pine mortality caused by blister rust may change the patterns of fire disturbance in these stands and over the landscape. However, I believe that the potential effects of high whitebark pine mortality on fire patterns may be very limited. In old stands (i.e., > 200 years) sampled in British Columbia, the death of whitebark pine trees is unlikely to have a significant effect on the susceptibility of the stand to fire because there are so few whitebark pine trees in these stands. In the short term, however, high whitebark pine mortality in young stands and on upper subalpine and timberline habitats, where the tree is more abundant, may make these stands more susceptible to fire through the creation of considerable fine fuels.

Populations of pathogenic fungi that evolve with their hosts are often relatively harmless to the populations they infect, allowing the reproduction and survival of both. The same pathogens, however, may have a serious impact on native species where the pathogen is newly introduced. White pine blister rust on whitebark pine represents the classical problems associated with introduced pathogens. Species affected by introduced pathogens are unable to evolve resistance mechanisms before their populations are drastically reduced. Unfortunately, whitebark pine may face the same fate as elms and chestnut trees that were virtually eliminated by introduced disease.

Chapter 4

Dynamics and age structure of whitebark pine stands in southern British Columbia

Introduction

Disturbance by natural fires has occurred periodically in forested ecosystems for millennia (Komarek 1964; Spurr and Barnes 1973) and the characteristics of fires, including type, size, intensity, and frequency, have long been recognized as critical factors controlling tree species distributions, forest structure and composition, forest dynamics, and the pattern of forests on the landscape (Ahlgren and Ahlgren 1960; Arno 1980; Cooper 1960; Habeck and Mutch 1973; Komarek 1964; Oliver 1981; Reiners and Lang 1979; Romme 1982; Rowe and Scotter 1973; Tande 1979; White 1979; Wright 1974). Fires can initiate new stands or, if of low enough intensity, maintain stands of relatively fire-tolerant tree species. Prior to widespread fire suppression, frequent low to moderate-intensity surfaces fires maintained shade-intolerant tree species like ponderosa pine (*Pinus ponderosa*) in western North America (Arno 1980); *Quercus* spp. in the southeastern U.S. (Abrams *et al.* 1995) and giant sequoia (*Sequoiadendron giganteum*) in the Sierra Nevada (Bonnicksen and Stone 1981; Hartesveldt 1964; Kilgore and Taylor 1979) on sites where they would otherwise have been successionally replaced by shade-tolerant tree species. In contrast, extensive and frequent stand-replacing fires account for the abundance and long-term persistence of lodgepole pine in landscapes of central British Columbia and the Rocky Mountains of Alberta (Day 1972; Meidinger and Pojar 1991). Even if stand-replacing fires are very infrequent, they can have a major effect on the forest landscape. For example, the ubiquity of Douglas-fir in the western Olympic Mountains suggests that fires have burned repeatedly in this area even though the climate is very wet (Huff 1995).

Fire disturbance is also thought to be important in the regeneration and maintenance of whitebark pine in subalpine forests of western North America (Arno 1980). Most of what is known about the frequency and behavior of fire in subalpine forests and timberline habitats containing whitebark pine comes from the northern Rocky Mountains. Fire-return intervals in forests containing whitebark pine vary from 29-300 years (Arno 1980; Arno and Peterson 1983; Morgan *et al.* 1994; Morgan and Bunting 1990; Tande 1979). Moist, cool north-slope communities burn much less frequently than those on drier slopes, with fires occurring on average, every 150 years (Arno 1980). Keane and Morgan (1994) found stand-replacing fires occurred on average every 144 years (ranging from 55-304 years) in western Montana. Stand-replacing fires are most common in forests where whitebark pine is a seral dominant and are increasingly more probable as stands age because of the formation of a dense understory of subalpine fir and the accumulation of downed woody fuel in older stands (Arno 1980; Fischer and Clayton 1983; Morgan and Bunting 1990). The probability of fire may also increase on sites where white pine blister rust and mountain pine beetle have created large patches of dead trees (Keane *et* al. 1990; Morgan *et al.* 1994). In western Montana, stand-replacing fires typically spread on the ground and may kill trees by scorching foliage or by heating the bole or roots to lethal temperatures (Lasko 1990). Because of their thin bark, whitebark pine trees are poorly adapted to survive these fires (Arno 1980; Fischer and Clayton 1983). Most stand-replacing fires are small; large ones usually only occur during windy conditions and after prolonged drought (Morgan *et al.* 1994). In Wyoming, fires are generally distributed evenly throughout the growing season of whitebark pine but large fires frequently occur late in the growing season (Morgan and Bunting 1990).

Through time, most whitebark pine forests experience a mixture of stand-replacement and low-intensity surface fires (Morgan *et al.*1994). Low-intensity surface fires are most common on dry sites and in forests near the timberline (Arno 1980; Fischer and Clayton 1983; Morgan and Bunting 1990; Morgan *et al.* 1994). These fires are often small and patchy in extent, particularly near the timberline where whitebark pine forests grade into subalpine meadows (Arno 1980; Agee 1993; Morgan and Bunting 1990). Large whitebark pine trees often survive low-intensity fires as evidenced by frequent fire scars found on trees in Wyoming (Morgan and Bunting 1990). Even low-intensity fires, however, generally kill young whitebark pine and most subalpine fir; when these fires occur frequently they can produce park-like stands of nearly pure whitebark pine (Arno 1980; Morgan and Bunting 1990).

Because whitebark pine is considered a moderately shade-intolerant species (Arno and Hoff 1989; Baker 1949; Day 1967; Krajina *et al.* 1982), fire disturbance is believed important to the regeneration and maintenance of whitebark pine in lower subalpine sites where it grows as a seral species in tall, closed-canopied forests with subalpine fir and Engelmann spruce (Arno 1986; Keane and Arno 1993; Keane *et al.* 1990; Morgan *et al.* 1994; Morgan and Bunting 1990). Whitebark pine is a pioneer on burned sites (Tomback 1982; Tomback *et al.* 1995; Weaver and Dale 1974) and becomes particularly abundant after high intensity stand-replacing fires because nutcrackers show a preference for caching seeds in clearings (Hutchins 1990; Tomback 1978; Tomback *et al.* 1990). Surface fires that remove a dense understory of shrubs and subalpine fir also create small openings in which whitebark pine regeneration occurs (Arno 1980; Keane *et al.* 1990). Only a limited number of studies have specifically examined the dynamics of whitebark pine stands following these initial regeneration stages (Morgan and Bunting 1990; Weaver *et al.* 1990). Various observations in subalpine habitats of the Rocky Mountains (Arno 1980, 1986; Arno and Peterson 1983; Loope and Gruell 1973; MacCaughey and Schmit 1990; Pfister *et al.* 1977) indicate that whitebark pine is eventually replaced by subalpine fir and Engelmann spruce during post-fire succession. Using a chronosequence approach to study post-fire succession in western Montana, Weaver *et al.* (1990) found that while whitebark pine seedlings established at rates of over 1000 /ha/year in forests of all ages, there was an exponential decrease in whitebark pine density with stand age; densities decreased from 4000 trees/ha in young stands to 1500 trees/ha in 200 year old stands and 1000 trees/ha in 400 year old stands. In Wyoming, however, whitebark pine abundance remained steady in young stands, increased in stands from 100 to 220 years and then decreased (Morgan and Bunting 1990).

In addition to mortality of whitebark pine caused by white pine blister rust and mountain pine beetle, this tree is threatened by widespread fire suppression (Arno 1986; Keane and Arno 1993). Successional replacement of whitebark pine by Engelmann spruce and subalpine fir in the absence of fire is cited as one of the important reasons for the rapid decline of this species in western Montana (Keane and Arno 1993; Keane *et al.* 1990; Keane *et al.* 1996; Keane and Morgan 1994; Morgan *et al.* 1994). However, very little specific information exists on the post-fire dynamics of stands containing whitebark pine, especially in British Columbia. The dynamics of whitebark pine is often thought or implied to parallel that of lodgepole pine (Fischer and Clayton 1983; Keane *et al.* 1990; Morgan *et al.* 1994), a comparison which may be inappropriate in many respects. Moreover, no information is available on age structure and successional development of whitebark pine stands west of the Rocky Mountains.

The objectives of this chapter are:

1. to examine how the composition and structure of whitebark pine stands change during successional development;

2. to describe the age structure characteristics of varying aged stands containing whitebark pine; and,

3. to compare the patterns of successional development of stands in the Coastal Mountains with those in the Columbia Mountains.

Materials and Methods

Study areas and stand selection

The age structure and development of whitebark pine stands following fire was examined using a chronosequence approach at two study areas in southern British Columbia. Thirteen post-fire stands (ranging in age from 34 to 505 years) were located in the Columbia Mountains near Cranbrook in southeastern British Columbia. The closest subalpine meteorological station is located about 70 km east of the Cranbrook study area at Natal Harmer Ridge (latitude 49°46' N; longitude 114° 50' W; elevation 1890 m). Mean annual snow fall at Natal Harmer Ridge is 661 cm and mean temperature of the coldest month is –10.7 °C; snow may remain on the ground well into July (B.C. Ministry of Environment 1997). Mean summer precipitation (May-September) is relatively low for subalpine forests (i.e., 272 mm) and this area may experience a short period of drought late in the summer (B.C. Ministry of Environment and B.C. Ministry of Forests, unpublished data, 1997, B.C. Ministry of Enivronment, Victoria, B.C.; Braumandl and Curran 1992; Ogilvie 1990). Natural fire disturbance was common in the study area. Blister rust was widespread but evidence of mountain pine beetle was rare. All sampled stands were on gentle slopes (i.e., slope inclination < 30%) of northerly aspects between 1940 and 2195 m in elevation. Major tree species in these stands were subalpine fir, Engelmann spruce, whitebark pine, and lodgepole pine. Sample stands were located on nutrient medium/poor, submesic to mesic sites with understories dominated by *Vaccinium myrtillus*, *Vaccinium scoparium* and *Menziesia ferruginea*. Understory herbs were sparse in older stands but pioneering herb species (e.g., *Lupinus arcticus*, *Epilobium angustifolium*, *Hieraceum albiflorum*) occurred with low cover in some young stands. Soils were predominantly shallow to moderately deep, well-drained eutric brunisols (Canadian Soil Survey Committee 1987) over colluvium.

A second chronosequence containing nine post-fire stands (ranging in age from 105 to 462 years) was established in the subalpine forests of the southern Coastal Mountains near Lillooet. The meteorological station closest to the Lillooet study area is located at Allison Pass about 100 km south of the Lillooet study area. The winter climate in these subalpine forests is relatively mild (compared to other subalpine environments in

British Columbia) because of its proximity to the Pacific Ocean (Green and Klinka 1994). Mean annual snowfall at the Allison Path weather station is 1431 cm and the mean temperature of the coldest month is –7.9 °C; as in the Cranbrook study area snow may remain on the ground well into July (B.C. Ministry of Environment 1997). Mean summer precipitation is 288 mm and late-summer soil water deficits may also be common (Ogilvie 1990). In addition to fire disturbance, white pine blister rust was widespread and evidence of past mountain pine beetle infestations were present in old stands. Snow avalanche tracks were common throughout the study area. The upper subalpine forests, where sampling took place, were dominated by subalpine fir, Engelmann spruce, and whitebark pine. Stands were sampled on steep (i.e., >30% slope inclination), south and southeast aspects between 1650 and 1900 m in elevation. Sample stands were located on nutrient poor to medium, mesic to submesic sites where *Vaccinium membranaceum*, *Rhododendron albiflorum*, and *Pachistima myrsinites* dominated the understory. *Orthilia secunda*, the dominant herb, occurred in most stands with a cover of 2-10%. Soils were shallow to moderately deep and well-drained orthic humo-ferro podzols (Canadian Soil Survey Committee 1987) over colluvium.

Forest cover maps, topographic maps, and aerial photographs were used to select stands of different ages originating from fire disturbance. Selected stands were then visited to assess their appropriateness for inclusion in the study. Stands were deemed appropriate if they had approximately the same edaphic properties, dominant understory vegetation, and indicator plant species. Because the stands at each study site have similar environmental properties they can be considered chronosequences of stand development (Brubaker 1981). Most of the stands for these studies were sampled in 1996; a few were sampled in 1995.

