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Regeneration dynamics of *Larix lyallii* in forests of the southern Canadian Rockies.

by

Brendan Charles Wilson ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Doctor of Philosophy
In
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University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Regeneration dynamics of *Larix lyallii* in forests of the southern Canadian Rockies, submitted by Brendan Charles Wilson in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Ecology and Environmental Biology.

M R T Dale

Dr. Mark R. T. Dale

Jens Roland.

Dr. Jens Roland

Dr. John Addicott

Dr. Philip Lee

Victor Lieffers

Dr. Victor J. Lieffers

Gary Bradfield

Dr. Gary Bradfield

Dedication

To my first teachers:

Barbara

Brian

Jeanne

Joan

Abstract

Alpine Larch (*Larix lyallii* Parl.) is a high elevation conifer that occurs over a limited area of the northern United States and southern Canada. This species is generally found near timberline, often forming the tree limit in these harsh environments. However, at the northern edge of the larch's distribution, the species forms extensive subalpine associations with Engelmann spruce (*Picea engelmannii* Parry.) and subalpine fir (*Abies lasiocarpa* (Hook) Nutt.). Because there was little known about the occurrence of the larch in these subalpine locations, my objective was to determine the importance of disturbance and the resultant forest structure in maintaining these peripheral populations over a range of forest ages present in the southern Canadian Rockies. I found alpine larch initially established following fire disturbance (< 40 years old) over a broad elevation range. Most larch regeneration occurred on northern aspects, although some seedlings were also found on shaded southern slopes. Seedlings were generally dispersed within 300 m of surviving parent trees and appeared to require moderate shrub cover for successful recruitment. In maturing forests (c.150 years), larch seedlings were not found in the lower subalpine zone, even though canopy larch were present. This was linked to the combination of increased fir basal area and increased shrub and canopy cover. In older forests (>300 years) larch recruitment remained inhibited at lower elevations where canopy height, canopy cover, and shrub cover was high, even though tree fall gap disturbance had started. However, at higher elevations, where there was a reduction in these competitive influences, larch regeneration reinitiated. This was linked to the changed gap structure. In these forests larch seedlings were found only in gaps. Larch gap fillers were more frequent at the northern edge of the larger (>70m^2), lighter gaps, and

where the surrounding average canopy height was less than 17 m. I suggest that the ability of larch to disperse into recent burns and the maintenance of a viable population within some part of the subalpine forest over time may be important for (1) maintaining genetic diversity between otherwise isolated timberline populations and (2) enabling migration as the climate changes.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Alpine Larch (*Larix lyallii* Parl.) is a deciduous conifer that generally occurs at, or near timberline over a limited area of the western cordillera in southern Canada and the northern United States (Arno and Habeck 1972). This tree is a distinctive feature of these high elevation sites, occupying the predominantly cooler, moist northern aspects. In many areas alpine larch is found growing well above the limits of other high elevation conifers, in what would otherwise be classified as alpine tundra (Figure 1.1a). However, in this species' northern distribution, it also forms associations with Engelmann spruce (*Picea engelmannii* Parry.) and subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) in continuous subalpine forest, well below the more open timberline ecotone (Figure 1.1b) (Corns and Achuff 1982). Although alpine larch is of little economic timber value, this species has a number other important values. These include high elevation slope stabilisation, wildlife habitat and forage, and providing an aesthetic component for human appreciation (Arno et al.1995, Blocker 1995).

1.1.1 Distribution and similar species

The northern extent of the alpine larch distribution is the upper end of the Bow River Valley in Banff National Park, Alberta (51° 40 north). The species occurs along the Rocky Mountains down to its southern limit in lower Montana and central Idaho (Figure 1.2). The most western populations of alpine larch are found on the eastern slopes of the Cascades in southern British Columbia and northern Washington. To the east of the Canadian Rockies the species is absent due to the lack of suitable high elevation topography (Arno 1970). Except for the latter case, these geographical limits appear to be related to larger scale climatic conditions. The semi-arid continental macroclimate that exists to the south and east of Montana likely inhibits establishment and early growth of seedlings. To the north, the cooler subarctic macroclimate prevalent in Alberta is the best

Figure 1.1a: Alpine larch saplings invading an alpine meadow at Healy Pass, Banff

Figure 1.1b: Alpine larch mixed with Engelmann spruce and subalpine fir in older forest around Pharaoh Lake, Banff National Park. Alberta.

correlate with the species' distribution boundary in this location (Arno 1995). The western and northwestern distribution limits of the species are less well understood, but may be related to a shorter growing season due to the greater depth and persistence of the spring snow pack.

There are 10 commonly recognised species of *Larix*, all of which occur in the northern hemisphere (Ostenfeld and Larsen 1930, Schmidt 1995). Alpine larch is one of three species that are endemic to North America. Tamarack (*Larix laricina* (Du Roi) K. Kock) is the most broadly distributed North American species, stretching from northwestern Alaska across the entire Canadian boreal forest to the northern United States on the Atlantic coast (Figure 1.2). The distribution of Western larch (*Larix occidentalis* Nutt.) is smaller than that of tamarack, and has striking similarities to the distribution of alpine larch.

The main differences between western and alpine larch are that western larch is more broadly spread over the lower subalpine slopes and montane valley bottoms, while alpine larch is confined to the higher elevation sites, which breaks the species' population up into smaller patches. The alpine larch population is also slightly further north (Figure 1.2). The consistent large scale overlap in these distributions highlights the strong similarity between alpine and western larch. Although the two species are generally separated by several hundred metres of elevation, there are several areas where the species overlap and form hybrids (Carlson and Ballinger 1995). There is no evidence of natural hybridization of tamarack with either western or alpine larch, as the populations do not overlap.