Sampling Methods

One to three 400m^2 (20mx20m) sample plots were placed in each stand (see Methods section of Chapter 2 for plot placement protocol). Site description, vegetation crown cover by species, blister rust, and mountain pine beetle data were collected in each plot as described in Chapters 2 and 3. The diameters (cm) of all trees greater than breast height (i.e., >1.3 m) in the sample plot were tallied into 5 cm diameter classes. Whitebark pine often occurred as multiple-stemmed trees. Each stem of a multi-stemmed whitebark pine was counted as an individual if stem fusion occurred below breast height (d.b.h.); trees fused above this point were considered single-stemmed trees. A grid of 16, 5x5m^2 subplots was laid out in the sample plot. Trees <1.3 m tall were counted in each 5x5m^2 subplot; larger trees were also recorded by subplot. For each tree species, diameter, height, and age data were collected for at least 3 trees in each 5 cm diameter class from trees in or near the plot. To determine tree age, increment cores were taken as close as possible to the base of sample trees. Cores were stored in numbered straws. Age of small trees (< 5 cm d.b.h.) was determined using basal disks, which were stored in paper bags. Because it can influence fire frequency and intensity (Agee and Huff 1987; Fryer and Johnson 1988; Keane *et al.* 1990; Lasko 1990), woody debris was sampled along the perimeter of the 20x20m sample plot. The diameter (cm) of each piece crossing the perimeter was recorded. When several small twigs (< 1 cm diameter) occurred in piles, the diameter (i.e., height) of the pile was measured as though the pile was one large piece.

Laboratory procedures and data analysis

The University of Victoria Tree-Ring Laboratory processed increment cores and basal disks. In the laboratory, cores and disks were sanded with successively finer grades of sandpaper until annual growth rings could be easily distinguished. Cores were mounted on grooved pieces of wood before sanding. Digital images of increment cores and basal disks were uploaded into WinDendro (a computerized tree-ring image processing system [Regent Instruments Inc. 1996]) using a scanner. WinDendro automatically marked annual growth rings based on differences in light intensity, which works well for conifers as they have good contrast between rings. However, some manual adjustment was required (e.g., addition of markers to faint growth rings and deletion of false rings). Annual growth rings were counted and the distance between growth rings was measured to the nearest 0.01 mm. Data were tabulated in decadal format. Some very old trees, especially old whitebark pine trees, had heartrot making age determinations impossible. Tree age data were not adjusted for core height; thus counts of cores represent minimum tree ages.

Individual tree ages and timing of release were used to estimate the time since the last major fire. The ages of the largest canopy trees in a stand often corresponded to the time of the last major fire disturbance. The ages of large lodgepole pine trees were particularly useful for estimating stand age because they often establish first and in great abundance immediately after fire disturbance and because subsequent recruitment is very low to non-existent and sporadic (Day 1972; Johnson *et al.* 1994). Although the age of the main fire-initiated cohort of lodgepole pine (and/or whitebark pine) was most often used to estimate stand age, growth release patterns of trees that survived fire disturbance were also useful for some stands. Following Lorimer and Frelich (1989), trees that exhibited slow growth followed by an abrupt increase with rapid growth (i.e., rates of growth at least double growth in previous years) for at least 15 years or more were considered survivors of fire disturbance. The time at which this change in growth rates occurred was presumed to be the time of the last fire disturbance. Growth release may be caused by other disturbances that open the forest canopy (e.g., windthrow, formation of canopy gaps caused by falling dead trees) and thus, the cause of growth release on any individual tree may be difficult to assess. However, fire was presumed to be the cause of the disturbance when little downed wood (that would result from widespread windthrow damage) was present, when more than 3 widely separated sample trees exhibiting the same growth patterns (i.e., rapid release at a particular time) occurred in the stand, and when evidence of fire (e.g., tree fire scars, charcoal in the soil) was present.

Structural and compositional characteristics are presented for individual stands arranged by stand age, which allows an examination of changes during the two chronosequences. The volume of woody debris in a stand was calculated following a formula modified from Harmon *et al.* (1986). First, depth (D) of debris was calculated: $D = \pi^2 (\Sigma d^2 / 8L)$; d = diameter (cm) of piece, L = length of transect used. D was then multiplied by 10 000 m^2 to obtain an estimate of the volume of downed woody debris per hectare.

To examine general tree size-age relationships of subalpine fir, Engelmann spruce, whitebark pine and lodgepole pine, size-age data taken from the Cranbrook and Lillooet study areas were combined with data collected at other sites. Only data from sites capable of producing large trees are included in scatter plots of height versus age; age data from very slow-growing forests on dry, rocky sites and from krummholz whitebark pine "stands" were excluded. I feel that combining these data is reasonable when examining general size-age relationships because size-age data from trees on very dry sites and in krummholz stands were excluded and because the remaining size-age data come from subalpine forests with submesic to mesic soil moisture regimes and poor to medium soil nutrient regimes. The strength of the association between tree size and age was measured using simple linear regression.

Because trees of different growth rates and size-age relationships often occur in the same stand, tree size-class analysis alone is usually insufficient to make interpretations about forest development and is the reason that age-class frequency distributions are more commonly used (Huff 1995; Stewart 1986). In this study, however, age frequency distributions could not be constructed because age data were collected from a pre-determined number of trees per diameter class per plot and thus are not necessarily a reflection of the proportion of trees of a given age in the sampled stand. However, scatter plots of tree size vs. age can be used to make inferences about the age structure of each tree species in individual stands. These plots, along with density and diameter distribution data, can be used to determine the dynamics of tree populations during post-fire succession in each stand. To determine how the age and size structure of each species changes from young to old stands, the stands were grouped into three broad age categories, young, medium-aged, and old-growth stands.

Results

Successional characteristics

Structural and compositional characteristics of different aged, post-fire stands comprising the Cranbrook chronosequence are summarized in Table 11. Whitebark pine and lodgepole pine dominated young, post-fire stands sampled near Cranbrook. Lodgepole pine grew faster than the other trees present and, when recruited abundantly after fire (e.g., the 65, 84, and 124 year-old stands), it formed dense pole stands with most whitebark pine, subalpine fir and Engelmann spruce in the understory or subcanopy. The density of both whitebark pine and lodgepole pine decreased with stand age, but the basal area of whitebark pine tended to be highest in old stands and the basal area of lodgepole pine decreased much less than density. Whitebark pine was often more abundant than lodgepole pine in old stands. Subalpine fir was abundant in most stands greater than 84 years old; in the oldest stands sampled, it formed a dense subcanopy. Subalpine fir, Engelmann spruce, and whitebark pine dominated old stands. Although the overall pattern of decreasing lodgepole pine and increasing subalpine fir with stand age is clear, considerable variation in density and basal area of all tree species among stands was unrelated to stand age. The 136 year-old and the 284-year old stands had less subalpine fir than would be expected for their age. The density of Engelmann spruce varied considerably among stands and showed only weak relationships to stand age. The 136 year-old stand had few lodgepole pine, which is likely the result of low initial establishment on this site.

Small whitebark pine were abundant in young stands and to a lesser degree in old stands but relatively infrequent in middle-aged stands, indicating that conditions for establishment are highly favourable in young stands and least favourable in middle-aged stands (Table 11). In contrast, establishment of lodgepole pine was almost completely restricted to a period immediately following fire; most trees were already >1.3 m tall in the youngest stand sampled (Table 11). Except for the 34 year old stand, subalpine fir < 1.3 m tall were comparatively sparse in young stands but increased in stands greater than 65 years old. Density of small Engelmann spruce was almost always considerably lower than that of subalpine fir, and varied considerably among stands, as did the density

Table 11. Structural and compositional characters of stands sampled in the Cranbrook study area.

Stand character	Stand age												
	34	55	63	65	84	124	136	150	155	284	339	346	505
Tree Density (# trees > d.b.h./ha)													
subalpine fir	725	300	225	75	1 075	2 150	275	1 350	2 775	525	1 313	2 350	3 263
Engelmann spruce	550	400	233	100	450	1 275	75	1 113	1 325	350	228	1 050	63
whitebark pine	400	4 600	2 517	2 850	1 850	175	1 725	1 012	225	375	228	325	138
lodgepole pine	125	150	1 017	3 825	2 925	825	50	1 175	325	25	177	175	13
Tree basal area (m^2/ha of trees > d.b.h.)													
subalpine fir	0.12	0.21	1.25	0.10	4.80	8.11	6.14	4.93	22.43	1.11	5.40	4.84	23.35
Engelmann spruce	0.50	0.28	1.63	0.10	2.12	14.33	3.80	2.81	5.14	9.94	9.94	7.65	0.71
whitebark pine	0.20	6.49	2.91	2.13	2.80	2.1	20.11	6.71	11.16	27.97	23.96	0.85	23.12
lodgepole pine	0.28	0.94	14.66	22.01	26.51	20.91	1.37	13.41	4.83	0.33	9.71	11.22	2.83
Density of trees <1.3 m tall (#/ha)													
subalpine fir	2 725	900	500	475	2 550	3 000	3 450	1 988	2 500	5 200	2 988	4 450	3 612
Engelmann spruce	1 000	1 225	200	375	225	50	50	413	75	0	175	725	138
whitebark pine	4 800	8 825	3 483	21 050	1 525	0	950	1 100	675	1 200	2 875	6 525	25
lodgepole pine	100	0	42	475	0	0	0	0	0	0	0	25	0
Total tree canopy cover (%)[a]	0	0	19	25	50	45	25	67	30	30	28	25	85
Maximum canopy height (m)	6	9.5	12.5	11.7	16.5	17.7	15.5	16.7	18.4	21.3	24.3	23.6	31.2
Total tree subcanopy cover (%)[b]	39	54	46	55	50	10	16	38	22	22	13	57	60
Total shrub cover (%)[c]	97	90	97	70	50	42	81	69	30	30	93	85	60
Total herb cover (%)	0.5	0	7	0	0.5	1	10	0.5	0	0	0	0.3	0
Understory Species Richness[d]	5	4	10	3	2	6	8	5	5	5	4	6	3
Downed woody debris (m^3/ha)	363	250	no data[f]	256	356	98	30	no data	49	66	32	137	no data
Density whitebark pine snags[e] (#/ha)	425	250	0	0	0	0	0	0	0	0	0	0	0
Average whitebark pine snag diameter (cm)	31	24	0	0	0	0	0	0	0	0	0	0	0

a Includes the cover of all trees greater than 10 m tall.

b Includes the cover of all trees less than 10 m tall.

c A complex of *Vaccinium* spp. dominate the understory with less cover of *Menziesia ferruginea* and *Rhododendron albiflorum*. The *Vaccinium* spp. complex is dominated by *V. myrtillus* (average cover = 32% over all stands; constancy = 77%). Average cover of V. *scoparium* is 15% with constancy of 54%. *V. membranaceum* is considerably less common (constancy = 15%) and had low average cover (3%).

d Species richness = number of understory shrub and herb species in a 400 m^2 plot.

e Snag = a dead but standing tree bole killed by the fire disturbance.

f Woody debris was not measured in stands sampled during 1995.

of larger trees.

Shrub cover was high in stands of all ages (Table 11). Herb cover was low in all stands (Table 11). Understory species richness was greatest in the 63 year-old and 136 year-old stands.

Some snags burned by fire were still standing and a large amount of woody debris from fallen snags was present in the youngest stands sampled (Table 11). Although variable, the volume of woody debris was consistently less in stands older than 84 years. Among stands greater than 84 years old, the 346 year-old stand had the highest amount of debris, whereas the 339 year-old stand had much less woody debris.

Structural and compositional characteristics of variously aged post-fire stands comprising the Lillooet chronosequence are summarized in Table 12. These stands were quite different from those observed at Cranbrook, the most notable difference being the absence of lodgepole pine in stands sampled near Lillooet. Subalpine fir and whitebark pine dominated stands of all ages; although the density of whitebark pine decreased considerably in stands older than 173 years, basal area was still fairly high (Table 12). Subalpine fir, whitebark pine and Engelmann spruce form a fairly open, main canopy in stands greater than 123 years old. In old stands, subalpine fir was the most abundant tree in both the subcanopy and the canopy, with scattered large whitebark pine and Engelmann spruce.

Small subalpine fir (<1.3 m tall) were considerably more abundant in the understory than either whitebark pine or Engelmann spruce, although the density of small subalpine fir varied considerably among stands (Table 12). Small whitebark pine were abundant only in the youngest stand (112 years old), which had a very open canopy; they were sparse or absent in the understory of all other stands, except the oldest (Table 12).

As in the Cranbrook stands, the cover of shrubs was high in most stands at the Lillooet study area. Herb cover, however, was much higher at Lillooet than at Cranbrook

Table 12. Structural and compositional characteristics of stands sampled in the Lillooet study area.

Stand character	Stand Age								
	112	123	129	154	170	173	269	310	462
Tree Density (# trees > d.b.h./ha)									
subalpine fir	3 050	800	2 325	3 813	3 750	2 350	3 400	2 750	7 425
Engelmann spruce	0	150	1 300	13	75	725	0	250	275
whitebark pine	1500	2 900	1 050	913	2 000	3 400	250	150	250
Tree basal area (m^2/ha of trees > d.b.h.)									
subalpine fir	8.74	9.23	25.59	22.86	20.89	14.88	32.87	27.44	29.14
Engelmann spruce	0	4.91	16.38	0	0.58	14.04	0	70.30	3.94
whitebark pine	5.25	25.20	10.82	13.68	36.04	62.02	16.87	16.18	17.36
Density of trees <1.3 m tall (#/ha)									
subalpine fir	3 313	975	525	600	1 450	675	900	1 850	7 075
Engelmann spruce	13	25	25	0	0	25	25	0	125
whitebark pine	2313	0	0	100	0	0	25	0	775
Total tree canopy cover (%)[a]	0.5	10	40	39	35	30	30	40	35
Maximum canopy height (m)	8.1	16.6	17.9	14.0	16	20.9	21.7	30.4	31.9
Total tree subcanopy cover (%)[b]	60	26	25	61	31	14	13	35	45
Total shrub cover[c] (%)	53	65	75	24	15	35	15	37	25
Total herb cover (%)	20	10	13	0.5	0	1	10	15	5
Understory Species Richness[d]	14	12	9	5	3	4	5	7	3
Downed woody debris (m^3/ha)	5	6	36	no data[f]	9	37	29	112	301
Density whitebark pine snags[e] (#/ha)	0	0	0	0	0	0	0	0	0
Average whitebark pine snag diameter (cm)	0	0	0	0	0	0	0	0	0

a Includes the cover of all trees greater than 10 m tall.

b Includes the cover of all trees less than 10 m tall.

c *V. membranaceum* dominates the understory (average cover = 16%; constancy = 100% with lesser covers of *Rhododendron albiflorum* (average cover = 9%; constancy = 88%) and *Pachistima myrsinites* (average cover =10%; constancy = 90%)

d Species richness = number of understory shrub and herb species in a 400 m^2 plot.

e Snag = a dead but standing tree bole killed by the fire disturbance.

f Woody debris was not measured in stands sampled during 1995.

(Tables 11 and 12). The youngest stand at Lillooet, which had a sparse tree layer, had the highest cover and diversity of herbaceous species. The volume of woody debris in the Lillooet stands was quite low in comparison to the Cranbrook stands except in the oldest stands sampled. The oldest stand had an amount of woody debris that was much greater than in any of the younger stands (Table 12).

Diameter class distribution

Diameter class distributions, by species, for stands of the Cranbrook chronosequence are summarized in Figure 9. The shape of tree diameter distributions of subalpine fir resembles the classic negative exponential distribution for shade-tolerant tree species in all stand age classes (Figure 9a). Trees in all diameter classes progressively increased in abundance with stand age, with small trees always much more abundant than large trees. Subalpine fir was represented in all diameter size classes in middle-aged and old stands, and all but the largest diameter class in young stands. Whitebark pine was also represented in all size classes in older stands and all but the largest size class in young stands (Figure 9b). However, the distribution of trees among size classes was very different than for subalpine fir. In middle-aged stands the decrease in abundance with size was much less pronounced for whitebark pine than for subalpine fir, and in old stands the size-class distribution of whitebark pine was bimodal with few trees of intermediate sizes. Although whitebark pine was able to establish in stands of all ages, individuals were unlikely to survive to maturity in old stands. In contrast to whitebark pine, the density of small lodgepole pine was very low in stands of all three age classes, indicating its inability to survive and establish below a forest canopy (Figure 9c). Engelmann spruce is represented in all diameter classes in middle-aged and old stands; however, its relative abundance in the smallest size class is much lower than for subalpine fir (Figure 9d). The somewhat bimodal distribution of Engelmann spruce in old stands suggests sporadic entry into the canopy in stands with dense subalpine fir.

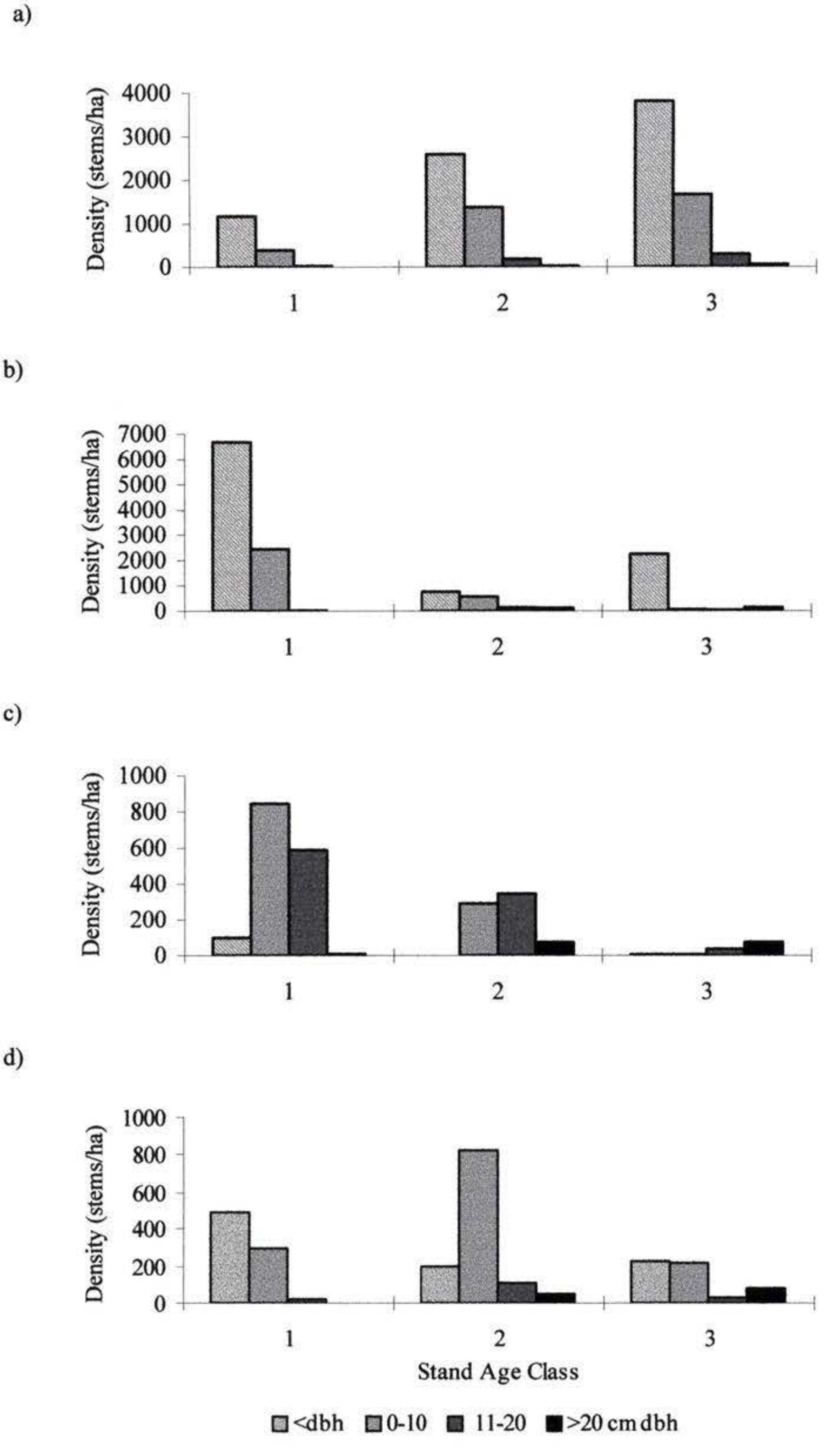


Figure 9. Diameter (cm) class distributions of a) subalpine fir, b) whitebark pine, c) lodgepole pine, and d) Engelmann spruce by stand age class for the Cranbrook chronosequence. Stand age classes are: 1 = < 125 years; 2 = 125–250 years; and 3 = >250 years.

Diameter class distributions, by species, for stands of the Lillooet chronosequence are summarized in Figure 10. Similar to stands of the Cranbrook chronosequence subalpine fir is represented in all diameter classes in all stand age classes with small subalpine fir generally considerably more abundant than large diameter trees (Figure 10a). However, the pronounced decrease in density with increasing size is not as apparent as in the Cranbrook chronosequence; trees in the second size class are generally more abundant than those in the youngest size class. In middle-aged stands recruitment was lower than expected with trees <1.3 m tall less than half as abundant as trees 0-10 cm d.b.h.; in old stands these two size classes had similar numbers of trees. Whitebark pine was represented in all diameter classes in young and middle-aged stands, but in old stands the tree size distribution was bimodal, the same pattern as occurred at Cranbrook (Figure 10b). The poor representation of whitebark pine in intermediate size classes in old stands reinforces the interpretation that recently recruited trees are unlikely to survive in old stands. Because Engelmann spruce is generally uncommon in the Lillooet stands, diameter distributions are difficult to interpret. However, the low numbers of trees in the smallest size class in all stand age categories and the absence of 11-20 cm diameter trees in the old stands suggest a limited ability to establish and ineffective or sporadic growth into the canopy.