Although the origins of the *Larix* genus were likely in Asia during the late the Cretaceous Period, some 60 million years ago, the North American species appear to have crossed the Beringia land bridge between Alaska and Asia in the late Tertiary, between 25 to 35 million years ago (LePage and Basinger 1995). Arno (1970) suggests that while it was possible that two separate types of larch crossed from Asia (a mountain species and a lower elevation boreal species), the lack of higher elevation habitat over the land

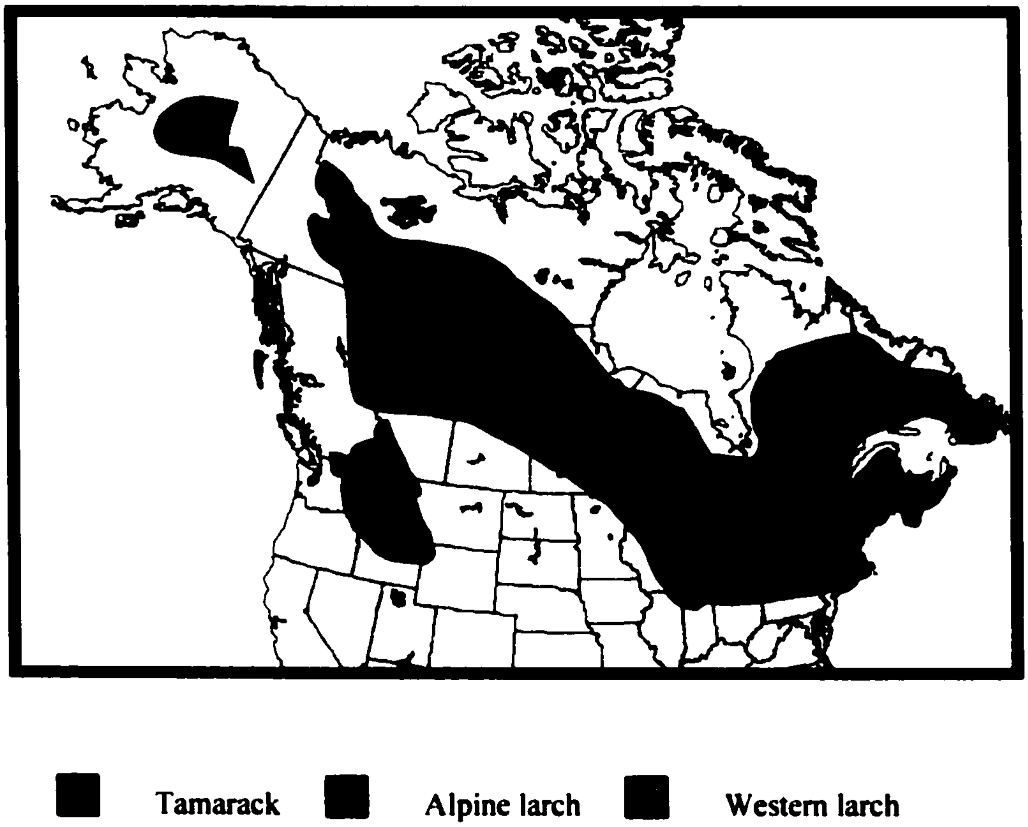


Figure 1.2: Distribution of the three North American larch species. Adapted from Johnston (1990), Arno (1990), and Schmidt and Shearer (1990).

bridge suggests the migration of one original North American species and subsequent speciation by climate change and mountain building. Richards (1981) suggests that two temporally separate migration events of different, or perhaps even the same species may also explain the present day species distribution.

1.1.2 Morphology, life history, and ecophysiology

Arno (1990) reports the tallest individual alpine larch to be 46 m. This was found in Montana's Cabinet Range. The tallest individual found in the current study was 21m, located in subalpine forest in the Redearth Creek drainage of Banff National Park. However, at timberline in the Canadian Rockies, the species rarely exceed 10m. The soft light green needles are borne in clusters 30-40 along branches that in older trees droop, but turn up at the end (Moss 1983). The needles flush in the spring, around the end of May to early June. This process appears to be controlled by a consistent rise in temperature during the preceding weeks (Worrall 1993). The larch's needles start to turn to a golden yellow usually in early October with leaf fall occurring later in the month. Worrall's (1993) study of this process indicates that timing of the fall is linked to the accumulated heat experienced during the summer.

Alpine larch is a long lived species. Arno and Habeck (1972) suggest that the average life span of the tree is about 500 years, with the oldest approaching 1000 years in some locations. Worrall (1990) speculates that there may even be individuals in Manning Provincial Park in British Columbia almost 2000 years old – making alpine larch Canada's oldest tree species. However, this is based on considerable extrapolation of the outer existing annual rings of trees where the inner two-thirds of the trunk have succumbed to heart rot. Nevertheless, these age ranges indicate that this species potentially is able to outlive all of the other high elevation species with which it occurs.

In a similar pattern, alpine larch generally do not become sexually mature until they reach ages of 80-100 years, and typically produce relatively little seed until the tree is several centuries old (Arno 1970). This kind of long term reproductive cycle the species in that it is able to wait out prolonged periods of time where there may not be the appropriate conditions for juvenile recruitment. The cone and seed development occurs over a two year period, with often low numbers of filled seed, due to low pollination rates and high levels of embryo abortion (Owens 1995). The winged seed matures in the cones by about September of the second year and then is dispersed by wind. Alpine larch appear to have large seed crops about once a decade and occasional moderate crops between these events (Arno 1990).