Tree size-age relationships

Subalpine fir and Engelmann spruce showed similar relationships between tree size and age (Figure 11). Tree height did not correlate well with tree age (Figure 11) nor did tree diameter (when tree age was regressed against tree diameter, $r^2 = 0.25$ for subalpine fir and $r^2 = 0.36$ for Engelmann spruce). Growth rates of both species were extremely variable; trees at any age between 150 and 250 years could vary from 5 m tall to 25 m tall. Subalpine fir and Engelmann spruce showed similar rates of growth in young stands (i.e., < 125 years old) and often reached 10 m in height within 75 to 100 years. However, growth rates of both species were highly variable in stands of all ages, and the ability of both subalpine fir and Engelmann spruce to withstand long periods

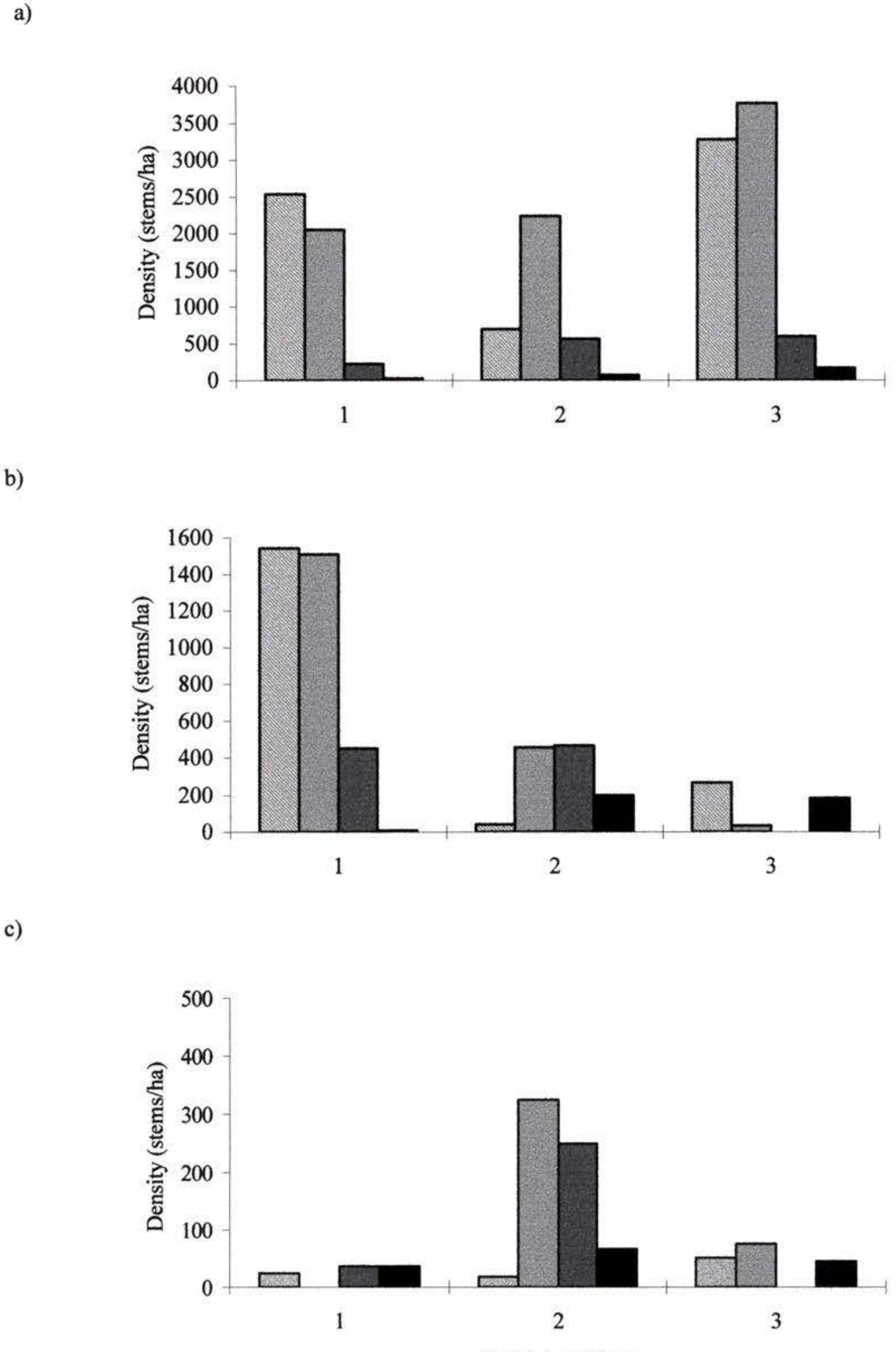


Figure 10. Diameter (cm) class distributions of a) subalpine fir, b) whitebark pine, and c) Engelmann spruce by stand age class for the Lillooet chronosequence. Stand age classes are: 1 = < 125 years; 2 = 125–250 years; and 3 = >250 years.

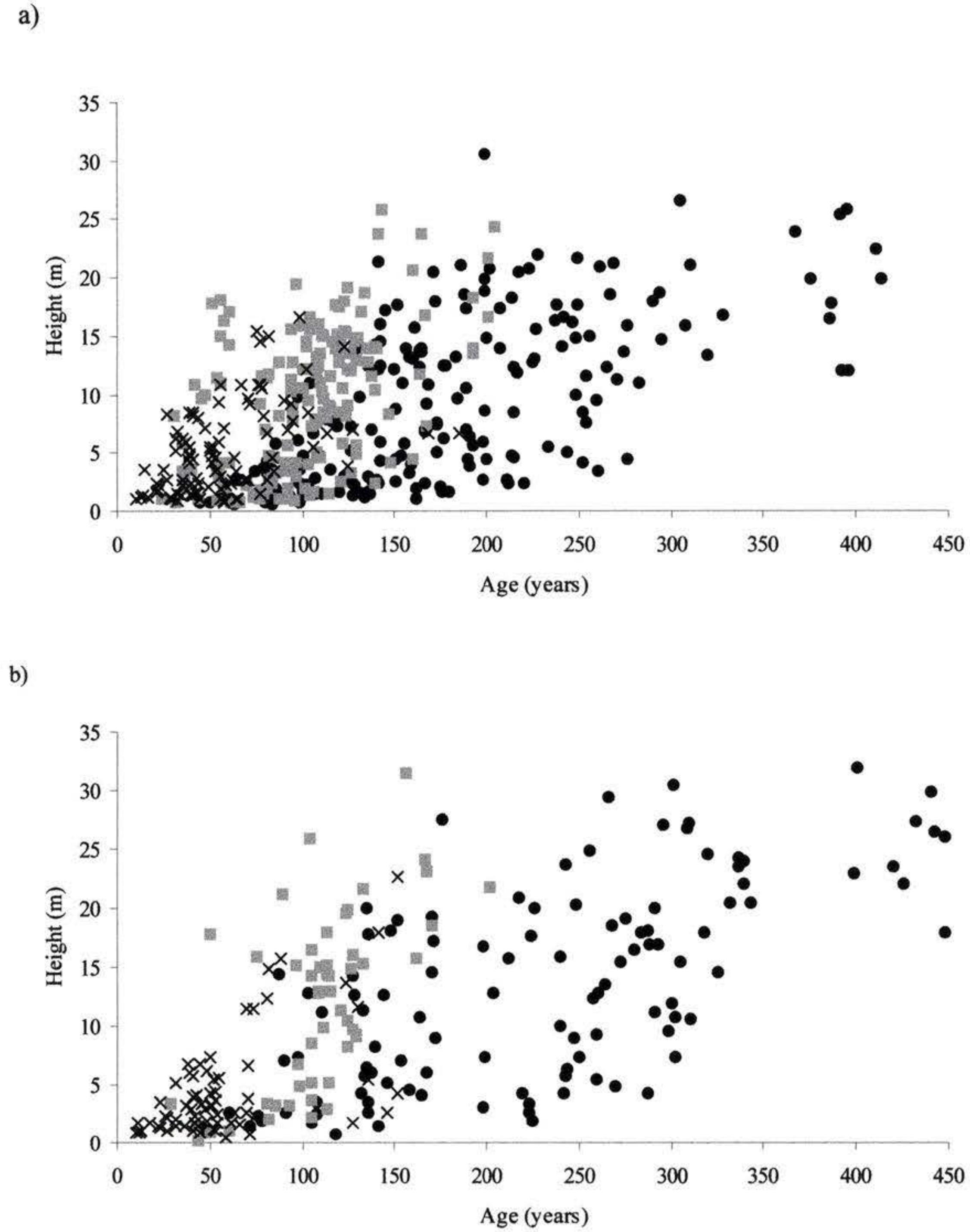


Figure 11. Scatter plots of tree height vs. age for a) subalpine fir and b) Engelmann spruce by stand age class. Stand age classes are: x = <125 years; ■ = 125-250 years; and • = >250 years. Krummholz "stands" and stunted stands on very dry sites are excluded. Squared correlation coefficients of height vs. age over all trees for subalpine fir are $r^2 = 0.27$ ($n = 417$) and for Engelmann spruce are $r^2 = 0.40$ ($n = 221$).

of suppression was clearly shown by the presence of trees up to 300 years but <10 m tall and below the main canopy. In old stands spruce appeared to grow very slowly, with few trees younger than 200 years that had reached greater than 10 m in height, suggesting that in contrast to fir, spruce establishing after a stand is 200 years old may reach the canopy very slowly if at all.

The size-age relationships of whitebark pine and lodgepole pine were similar to one another but greatly differed from those of subalpine fir and Engelmann spruce (Figure 12). The age of lodgepole pine is weakly correlated with both height (Figure 12) and diameter ($r^2 = 0.40$). Correlations of tree height and age were higher for whitebark pine (Figure 12) with similar findings when tree age was regressed against diameter ($r^2 = 0.53$). Early growth of lodgepole pine was considerably faster than that of whitebark pine. Lodgepole pine trees of young stands reaching 10 m in height between 40 and 50 years following disturbance, whereas whitebark pine trees were more likely to reach this height between 60 and 100 years. In middle-aged stands, most lodgepole pine trees occurred in the tree canopy; whitebark pine trees also occurred in the canopy but were still frequent in the understory after 100 years. In old stands, lodgepole pine trees were almost all tall and old with none in the understory. Tall whitebark pine trees were also present in old stands but unlike lodgepole pine there was still recruitment of whitebark pine in the understory. Some small whitebark pine trees were able to persist, with suppressed growth, in the subcanopy for nearly 200 years. Like lodgepole pine, though, there is a distinct absence of intermediate sized trees in old stands. Differences in tree growth and size in different aged stands and the presence of small trees in older stands suggests that whitebark pine will tolerate more shade than lodgepole pine.

Stand age structure

Scatter plots of tree height vs. age for individual stands sampled near Cranbrook indicate that subalpine fir, Engelmann spruce, lodgepole pine, and whitebark pine can all occupy sites within about a 20 year period following fire (Figures 13, 14, 15). In the 63

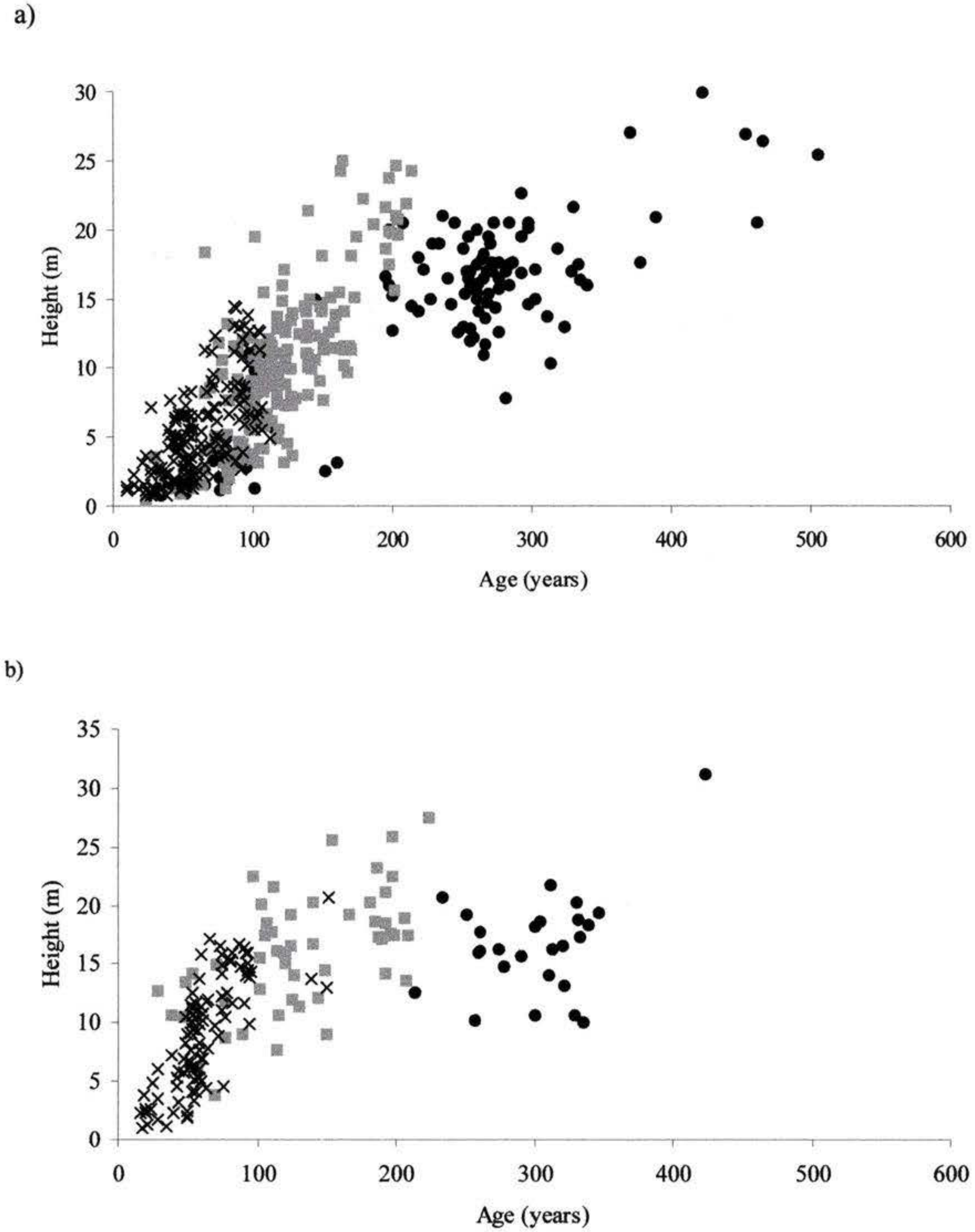


Figure 12. Scatter plots of tree height vs. age for a) whitebark pine and b) lodgepole pine by stand age class. Stand age classes are : **x** = <125 years; ■ = 125-250 years; and • = >250 years. Krummholz "stands" and stunted stands on very dry sites are excluded. Squared correlation coefficients of height vs. age over all trees are $r^2 = 0.62$ ($n = 467$) for whitebark pine and $r^2 = 0.40$. ($n = 180$) for lodgepole pine .

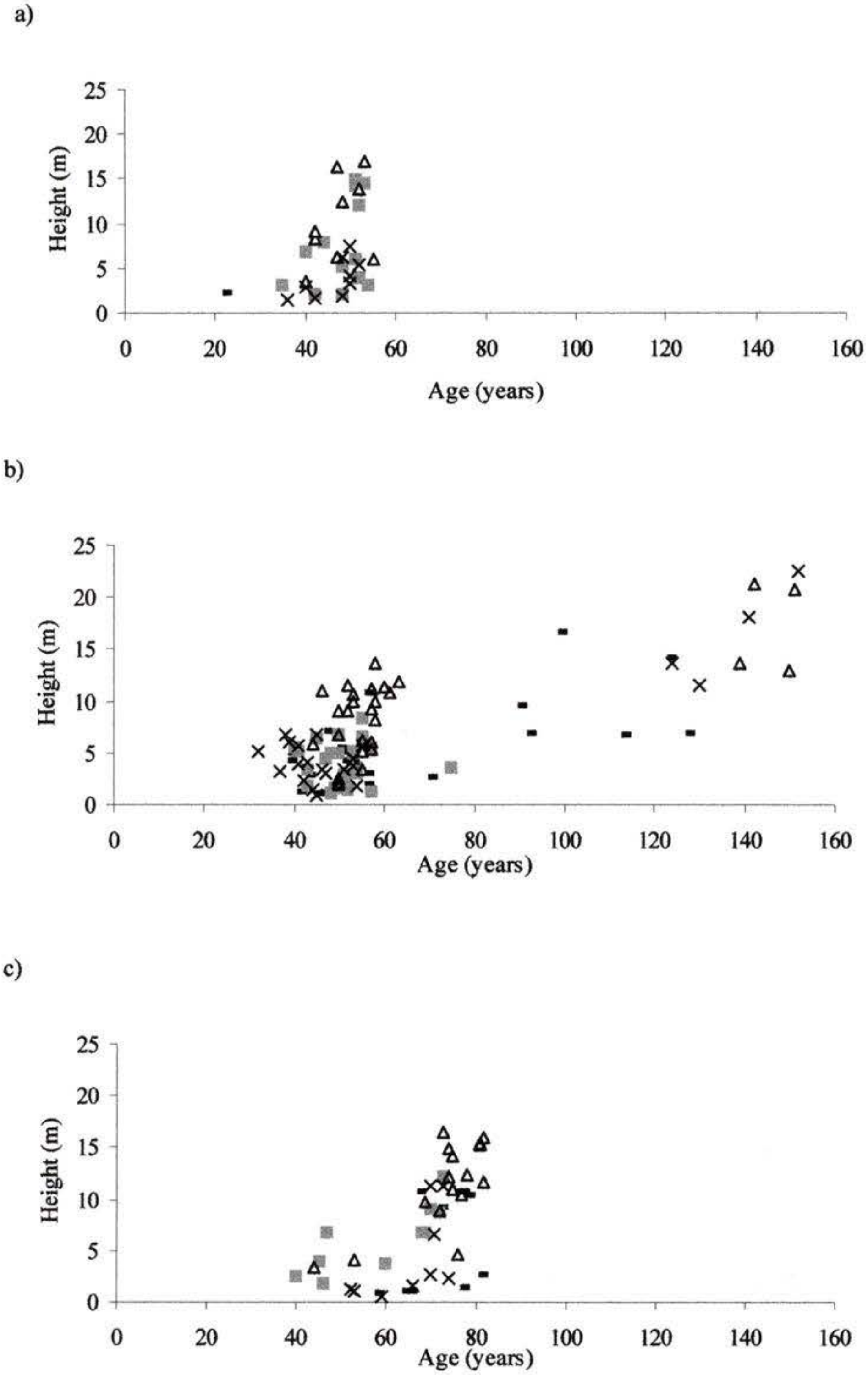


Figure 13. Scatter plots of tree height vs. age for selected young stands (i.e., < 125 years old) of the Cranbrook chronosequence. Presented are data for a) the 55 year-old stand; b) the 63 year-old stand; and, c) the 84 year-old stand. Subalpine fir = - ; whitebark pine = ■ ; lodgepole pine =△; Engelmann spruce = ×.

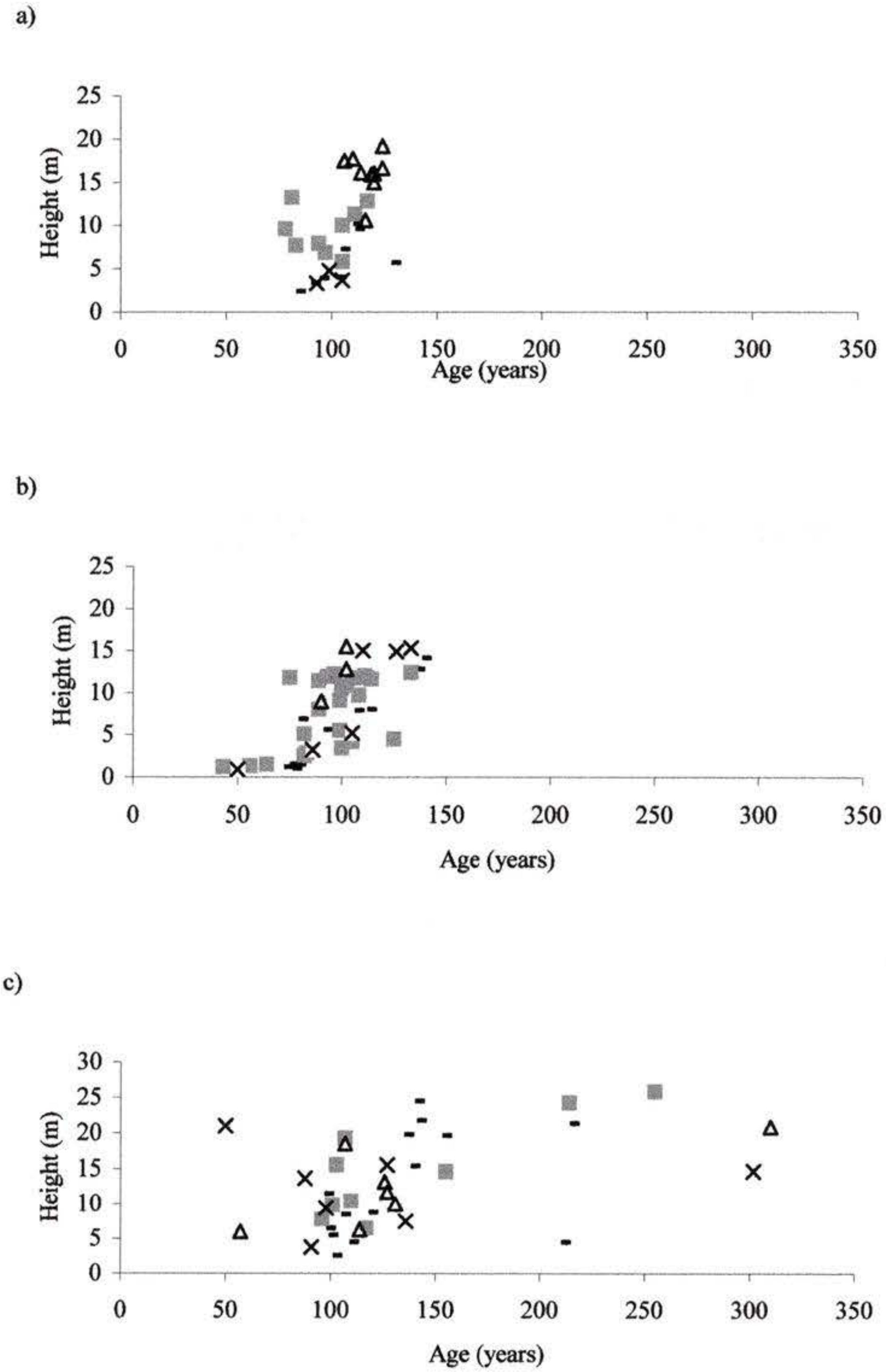
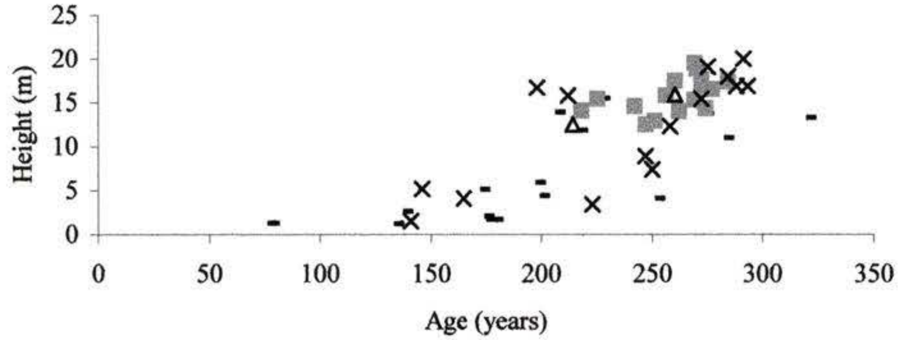
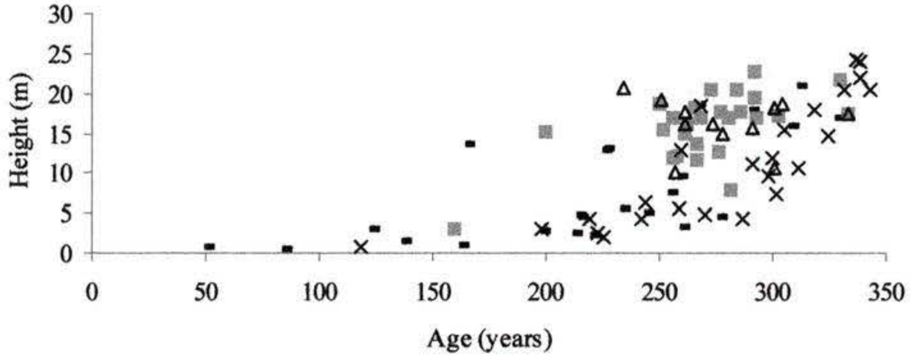


Figure 14. Scatter plots of tree height vs. age for selected middle-aged stands (i.e., 125–250 years old) of the Cranbrook chronosequence. Presented are data for a) the 125 year-old stand; b) the 136 year-old stand; and, c) the 155 year-old stand. Subalpine fir = - ; whitebark pine = ■ ; lodgepole pine = Δ ; Engelmann spruce = ×.

a)



b)



c)

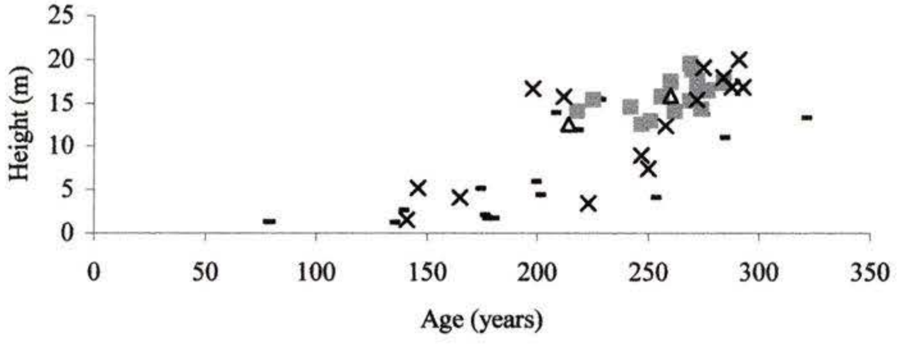


Figure 15. Scatter plots of tree height vs. age for selected old stands (i.e., > 250 years old) of the Cranbrook chronosequence. Presented are data for a) the 284 year-old stand; b) the 339 year-old stand; and, c) the 346 year-old stand. Subalpine fir = - ; whitebark pine = ■ ; lodgepole pine = △ ; Engelmann spruce = ×.

and the 84 year-old stands (Figures 13b and 13c) lodgepole pine appears to have colonized sites first, but they were quickly followed by establishment of slower growing whitebark pine, subalpine fir, and Engelmann spruce. In most stands, establishment of lodgepole pine occurred over about a 20 year period following disturbance. In the 136 year-old and the 284 year-old stands (Figures 14b and 15a), lodgepole pine appears to have not been part of the post-fire cohort; these sites were colonized by whitebark pine, subalpine fir, and Engelmann spruce following fire.