Richards' (1981) study of the ecophysiology of alpine larch identified several useful adaptations to aid seedling establishment and survival in the high elevation timberline environment. Seedlings appear to initially invest substantial energy in to developing deep tap roots and sinking lateral roots to reach a consistent summer water supply. During this initial growth period the young alpine larch seedlings keep their needles for two full seasons. These "wintergreen" needles are more effective at limiting summer desiccation than the larch's normal deciduous needles, due to more rapid stomatal closure during period of low atmospheric humidity. The wintergreen needles also lengthen the summer growing season while the root development takes place. However, these needles have a much higher light compensation point than the deciduous needles and only remain on the seedling during winter where there is a sufficient snow pack to keep them covered.

Trees living within the timberline environment have to cope with a number of general problems including cold temperatures, short growing seasons and potentially damaging winds (Daubenmire 1974). Winter conditions in these high altitude habitats present trees that reach above the snow pack with two additional problems that severely affect the overall vigour of individuals. These are (1) abrasion caused by wind-blown snow and ice to exposed needles, and (2) desiccation caused by warm air events such as inversions and Chinooks (Tranquillini 1979). Krummholtz, or shrub-like patches of conifers, in the exposed timberline areas are generally a vegetative response to the "pruning" action of wind blown snow and ice particles on soft tissues exposed above the winter snow pack (Arno and Hammerly 1984). Desiccation of needles and adjacent branches can occur when the soil is still frozen and the tree is unable to replace the lost water (Richards

1981). Evidence of desiccation is often indicated by the presence of necrotic needles on high elevation conifers.

The loss of the deciduous needles of the larger alpine larch before winter eliminates the water loss through needle-leaf surfaces caused by occasionally warmer air temperatures, and limits the damage due to wind borne particle abrasion for limbs that are raised above the snow. The larch also appear to be able to isolate the over-wintering buds from the xylem in the adjoining branchs, reducing the amount of water loss from these structures. This remaining soft tissue and the associated small woody branches also are resistant to extremely low water potentials. Even if severe water loss does occur, the species is able rehydrate in the spring and proceed with rapid needle growth with little apparent damage (Richards 1981).

The energetic trade-offs to the benefits of deciduousness are that alpine larch need an adequate, constant water supply in the summer and high levels of light to support a higher rate of photosynthesis. This greater rate of carbon fixation is required to make a new set of needles at the start of each growing season and to generate overall growth. The high moisture requirements of alpine larch help explain its distribution on a local scale. Alpine larch are generally limited to the mesic, northern slopes or other areas where they can obtain an adequate supply of water. In addition, this species' ability to avoid winter desiccation and abrasion explains why it is able to maintain an upright tree form in areas that would otherwise contain only patchy evergreen krummholtz or treeless alpine meadows (Arno 1970, Richards 1981).

For these reasons, alpine larch seems particularly well adapted to filling a niche as timberline specialist, and relatively poorly suited to compete in lower subalpine forest where available moisture and light are typically in high demand. However, at the northern edge of the species' distribution in the southern Canadian Rocky Mountains, alpine larch do appear in subalpine forests of a variety of different ages, a phenomenon that has not been studied before. The entry of alpine larch to these subalpine forests, and the persistence of the species within them raises a number of questions about how these patterns might occur and possibly be maintained. The following is a brief review of subalpine forest regeneration dynamics to provide some background for considering the presence of alpine larch in these environments.

1.1.3 Subalpine regeneration dynamics

Plant communities, particularly forests, exist in a mosaic of different successional stages, each initiated by previous disturbance (Watt 1947, White 1979). Disturbance creates openings that change the quantity and quality of available light, moisture, nutrients, and other environmental gradients that are necessary for the successful recruitment of tree seedlings (Goh and Philips 1991, Casper and Jackson 1997, Lieffers et al. 1999). In the Pacific Northwest of the USA, fire is the most prominent type of disturbance that affects forests (Agee 1993, Pyne 1984). Different types of fire regimes produce a range of intensity and frequency of canopy disturbance (Agee 1990, Arno et al. 1995, Turner et al. 1997). The north facing Engelmann spruce – subalpine fir, and occasionally lodgepole pine vegetation types are most often associated with subalpine distribution of alpine larch in the Canadian Rockies (Wilson 1997). These forest types are described as having a low frequency, high intensity fire regime where, on average, the cooler, more moist subalpine conditions limit the spread of lightening ignition events to relatively infrequent large, or "coarse scale" disturbances (Tande 1979, Spies and Franklin 1989, Agee 1990, Johnson and Miyanishi 1991).

This type of disturbance creates large open areas where most of the above-ground vegetative structure is removed, dramatically changing environmental gradients through the destructive reduction of competition (Dubé 1976). Typically, fire frequency for these forests is highly variable; estimated from 100 years to greater than 400 years (Tande 1979, Masters 1990, Agee 1993, Barrett 1996, Rogeau 1996). Where the fire return interval is at the lower end of this range, some pioneer, or "early successional" species have adapted life history strategies to take advantage of this kind of coarse scale disturbance regime. For example, lodgepole pine is a relatively short lived species (150-300 years) capable of rapid growth (Uchytil 1992). In the Canadian Rockies, this shade intolerant pine has mostly serotinous cones that release seed once the resin holding the cone scales closed is heated during the course of a fire (Lotan and Perry 1983). Therefore this species' seeds will be some of the first to germinate and grow within newly disturbed areas, providing the pine with an important advantage over other later arrivals to the same site (van der Valk 1992). However, for lodgepole pine to maintain a presence in an area, the fire return interval needs to remain at the lower end of the 100 to 400 year range.

Although both Engelmann spruce and subalpine fir will effectively colonize recently burned areas as pioneers, seedlings of these species are shade tolerant and also able to germinate and establish in more competitive situations. As the fire frequency starts to exceed the average longevity of both Engelmann spruce and subalpine fir, regeneration in older stands is facilitated by smaller, or "fine scale" gap disturbance (Veblen 1986, Aplet et al. 1988, Veblen et al. 1991). Here, the changes to environmental gradients are subtler. The removal of one or more canopy individuals creates a break in the overstory. Understory vegetation, including conifer seeds and seedlings, are then able to use the increases in light and nutrients, and changes in other environmental gradients to grow.