Trees less than about 150 years old in the two oldest stands were small and suppressed (Figure 15). Most lodgepole pine and whitebark pine in the 339 year-old stand established about 40-90 years after the oldest trees in the stand (Figure 15b). However, the oldest trees in this stand showed no marked increase in growth rates during the period of time in which whitebark pine and lodgepole pine established, suggesting that the older Engelmann spruce and subalpine fir trees were not affected by disturbance. Most trees establishing after the stand was about 100 years old grew very slowly, indicating that a full canopy developed on this site, but only very slowly. The tree canopy in this stand was only weakly multi-layered with a relatively low subcanopy cover. In contrast, the subcanopy of the 346 year-old stand was fairly dense (Table 11), and growth of subalpine fir that established up to 200 years after stand initiation was still fairly rapid (Figure 15c).

Several trees appear to have survived fire in the 63 and 155 year-old stands (Figure 13b, 14c). Both small and large trees survived the fire that initiated the 63 year-old stand. However, only two small subalpine fir (the 113 and 127 year-old trees) showed clear evidence of release from suppressed growth around 63 years ago; all other surviving trees showed no changes in growth rates at the time of fire and most of these trees had good, steady growth. The older residual trees in this stand result from a combination of trees surviving in patches and occasional small trees surviving in the understory during fire. The age structure of the 155 year-old stand appears to be the result of a fire through which some small trees survived (Figure 14c). All trees surviving the fire about 155 years ago were small with basal diameters of < 5 cm when the fire occurred. The 214 and 250 year-old whitebark pine showed a distinct release from suppressed growth between 150 and 160 years ago, and a single large Douglas-fir (219 years old, height = 19 m) showed a pronounced increase in radial growth about 165 years ago. One small, suppressed, subalpine fir that survived the fire maintained a slow rate of growth over its 211 year life time. The 5 subalpine fir and 1 whitebark pine between 136 and 150 years old likely established after the fire; they all showed good growth until about 50 years ago when growth decreased considerably.

Scatter plots of tree height vs. age were also used to examine the development of individual young, middle-aged and old stands sampled near Lillooet (Figures 16, 17, and 18). Whitebark pine, subalpine fir and Engelmann spruce were all part of the post-fire cohort in the 129, 173, and 310 year-old stands (Figures 17a, c, and 18b). Whitebark pine was the first to colonize the youngest stands sampled (Figure 16), and was followed by subalpine fir and Engelmann spruce 10 to 25 years later. Subalpine fir and whitebark pine comprised the post-fire cohort of the 170 and 261 year-old stands with Engelmann spruce establishing about 50 years later in the 170 year-old stand but never establishing in the 261 year-old stand (Figures 17b and 18a). The post-fire cohort of the oldest stand sampled appeared to be comprised of whitebark pine and Engelmann spruce (Figure 18c). Young and middle-aged stands had a wide distribution of tree ages for subalpine fir, whitebark pine, and Engelmann spruce. The oldest stand had a wide distribution of tree ages for subalpine fir but whitebark pine and Engelmann spruce trees were either large and old (> 200 years) or very young (Figure 18c).

Only the 173 year-old stand contained trees that had survived the most recent fire (Figure 17c). Examination of growth ring widths indicated that both surviving whitebark pine trees showed slow growth except for a period of relatively rapid growth between 146 and 196 years ago. A gap in tree regeneration appears to occur between about 280 and 360 years ago in the 462 year-old stand (Figure 18c). This regeneration gap was not obvious with visual inspection of the stand because subalpine fir of varying sizes formed a multi-layered canopy. Most of the subcanopy and some of the canopy trees, however, were less than 280 years old.

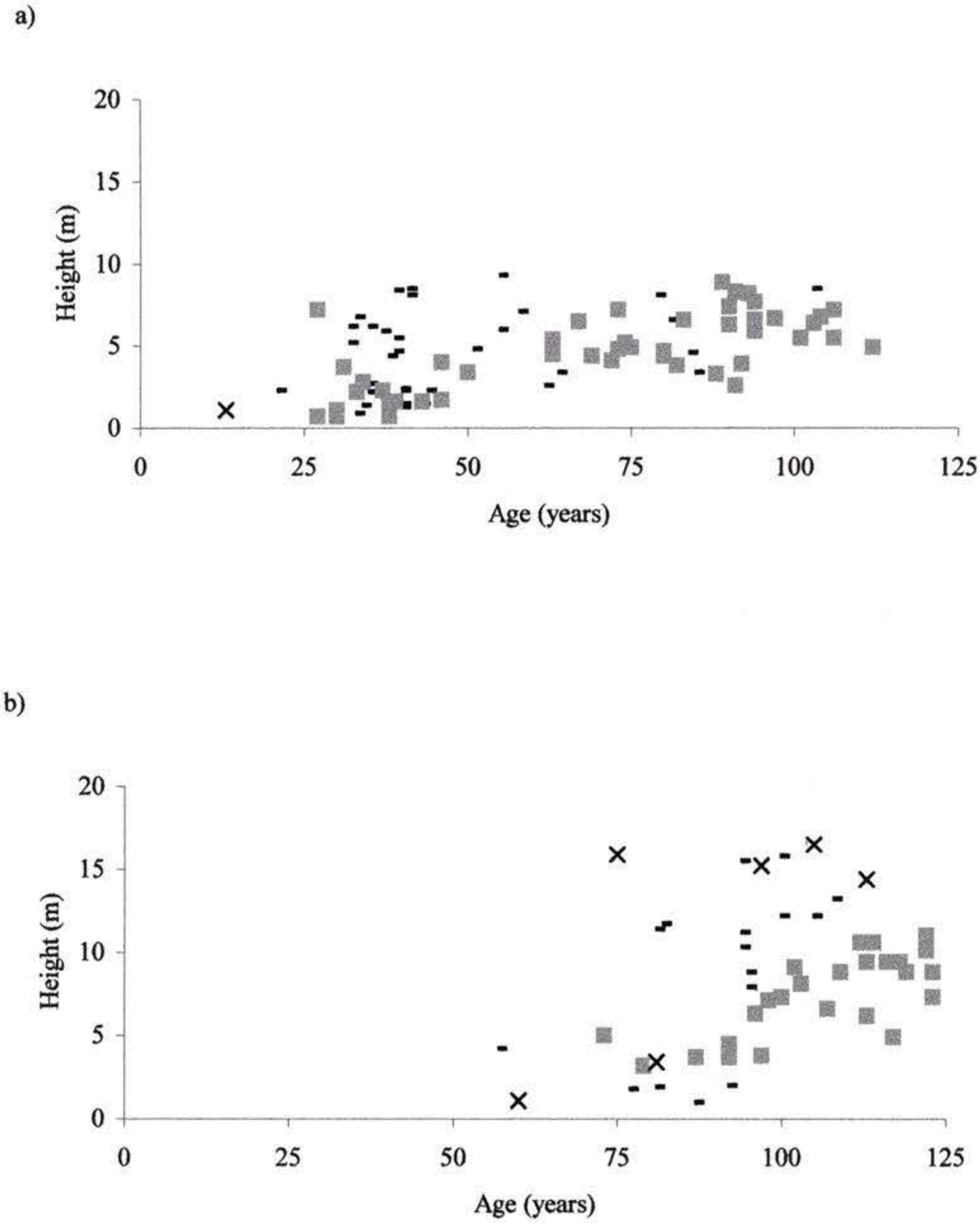


Figure 16. Scatter plots of tree height vs. age for selected young stands (i.e., < 125 years old) of the Lillooet chronosequence. Presented are data for a) the 112 year-old stand; and, b) the 124 year-old stand. Subalpine fir = -; whitebark pine = ■ ; Engelmann spruce = ×.

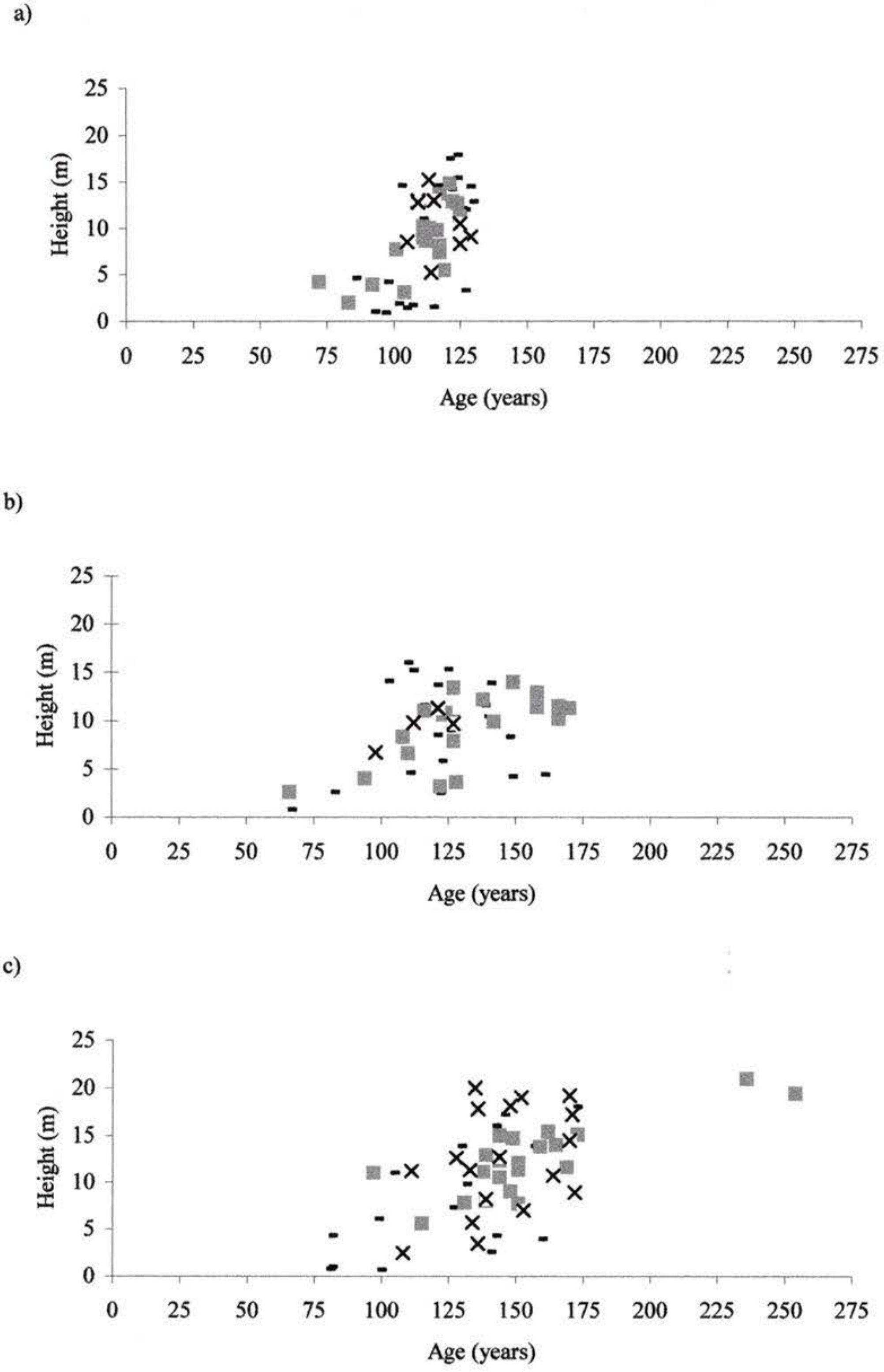


Figure 17. Scatter plots of tree height vs. age for selected middle-aged stands (i.e., 125–250 years old) of the Lillooet chronosequence. Presented are data for a) the 129 year-old stand; and, b) the 170 year-old stand; and, c) the 173 year-old stand. Subalpine fir = - ; whitebark pine = ■ ; Engelmann spruce = ×.

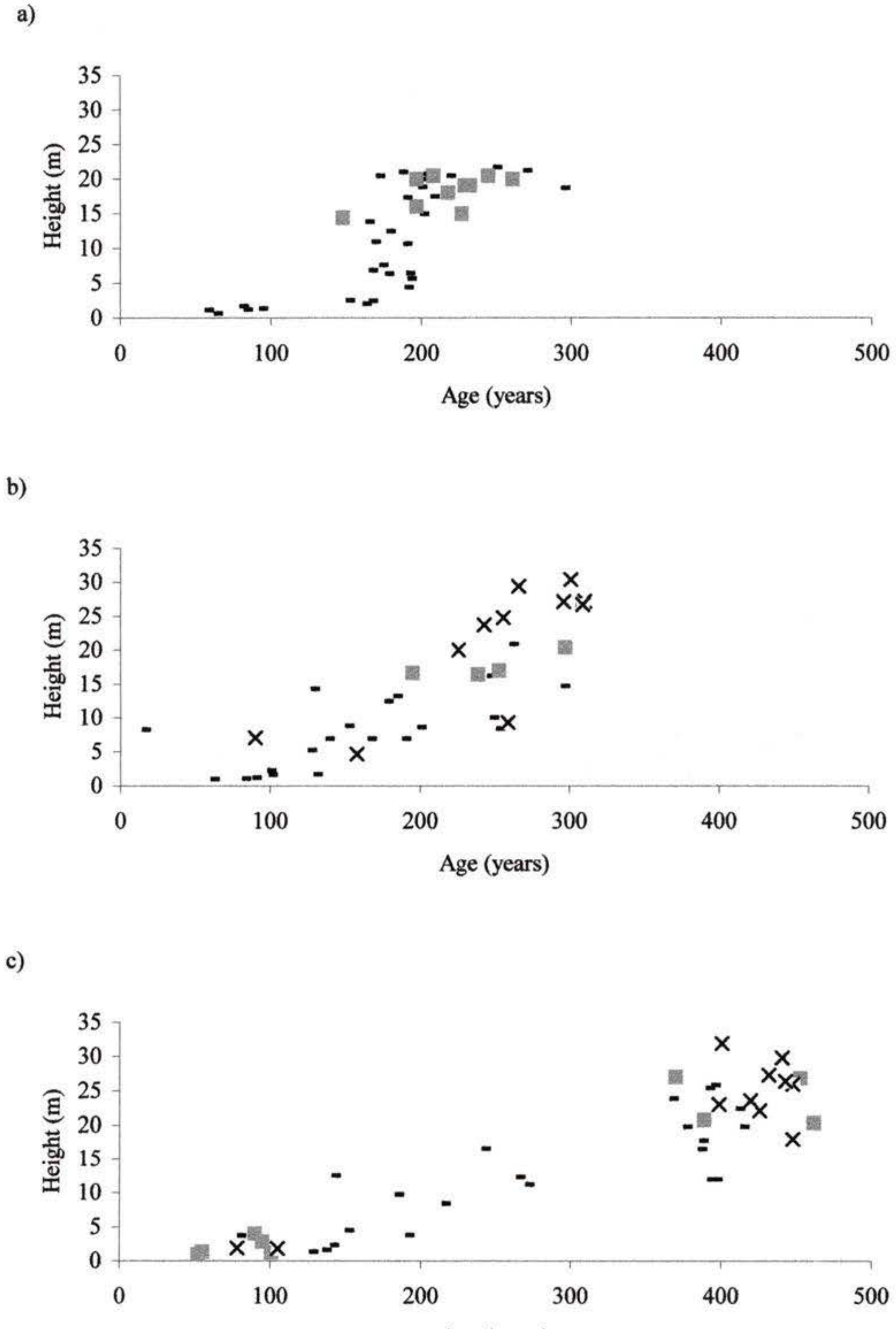


Figure 18. Scatter plots of tree height vs. age for selected old stands (i.e., >250 years old) of the Lillooet chronosequence. Presented are data for a) the 261 year-old stand; and, b) the 310 year-old stand; and, for c) the 462 year-old stand. Subalpine fir = - ; whitebark pine = ■ ; Engelmann spruce = ×.

Discussion

Patterns of fire disturbance

Fire is an important agent of disturbance in both the Cranbrook and Lillooet study areas. Field reconnaissance and stand age structure data indicated that at least the most recent fires at both the Cranbrook and the Lillooet study areas were largely stand-replacing fires. However, some trees survived these fires on sites sampled at both Cranbrook and Lillooet. The presence of large Engelmann spruce and subalpine fir trees within the area of a stand-replacing fire suggests the patchy nature of some of the fires that occurred in the Cranbrook study site. Because of their thin bark and low branching habit, both Engelmann spruce and subalpine fir are poorly adapted to survive fire (Flint 1925; Lasko 1990). The degree to which a fire is patchy depends greatly on the nature of the tree canopy, the amount and distribution of surface fuel, and the density of understory shrubs and small trees (Arno 1980; Lasko 1990; Tande 1979). The 63 and the 165 year-old stands sampled at Cranbrook had many surviving trees, indicating that fuels may have been especially sparse or patchy in these sites prior to the fires, or that weather conditions at the time of the fires were marginal for burning. The survival of trees, particularly large reproductively mature trees, can have a major impact on regeneration (and successional development) in the post-fire stands (e.g., Stewart 1986) and explains, in part, the higher than expected densities of Engelmann spruce and subalpine fir found in some very young stands sampled at Cranbrook (e.g., the 34 and 55 year-old stands). Some small, suppressed subcanopy trees and saplings also survived fires that appear to have killed the entire tree canopy (e.g., 34, 63, and 155 year-old stands in the Cranbrook study area). Some of these trees had an abrupt increase in radial growth following the disturbance.

An interesting finding with regard to stand age structure is the virtual absence of intermediate aged trees (and intermediate sized trees) in some older stands sampled at both the Cranbrook and Lillooet study areas. Gaps in conifer regeneration are common in many kinds of forests (e.g., *Libocedrus bidwillii* stands in New Zealand, Veblen and Stewart 1982) and occur for a variety of reasons. Similarly, there are several potential explanations for the occurrence of the gaps in conifer regeneration found at the

Cranbrook and Lillooet study areas. The occurrence of low-intensity surface fires is one possible explanation. In subalpine whitebark pine/subalpine fir forests of Wyoming, gaps in tree regeneration, corroborated with tree fire scars, has been attributed to frequent occurrence of low-intensity surface fires in the late 1700's and early 1800's (Morgan and Bunting 1990). The short interval between fires during this time is believed to have prevented all conifer regeneration. Surface fires were common in various kinds of forests in British Columbia (e.g., ponderosa pine, Douglas-fir, and some lodgepole pine forests), and occurred frequently in the low-elevation forests below both the Lillooet and Cranbrook study areas (K. Lertzman, pers. comm. Feb. 1998; J. Parminter, pers. comm. Feb. 1998). The 346 year-old stand sampled at Cranbrook appeared to have virtually no trees that established between about 200 and 280 years ago. Because many of the lodgepole pine and whitebark pine in the stand would have been large enough by this time to survive low-intensity fires (Arno 1986; Morgan and Bunting 1990), it is plausible that surface fires may have been responsible for the gap in conifer establishment. Although the 462 year-old stand sampled at Lillooet lacked trees between the ages of about 280 and 360 years, many of the oldest trees in the stand were subalpine fir or Engelmann spruce, which are poorly adapted to survive fire. However, subalpine fir can survive fires in the study areas as indicated by the age structure data of a few stands and charred lower branches on trees in the 129 year-old stand sampled at Lillooet. Alternatively, the gap in conifer regeneration could result from an inability of trees to establish under a dense canopy in young stands. Johnson *et al.* (1994) show that the empty middle-age classes in stand age-class distributions of Engelmann spruce/lodgepole pine forests were caused by low recruitment and high mortality of trees establishing under the main canopy. However, this explanation seems unlikely at least for subalpine fir, which is extremely shade tolerant (Kobe and Coates 1997). It is also possible that if more age data were collected in the stands, the gap in conifer establishment would be less pronounced.

Though stand-replacing fires were the most prominent type of recent fire disturbance in the Cranbrook and Lillooet study areas, the pattern of fire disturbance in whitebark pine stands may be very heterogeneous with complete stand-replacing fires, stand-replacing fires with surviving patches of trees or scattered trees (sometimes only small trees), and low-intensity surface fires all occurring in these forests. Over time, one or a combination of these fire types may occur in any stand. There is still much information about fire behavior in these habitats that could be obtained through dendroecological work with tree fire scars and more intensive stand reconstructions (*sensu* Fastie 1995; Johnson and Fryer 1989; Johnson and Gutsell 1995).

Succession

Major disturbances greatly alter the structure and composition of forest communities (Oliver 1981). Succession theory indicates that vegetation development after disturbance is driven by life history traits of individual species and follows a general pattern in which species with progressively greater maximum size, longevity, and shade tolerance but progressively lower maximum growth and dispersal rates become more abundant with time (e.g., Clements 1928; Connell and Slayter 1977; Egler 1954; Grime 1979; MacArthur and Wilson 1967; McCook 1994). Many foresters and plant ecologists believe that forest succession is largely driven by interspecific differences in shade tolerance, with slow-growing shade-tolerant trees replacing relatively shade intolerant colonizers in the absence of major disturbance (Kobe and Coates 1997; Kobe *et al.* 1995; Shugart 1984). From studies of lodgepole pine/Engelmann spruce forests in the northern Rocky Mountains, Johnson *et al.* (1994), on the other hand, assert that forest succession cannot be viewed as a simple sequence of species replacements based on shade tolerance as other factors contributing to mortality are important. Other researchers have also shown that patterns of successional development on a site are the result of numerous factors (e.g., species availability, disturbance levels, history) (Fastie 1995; Halpern 1988; McCook 1994). The results of this study support this view, and indicate that patterns of vegetation change following disturbance can result from the combined effects of tree species life history characteristics (e.g., shade tolerance), availability of seed sources (which are affected by the nature of the disturbance [e.g., type, size, intensity, frequency]), characteristics of the pre-disturbance vegetation, and characteristics of vegetation in the surrounding landscape.