There has been some debate as to whether the fine scale disturbance that is associated with these older subalpine forests can allow the coexistence of two or more species independently of the coarse scale disturbance process (Aplet et al. 1988, Shea, 1985). Studies examining the Engelmann spruce-Subalpine fir forest in the Rocky Mountains indicate that this forest association is likely in a dynamic equilibrium, but there are several non-mutually exclusive hypotheses on how this occurs. Veblen (1986) generally attributes the coexistence to the difference in life history strategies of the two species, where fir had greater numbers of seedlings and faster growth rates, compared to spruce, which experienced greater longevity in the canopy (also see Veblen et al. 1991). Shea (1985) also considers these life history aspects to be important. However, her hypothesis included the importance of niche differentiation among the wet and dry microsites present in her study area. Aplet et al. (1988) put forward an interesting model of spruce - fir coexistence. The main point of this model describes a switching dominance of the two canopy trees, similar in nature to the "cohort senescence theory" described by Mueller-Dombois (1991). Here, spruce predominately reinitiate only after mature individuals of the same species senesce, creating slightly larger gaps than those of the senescing fir, allowing the reportedly less shade tolerant spruce a chance to regenerate. Fir appears to maintain a high recruitment level throughout these spruce cycles.

Many of these studies point to the importance of environmental heterogeneity as the key factor maintaining recruitment of different species within forests. Perhaps highlighting this recurrent theme is the continued popularity of Grubb's (1977) presentation of how spatial and temporal environmental heterogeneity enables the early life stages of plants to capture a community place. Hence, a species' "regeneration niche" describes a fundamental relationship between the broader occurrence of a species' population on the landscape (its more general realised niche; Austin and Smith 1989) and finer scale interaction of life history, physiology, and the local environment.

This information suggests that determining how alpine larch responds to the different kinds of environmental conditions present following natural disturbance will be one of the important factors in describing the species' population dynamics within subalpine forest. Obtaining this kind of knowledge for less well known forest species is now of great importance as management practices may be altering the natural disturbance regimes that maintain the range of regeneration opportunities in high elevation forests. Disturbance and the resulting forest structure are now actively managed throughout federally and provincially administered lands by fire suppression, fire prescription, logging, and associated silvicultural practices (Canadian Heritage 1997, Ministry of Forests 2001). Furthermore, rapidly changing global climatic conditions will alter the rates at which plant species grow, reproduce, and disperse (Prentice 1992, Grabherr et al.1994, Graumlich 1994). To help address this problem, specific research is required into the regeneration dynamics of less well-known species, such as alpine larch, that may be threatened by the altered environmental conditions.

1.1.4 Thesis objectives and outline

The general study objectives were to determine the importance of disturbance and the resultant forest structure in maintaining the peripheral populations of alpine larch found in subalpine forests at the northern edge of this species' distribution.

In Chapter 2, I first explore the response of alpine larch regeneration to the environmental variation within two recent large fire events that stretch over several hundred metres in elevation. I document the patterns of recruitment for alpine larch compared to the other subalpine conifers and returning understory vegetation within these areas. I also identify the important factors describing the regeneration niche of alpine larch in these regenerating environments.

Chapter 3 examines the fate of alpine larch populations in later stages of forest succession. In this part of the study, I describe the realised niche of the species as a function of the stand structure associated with maturing and older forests over the elevation range where larch is present.

In Chapter 4, I look at the process of fine scale disturbance and whether the gaps created in older subalpine forests by treefall are sufficient to maintain the presence of alpine larch in those systems.

Finally, I summarise the findings of these three parts of my study in Chapter 5. I then suggest several hypotheses for the occurrence of subalpine distribution of alpine larch in the Canadian Rockies, and present a number of suggestions for further research and long-term management of the species.

1.2 Literature cited

Agee, J. K. 1990. The historical role of fire in Pacific Northwest forests. Pages 25-38 *in:* Walstad J. D., S. V. Radosevich, and D. V. Sandberg, editors. Natural and prescribed fires in Pacific Northwest forests. Oregon State University Press. Corvallis, Oregon, USA.

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press. Washington, DC, USA.

Aplet, G. H., Laven, R. D., and Smith, F. W. 1988. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. Ecology. **69:** 312-319.

Arno, S. F. 1970. Ecology of alpine larch in the Pacific Northwest. PhD thesis University of Montana, Missoula, MT, USA.

Arno, S. F. 1990. Alpine Larch (*Larix lyallii* Parl). Pages 152-158 *in:* Burns R. M. and B. H. Honkola, editors. Silvics of North America. **Agricultural Handbook 654**. Forest Service, US Department of Agriculture. Washington, DC, USA.

Arno, S. F. 1995. The distinctive distribution of alpine larch: clear patterns and enigmas. Pages 469-472 *in:* Schmidt W. C. and C. J. Mc Donald, Compilers. Ecology and management of Larix Forests: a look ahead. **GTR-INT-319.** 469-472. US Department of Agriculture, Forest Service. Ogden, UT, USA.

Arno, S. F. and Habeck, J. R. 1972. Ecology of Alpine Larch (*Larix lyallii* Parl) in the Pacific Northwest. Ecological Monographs. **42:** 418-450.

Arno, S. F. and Hammerly, R. P. 1984. Timberline: Mountain and Arctic Forest Frontiers. The Mountaineers. Seattle, USA.

Arno, S. F., Worrall, J., and Carlson, C. E. 1995. *Larix Lyallii:* colonist of tree-line and talus sites. Pages 72-78 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and Management of Larix Forests: A Look Ahead. **GTR-INT-319.** US Department of Agriculture, Forest Service. Ogden, UT, USA.