The chronosequence studies reported here provide some support for the general successional trends reported in other studies of whitebark pine forests (e.g., Keane *et al.* 1990; Morgan and Bunting 1990; Morgan *et al.* 1994; Weaver and Dale 1974). That is, whitebark pine and sometimes lodgepole pine establish in abundance shortly after fire and, because of the relative shade intolerance of these species, they are eventually replaced by subalpine fir and Engelmann spruce. However, my results indicate that this view of succession in whitebark pine forests is somewhat over-simplified and that the replacement of whitebark pine is equivocal. At both the Cranbrook and Lillooet study areas, stands on similar sites showed considerable variability in species composition that cannot be attributed to stand age; that is, composition was different than expected considering their position in the chronosequence. Because of this, I suggest that forests containing whitebark pine in southern British Columbia may have developed along more than one successional pathway. Multiple pathways of succession are often detected in chronosequence studies (e.g., Abrams *et al.* 1985; Cattelino *et al.* 1979; Fastie 1995; Halpern 1988). In whitebark pine forests, three major successional pathways can be identified.

The differences among the three major pathways depend on the amounts of lodgepole pine establishing in post-fire stands. The first major pathway is distinguished by abundant colonization of burned sites by lodgepole pine. Where it was common in the pre-disturbance stand, lodgepole pine often establishes rapidly and abundantly following fire, because large amounts of seed are released from serotinous cones (Lotan 1974; Muir and Lotan 1985) (e.g., 84 year-old and 124 year-old stands in the Cranbrook study area). At all sites, whitebark pine established in post-fire stands at the same time or very shortly after lodgepole pine. Tomback (1994) observed whitebark pine regeneration within 2-3 years of fires. The initial growth rates of lodgepole pine were greater than those of whitebark pine on all sites sampled. Because of this, when lodgepole pine was abundant, it formed dense pole stands (between about 60-120 years) with slower-growing whitebark pine, subalpine fir and Engelmann spruce in the subcanopy. This successional stage appears to have a critical effect on the abundance of whitebark pine in future stands; whitebark pine was markedly less abundant in these stands compared to stands where lodgepole pine was less dense. The low abundance of whitebark pine can be attributed to some combination of relatively high mortality rates because of competition and low recruitment rates during this successional stage.

Some researchers in the U.S. consistently report that Clark's nutcracker prefers to cache seed in open areas (Morgan *et al.* 1994; Tomback 1990; Tomback *et al.* 1995) but give no empirical evidence to support this. Hutchins (1990) and Hutchins and Lanner (1982) suggest that it is advantageous for nutcrackers to cache seed in open areas as they are less subject to predation by red squirrels, although they also observed nutcrackers caching seed in dense forests in Wyoming. If nutcrackers do cache fewer seeds in dense stands, this would partly explain the low densities of small whitebark pine in stands where lodgepole pine is dense and also why recruitment appears bimodal during the chronosequences at both study sites. However, high mortality rates caused by competition are an equally or more likely explanation. Low initial establishment rates of whitebark pine on sites where lodgepole pine is abundant is a further alternative explanation, but this seems unlikely in the Cranbrook study area because many nearby recently burned sites had abundant whitebark pine. However, Tomback *et al.* (1995) observed lower than expected densities of whitebark pine seedlings on burned sites in Idaho. They suggested that this was due to poor seed crops in adjacent mature stands that had been heavily affected by blister rust; blister rust may quickly kill the upper cone-bearing branches of large trees.

When the canopy of stands with abundant lodgepole pine begins to open (e.g., 124 year-old stand at Cranbrook), subalpine fir and Engelmann spruce become more abundant in the understory. Some small, suppressed whitebark pine, which appear more shade tolerant than lodgepole pine, survive through the pole stage and become the large trees observed in the older successional stages at the Cranbrook study area. However, the abundance of whitebark pine would in most cases be relatively low in old stands that developed through a dense lodgepole pine stage.

The second major successional pathway is distinguished by low lodgepole pine abundance in post-fire stands. In some young post-fire stands at the Cranbrook study area, lodgepole pine was sparse (e.g., the 34, 55, and 63 year-old stands), probably because it was not abundant in the stand that burned. Though lodgepole pine grew faster than whitebark pine on these sites, its low density precluded the formation of dense-canopied stands. Whitebark pine was relatively abundant on these sites, but because of its growth form and the manner in which seeds are dispersed, it tended to form more open-canopied stands in which relatively abundant small whitebark pine could survive into mid-late seral stages (e.g., the 136 and 150 year-old stands at Cranbrook). A similar phenomenon was observed on sites where lodgepole pine was absent from the post-fire cohort (i.e., the 136 year-old stand at Cranbrook and all of the stands in the Lillooet study area). The complete absence of lodgepole pine on post-fire sites distinguishes the third major successional pathway. With no lodgepole pine to compete with, abundant whitebark pine of all sizes survive into mid-seral stages. However, despite the absence of lodgepole pine and a relatively open canopy, stands of the Lillooet chronosequence indicate that there is a major reduction in the density of whitebark pine in older successional stages. Part of this decline in density results from the poor ability of seedlings to establish on these sites; though the canopy is relatively open, old stands usually have a dense understory of subalpine fir and shrubs that could prevent most seedling establishment. Additionally, many large, old trees have heartrot, which can lead to mortality and further reductions in density. These findings are not restricted to old stands in the Lillooet study area; similar situations were observed in old stands at the Cranbrook study area and in other old stands throughout the range of whitebark pine in British Columbia.

Further variation in species composition among stands occurs because of the amounts of Engelmann spruce. Unusually large amounts of spruce were found in some stands at both the Lillooet and Cranbrook study areas (e.g., the 346 year-old stand at Cranbrook and the 310 year-old site at Lillooet). Large seed crops near the time these sites were burned, or potentially coincidental wind direction and seed dispersal (see Tomback 1994) may have resulted in greater recruitment of Engelmann spruce on these sites.

Dynamics of whitebark pine in subalpine forests

Although whitebark pine is considered to be able to persist indefinitely in the absence of disturbance on very harsh sites where other trees do poorly, it is generally thought to be maintained on more productive sites by disturbance. This view of whitebark pine as largely a pioneer species is inadequate. Although density decreases greatly in old stands, new trees are occasionally able to establish and survive, indicating that long-term persistence of the species on many sites, albeit in low abundance, is plausible in the absence of disturbance. Contrary to expectations for a shade-intolerant, pioneer species, whitebark pine can withstand suppression for long periods; trees less than 1.3 m tall but almost 100 years old occur in forest understories. Extremely slow growth rates like this are more typical of late successional species, such as subalpine fir, than of pioneer species. Thus the comparisons made with lodgepole pine are largely inappropriate; the ecology of the two species differ greatly. Where these two species occur together, they differ in growth rates and timing of establishment, with lodgepole pine exhibiting classical characteristics of a pioneer tree species – rapid growth, establishment restricted to the immediate post-disturbance period, and little ability to survive suppression – whereas whitebark pine is more variable in its characteristics. Thus, whitebark pine should be viewed as a species that, although establishing in abundance after fire, can also recruit in many stands of all seral stages, and that has major differences from all other sympatric tree species, not only in its unusual mode of seed dispersal, but also in its basic ecological characteristics related to disturbance and succession.

CHAPTER 5

CONCLUSIONS

Prior to this study, the structure and composition of forested ecosystems containing whitebark pine in British Columbia remained virtually undescribed. Knowledge about how the abundance of whitebark pine varied over its geographic range and among different habitats was absent. This, coupled with a forest ecosystem classification system based on potential dominant climax vegetation, has given the impression that whitebark pine is uncommon in British Columbia. Whitebark pine however, occurs on most major mountain ranges in British Columbia south of 55°N, and in all but the wettest mountain ranges it is be quite consistently found in upper subalpine forests and at the timberline. The species occupies a diverse array of habitats in British Columbia from productive lower subalpine forests to unproductive sites such as rock outcrops and timberline stands. Whitebark pine is most abundant on sites with harsh environmental conditions and where competition with other species is low (e.g., rock outcrops, timberline sites, and some recent burns); it is clearly a stress-tolerant species.

The patterns of successional development of stands containing whitebark pine are often more complex than the simple generalization that whitebark pine is replaced by more shade-tolerant subalpine fir and Engelmann spruce. Influenced by the combined effects of tree species life history traits, availability of seed sources, the nature of the fire disturbance (i.e., fire frequency, intensity, etc.,), characteristics of pre-disturbance vegetation, and characteristics of the vegetation in the surrounding landscape, forests containing whitebark pine in this study developed along three major successional pathways. The differences among these pathways depended largely on the relative amounts of lodgepole pine that colonize with whitebark pine following fire disturbance (i.e., none, some, abundant lodgepole pine). The interactions between these two species in early seral stages is an important determinant of the abundance of whitebark pine in later seral stages. Without competition from lodgepole pine, slower growing whitebark pine may become an important stand component in late successional stands. Unlike lodgepole pine, whitebark pine may persist, albeit at low abundance, in the absence of disturbance on productive sites and can recruit in stands of all seral stages.

Fire is a key process for maintaining abundant whitebark pine over the landscape. Fire suppression programs of the last century have been cited as an important reason for the decline of whitebark pine in the United States (Keane and Arno 1993). In Canada however, fire suppression programs of the last century have been limited primarily to the southern portions of the Canadian provinces (Hawkes 1990), and despite this, fires still continue to burn in the southern portions of British Columbia. The small size of recent fires in both the Cranbrook and Lillooet study areas is likely the result of successful fire suppression over the last several decades. Both study areas were located relatively close to human populations and areas of recreational use. Most whitebark pine habitats in British Columbia, however, occur on steep, rugged terrain isolated from human populations. Moreover, many of these forests occur outside of major parks (where fire suppression has been extensive). For these reasons, and from widespread surveys throughout the range of whitebark pine in British Columbia, there is little evidence that fire suppression programs of the last several decades have posed a significant threat to whitebark pine in this province.

Having reached epidemic levels, white pine blister rust currently poses a serious threat to whitebark pine in British Columbia. Virtually all stands sampled in this study contained whitebark pine trees infected by white pine blister rust and the incidence of infection within stands was frequently high. Contrary to some U.S. research, however, high levels of whitebark pine mortality due to blister rust were not common. However, it is likely that many of the infected stands will experience high levels of whitebark pine mortality over the next few decades, significantly reducing whitebark pine throughout its geographic range in British Columbia. A dramatic reduction in whitebark pine will likely have serious implications for the structure and dynamics of subalpine forests and on plant communities near the timberline. It will probably also have a significant impact on the wildlife that depend on whitebark pine seeds for food.

Tree species are very vulnerable to destruction by introduced pathogens because of the long time required to replace mature trees. Dramatic losses of the American chesnut and elm trees due to introduced fungi are good examples of the potentially devastating effects of introduced diseases. Potential economic, and in the case of whitebark pine, important ecological losses, make their need for protection a high priority. However, protecting trees from diseases are amongst some of the most difficult forest management challenges. Because the spread of blister rust is independent of human activities, conservation of the species in isolated wilderness areas and parks will afford whitebark pine little protection. Early efforts to control the spread of white pine blister rust on western white pine through widespread eradication of the alternative host (*Ribes* spp.) and applications of fungicide failed (Hoff and Hagel 1990) and, thus are not practical options for the control of blister rust on whitebark pine. About 1 to 8 percent of whitebark pine in a stand may be genetically resistant to blister rust (Arno and Hoff 1989; Bingham 1971; Hoff *et al.* 1980). While these current levels of natural resistance may permit the maintenance of whitebark pine in landscapes it is likely not high enough to maintain whitebark pine at its current population levels (Keane and Morgan 1994). However, the fact that whitebark pine currently exhibits some resistance to the disease holds some promise for the future of the species. The use of this natural resistance to breed rust-resistant whitebark pine could play an important role in future conservation efforts. Though rust resistant seedlings are currently not available, the U.S. Forest Service is locating phenotypically resistant trees (i.e., those which exhibit overt signs of blister rust resistance [e.g., bark reactions, fungicidal short shoots]) that could be used to produce resistant seedlings for planting (Hoff *et al.* 1994). There has been little effort directed toward the production of resistant whitebark pine in British Columbia. Traditional breeding and selection programs, however, require the commitment of large amounts of land, labour, funding, and time. With currently limited financial resources, the development of a program for breeding and replanting blister rust resistant whitebark pine in burned and cutover areas will be a challenge particularly because the species holds little commercial value.

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