Austin, M. P. and Smith, T. M. 1989. A new model for the continuum concept. Vegetatio. **83:** 35-47.

Barrett, S. W. 1996. The historic role of fire in Waterton Lakes National Park, Alberta. **KWL 30004**. Parks Canada contract report. Waterton, AB, Canada.

Blocker, L. 1995. Aesthetics of larch forests. Pages 147-150 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and Management of Larix Forests: A Look Ahead. **GTR-INT-319.** US Department of Agriculture, Forest Service. Ogden, UT, USA.

Canadian Heritage 1997. Banff National Park management plan. Minister of Public Works and Government Services. Ottawa, ON, Canada.

Carlson, C. E. and Ballinger, D. 1995. Germination, growth, and mortality of alpine larch, western larch, and their reciprocal hybrids: preliminary observations. Pages 408-411 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and management of Larix forests: a look ahead. **GTR-INT-319.** U S Department of Agriculture, Forest Service. Ogden, UT, USA.

Casper, B. B. and Jackson, R. B. 1997. Plant competition underground. Annual review of ecology and systematics. **28:** 545-570.

Corns, I. G. W. and Achuff, P. L. 1982. Vegetation: vegetation type descriptions. Pages 75-141 *In* Holland W. D. and G. M. Coen, editors. Ecological (biophysical) land classification of Banff and Jasper National Parks. **SS-82-44.** Alberta Institute of Pedology, University of Alberta. Edmonton, AB, Canada.

Daubenmire, R. F. 1974. Plants and the environment. Wiley. New York, NY, USA.

Dubé, D. E. 1976. Early plant succession following a 1968 wildfire in the subalpine zone of the Vermilion Pass, Kootenay National Park. M.Sc. thesis, University of Alberta. Edmonton, AB, Canada.

Goh, K. M. and Phillips, M. J. 1991. Effects of clearfell logging and clearfell logging and burning of a *Nothofagus* forest on soil dynamics in South Island, New Zealand - changes in forest floor organic matter and nutrient status. New Zealand Journal of Botany. **29:** 367-384.

Grabherr, G., Gottfried, M., and Pauli, H. 1994. Climate effects on mountain plants. Nature. **369:** 448.

Graumlich, L. J. 1994. Long-term vegetation change in mountain environments. Pages 167-179 *in:* Beniston M., editor. Mountain environments in changing climates. Routledge. New York, NY, USA.

Grubb, P. 1977. The maintenance of species-richness in the plant communities: the importance of the regeneration niche. Biological Review. **52:** 107-145.

Johnson, E. A. and Miyanishi, K. 1991. Fire and population dynamics of lodgepole pine and Engelmann spruce forests in the southern Canadian Rockies. Pages 77-91 *in:* Nakagoshi N. and F. B. Golley, editors. Coniferous forest ecology from an international perspective. Academic Publishing. The Netherlands.

Johnston, W. F. 1990. *Larix laricina* (Du Roi) K Koch Tamarack. Pages 141-151 *in:* Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC, USA.

LePage, B. A. and Basinger, J. F. 1995. The evolutionary history of the genus *Larix* (Pinaceae). Pages 19-29 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and management of Larix forests: a look ahead. **GTR-INT-319.** U S Department of Agriculture, Forest Service. Ogden, UT, USA.

Lieffers, V. J., Messier, C., Stadt, K. J., Gendron, F., and Comeau, P. G. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal Forest Research. **29:** 796-811.

Lotan, J. E. and Parry, D. A. 1983. Ecology and regeneration of lodgepole pine. **Agricultural Handbook 606**. US Department of Agriculture, Forest Service. Washington DC, USA.

Masters, A. M. 1990. Changes in forest fire frequency in Kootenay National Park, Canadian Rockies. Canadian Journal of Botany. **68:** 1763-1767.

Ministry of Forests 2001. Forest practices code. Government of British Columbia. Available at: http://www.for.gov.bc.ca/tasb/legsregs/fpc/fpc.htm [2001]

Moss, E. H. 1983. Flora of Alberta. University of Toronto Press. Toronto.

Mueller-Dombois, D. 1991. The mosaic theory and the spatial dynamics of natural dieback and regeneration in Pacific forests. Pages 162-172 *in:* Remmert H., editor. The mosaic-cycle concept of ecosystems. Springer-Verlag. Berlin.

Ostenfeld, C. H. and Larsen, C. S. 1930. The species of the genus *Larix* and their geographical distribution. Kongelige Danske Videnskabernes Selskab Biologiske Meddelelser. **9:** 1-106.

Owens, J. N. 1995. Reproductive biology of larch. Pages 97-109 *in*: Schmidt W. C. and K. J. McDonald, Compilers. Ecology and management of *Larix* forests: a look ahead. **GTR-INT-319.** U S Department of Agriculture, Forest Service. Ogden, UT, USA.

Prentice, C. 1992. Climate change and long-term vegetation dynamics. Pages 293-339 *in:* Glenn-Lewin D. C., R. K. Peet, and T. T. Veblen, editors. Plant succession: theory and prediction. Chapman and Hall. London, UK.

Pyne, S. J. 1984. Introduction to wildland fire: fire management in the United States. John Wiley & Sons. New York, NY, USA.

Richards, J. H. 1981. Ecophysiology of a deciduous timberline tree, *Larix lyallii* Parl. PhD thesis, Department of Botany, University of Alberta. Edmonton, Alberta.

Rogeau, M. P. 1996. Understanding the age-class distribution in the southern Canadian Rockies. M.Sc. Thesis, Department of Forest Science, University of Alberta. Edmonton, AB, Canada.

Schmidt, W. C. 1995. Around the world with *Larix*: an introduction. Pages 6-18 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and Management of *Larix* Forests: A Look Ahead. **GTR-INT-319.** US Department of Agriculture, Forest Service. Ogden, UT, USA.

Schmidt, W. C. and Shearer, R. C. 1990. *Larix occidentalis* Nutt Western Larch. Pages160-172 *in*: Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC, USA.

Shea, K. L. 1985. Demographic aspects of coexistence in Engelmann spruce and subalpine fir. American Journal of Botany. **72:** 1823-1833.

Spies, T. A. and Franklin, J. F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology. **70:** 543-545.

Tande, G. F. 1979. Fire history and vegetation pattern of coniferous forest in Jasper National Park, Alberta. Canadian Journal of Botany. **57:** 1912-1931.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European alps. Springer-Verlag. New York, NY, USA.

Turner, M. G., Romme, W. H., Gardner, R. H., and Hargrove, W. W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs. **67:** 411-433.

Uchytil, R. J. 1992. *Pinus contorta* var. *latifolia*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (2001, February). Fire Effects Information System, [Online]. Available: http://www.fs.fed.us/database/feis/ [2001/03/01]

van der Valk, A. G. 1992. Establishment, colonization and persistence. Pages 60-102 *in:* Glenn-Lewin D. C., R. K. Peet, and T. T. Veblen, editors. Plant succession: theory and prediction. Chapman and Hall. London, UK.

Veblen, T. T. 1986. Treefalls and coexistence of conifers in subalpine forests of the central Rockies. Ecology. **67:** 644-649.

Veblen, T. T., Hadley, K. S., and Reid, M. 1991. Disturbance and stand development of a Colorado subalpine forest. Journal of Biogeography. **18:** 707-716.

Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology. **35:** 1-22.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. The Botanical Review. **45:** 229-299.

Wilson, B. C. 1997. The ecology of alpine larch in the northern Rocky Mountains. Cordillera. **3:** 8-11.

Worrall, J. 1990. Subalpine larch: Oldest trees in Canada? Forestry Chronicle. October: 478-479.

Worrall, J. 1993. Temperature effects on bud-burst and leaf-fall in subalpine larch. Journal of Sustainable Forestry. **1:** 1-18.

CHAPTER 2: ESTABLISHMENT PATTERNS OF ALPINE LARCH FOLLOWING FIRE IN THE CANADIAN ROCKIES

2.1 Introduction

Alpine larch (*Larix lyallii* Parl.) is a deciduous conifer that is found most commonly on cool, north-facing slopes near timberline in the northern Rockies and on the eastern slopes of the Cascades (Arno 1990). The common name "alpine larch" describes the species' tendency to invade alpine tundra, above the krumholtz of the other high elevation tree species (Arno 1970). However, at the northern extent of the larch's distribution it often forms extensive subalpine associations with Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* (Hook) Nutt). It has been suggested that in these regions alpine larch may be regenerating in recently burned areas (Arno et al. 1995, Wilson 1997), well below where one might expect to find this apparently poor subalpine competitor (Richards 1981).

Land management practices, such as fire suppression and intensive silviculture, may be altering the natural disturbance regimes that maintain the range of regeneration opportunities in high elevation forests (White and Vankat 1993). There is now concern that these practices and rapid climate change are leading to declining biodiversity (Agee 1990, Grabherr et al. 1994, Cameron-Duffy and Meier 1995, Holt 2000). To help address this problem, specific research is required into the regeneration dynamics of less well-known species, such as alpine larch, that may be threatened by the altered environmental conditions.

The role of fire in subalpine forest regeneration in the northern Rocky Mountains has been investigated for many of the commercially important species (Day 1972, Tande 1979, Romme and Knight 1981, Johnson and Miyanishi 1991). Although the effect of large scale pest outbreaks and blowdown events (Alaback and Tappeiner 1991, Veblen et al. 1991) have been identified as important factors in forest regeneration, fire has been recognised as the dominant form of coarse-scale disturbance that structures these forests at the landscape scale (Pyne 1984, Johnson 1992, Agee 1993). Previous research examining how tree populations respond to fire has often been directed at obtaining a stand level response for the most common species (Johnston and Fryer 1989, Agee 1993). However, this approach provides no information as to how the minor species that may occupy the same stand are able to co-exist given the apparent broad overlap in their realised niches (Austin and Smith 1989). Because coarse-scale disturbance can create substantial within-stand environmental heterogeneity, assuming an "average" or "representative" stand response may be an over-simplification of the dynamics, even at the landscape level (Shugart et al. 1988, Turner et al. 1997, Lertzmann et al. 1998, Miller and Urban 1999). This may be especially true in mountainous regions where disturbed areas can range over large differences in elevation that often correspond to changes in species distributions.

The concept of a plant species' "regeneration niche" (Grubb 1977), and that of the "safe site" (Harper 1977) for dispersed seeds has led to an understanding that smaller scale heterogeneity in environmental conditions created by disturbance, and its effects on recruitment of different species, is important in structuring plant communities. This kind of focus has been taken in fine scale disturbance studies that have looked at the effect of changed forest structure, and associated environmental gradients, on the recruitment of tree species (Runkle 1981, Denslow 1985, Brokaw and Scheiner 1989, Lertzman 1992, Heinemann et al. 2000). However, this kind of approach for examining recruitment following coarse scale disturbance is still gaining popularity (e.g., Callaway 1998), and may be a useful approach for examining the factors that enable alpine larch regeneration below its characteristic habitat.

2.1.1 Objectives

The objective of this Chapter is to describe the regeneration niche of alpine larch following coarse scale stand replacing fire in subalpine forest. There is little information on the kinds of environmental conditions that are important for the establishment of this species, especially in this peripheral lower elevation environment. Specifically, I wished:

1. To document the patterns of regeneration within the burns for the dominant vegetation types, with emphasis on conifer recruitment.
2. To compare the regeneration niche of alpine larch to those of the other subalpine conifers as a function of the broader plant community response to both landscape and environmental microsite gradients.
3. To examine the direct relationships of alpine larch seedlings with measured environmental gradients, to help explain this species subalpine distribution.

2.2 Methods

2.2.1 Study area

The study area was located on the continental divide formed by the southern Canadian Rockies along the border of Alberta and British Columbia. I studied two fires: the Vermilion Pass fire of 1968 (51 ° 12' N, 116 ° 7' W), in Kootenay and Banff National Parks, and the Rock Canyon Creek fire of 1960 (50° 10'N, 115 ° 15' W), approximately 125 km further southeast in the Invermere Forest District of B.C. (Figure 2.1).

Lightening started the Vermilion Pass fire. The burn covered approximately 2630 hectares and ranged in elevation from 1530 m to 2280 m (Dubé 1976). Although the main pass is oriented on a northeast-southwest axis, the numerous side valleys provide a range of different aspects. This area lies between the montane and the subalpine southern cordilleran ecoclimatic regions (EWGCCELC 1989). The weather is characterised by cool summers and cold winters, but there are occasionally settled high pressure systems in this region of the Rockies that create prolonged hot, dry, forest fire conditions in the summers (Johnson and Miyanishi

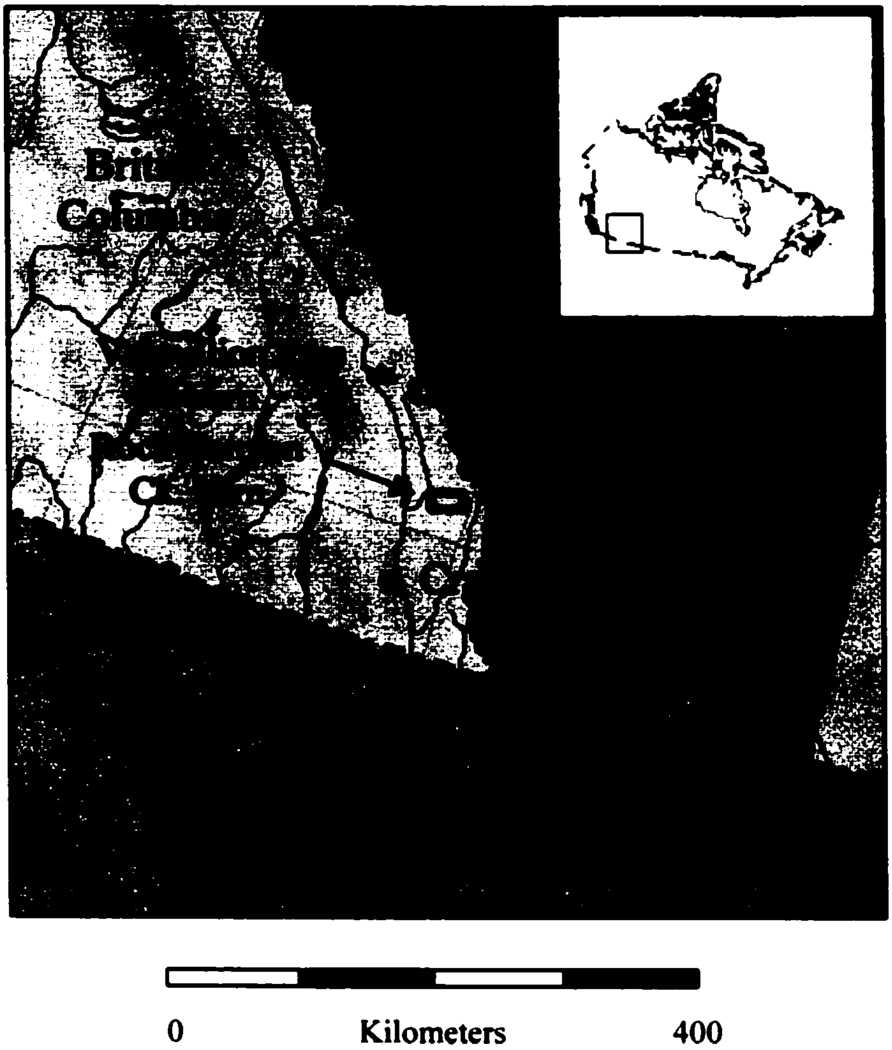


Figure 2.1: General location of the study sites in south-western Canada.

1991). Data from the nearest weather station in Banff, Alberta (approximately 30 km away and 150 m lower) show a mean maximum air temperature in July of 22.1° C, and a mean maximum temperature in January of –5° C. The average yearly precipitation at Banff is 468.0 mm, with the greatest precipitation occurring in the summer between May and August (Anonymous 1999). The major soil types found in the burn area are humo-ferric podzols, regosols, and brunisols (Dubé 1976, Walker et al. 1984).

The Rock Canyon Creek burn is smaller (1675 ha.) than the Vermilion Pass burn but the topography, soil types, and elevation range are similar (Lacelle 1990). This burn lies in the vertically stratified subalpine interior cordilleran ecoclimatic region (EWGCCELC 1989) and experiences slightly warmer and drier summer condition. The nearest weather recording station at Cranbrook B.C. is approximately 100 km southwest and nearly 500 m lower in elevation and its records probably exaggerate this warmer, drier trend. At Cranbrook, the mean maximum air temperature in July is 25.7° C and the mean maximum in January is –3.9° C. The mean annual precipitation is 384.5 mm (Anonymous 1999).

At both burns, the surrounding forest is dominated by mature Engelmann spruce and subalpine fir. At lower elevations, lodgepole pine (*Pinus contorta* Dougl. *var. latifolia* Engelm.) replaces subalpine fir as the co-dominant species. Whitebark pine (*Pinus albicaulis* Engelm.) is present in the higher south-facing stands surrounding both burns. At approximately 1800 m, alpine larch is present as a subdominant species and increases in importance with elevation. Mature larch are found in greater abundance on the northern aspects, although protected southerly aspects on gentle slopes also support locally abundant populations adjacent to the burn areas.

2.2.2 *Data collection*

I used a stratified random sampling procedure in each burn area to provide roughly equal sampling intensity across the environmental gradients of altitude, aspect, and distance to the mature forest edge. I established a starting position in each of these defined strata using a hand-held GPS unit. I used random distances on bearings that maintained the same altitude to locate sample plots, ensuring that plots did not overlap. There were 72 circular plots ($100m^2$) in the Vermilion burn and 30 plots of equal size in the Rock Canyon Creek burn.

To determine the importance of spatial scale in the regeneration niche of alpine larch and the other conifers, I measured environmental gradients at two spatial scales. Gradients that varied within a plot, such as vegetation cover, were treated as microsite gradients, and those gradients that varied on a larger scale, such as aspect or elevation, were considered landscape gradients.

2.2.2.1 *Microsite gradients*

2.2.2.1.1 *Vegetation structural characteristics*

I recognised four forest structural layers present within the burned areas. These were: (1) tall shrubs: woody species ≥2 m; (2) low shrubs: woody species ≥30 cm, and <2 m; (3) herbs: all woody species <30 cm and any sized forbs or grasses; and (4) forest floor: terrestrial bryophytes and lichens, rocks, decaying wood, organic matter, and mineral soil. Tall shrub cover was estimated with a convex densiometer from the four cardinal points of each plot. The measurements were taken standing at the edge of the plot reading the densiometer value while facing toward the plot centre. The meter was held level at 1 m above the ground. I performed a calibration of the measured percent cover values to the actual light attenuation experienced under a range of forest canopy (Appendix I). This test indicated that there was close to a directly proportional relationship between these values over a large range of the data. Low shrub cover was estimated by drawing the plot cord toward each cardinal direction and determining the average proportion of intersection with the underlying shrubs. This line intercept procedure (Bonham 1989) was also used to determine the percent cover of the herb layer, and the percent cover of the forest floor components. To complete the structural description of the community, I measured the average height of the shrub and herb layers from four randomly chosen locations within each plot. However, at this stage of development in these burn sites, the shrub layer generally varied continuously in height, largely due to the range of different broad-leafed shrub and conifer species, and their respective growth responses. Therefore, I pooled the shrub categories and measured the average height of the shrubs as one layer.

2.2.2.1.2 Soil moisture and nutrient status

A small soil pit was dug at each plot to determine the thickness of the duff, A_x horizon, and B horizon layers. Soil colour, texture and percent coarse fraction were also noted. This information, along with the percent slope and the topographical position that each plot occupied with respect to the slope (i.e., ridge crest, upper slope, mid slope, toe of the slope, flat ground, depression) were used to derive both a soil moisture and soil nutrient scalar following the key provided in Braumandl and Curran (1996). This is a qualitative approach that provides ordinal values from 0 to 8 for very xeric to subhydric soil moisture and from 1 to 5 for very poor to very rich soil nutrient content. These were included in the analyses as ordinal variables with three levels corresponding to high, medium and low values.

2.2.2.2 Landscape gradients

At the larger scale, I included geographic area (Vermilion Pass and Rock Canyon Creek) as a nominal variable in the analyses to determine the generality of the study findings. The shortest distance to a larch seed source at the forest edge, and more generally, the distance to the forest edge itself, were measured for each plot. At each plot, the altitude above mean sea level was recorded with a Casio electronic altimeter. The aspect of a plot was measured to within one degree of true north with a hand-held compass. As the main topographically controlled environmental changes for plants occur over a north-south gradient, the data were converted to a linear aspect gradient by taking the arcsine of the cosine of the compass bearing. These new data were then standardised, dividing each by the maximum absolute value, to give a value between 1, for due north and –1 for due south.

2.2.2.3 *Tree population structure*

To describe the tree population structure, I identified to species and measured the height of each tree within the sample plot. Because recent conifer germination was more likely associated with the present local conditions than the larger, older plants, I grouped both the live and dead trees into two size cohorts that would likely reflect the differences in their recruitment ages: "seedlings" were individuals that were less that 30 cm tall; "saplings" were individuals greater that this.

To provide an estimate of the average age of each tree cohort, I collected both increment cores, and destructively sampled individuals from the size range of each species. Trees that were greater than approximately 3 m tall were bored as close to the ground as possible. Complete disk samples from individuals smaller than this were taken by cutting the stem at the root collar. Both increment cores and disks were mounted on wooden holders and either sanded with successively finer sandpaper following Arno and Sneck (1977), and/or lightly planed using a razor blade depending on the quality of the wood. The numbers of annual growth rings were counted on the prepared samples under a dissecting microscope in the lab.

2.2.2.4 *Vegetation composition*

To document the local plant community and provide a "floristic characterization" of the environmental influence at each plot, I chose to record the presence and 'importance' of all vascular plant species, and some nonvascular indicator species, that were present in geometrically increasing zones within each $100m^2$ plot (Morrison et al.1995). Using this method, the occurrence of a species was only recorded once, the first time it was encountered, searching from the smallest zone around the centre of the plot outwards. An importance score was assigned to the species depending on the size of zone it is first found in (the greater area searched, the less importance assigned). This method provides not only frequency data, but also a quantitative estimate of relative species abundance when scores are averaged for a given area (Morrison et al. 1995, Wilson and Stuart-Smith 2000). Appendix II presents the details of this method.

2.2.3 *Data Analysis*

2.2.3.1 *General vegetation characteristics*

There was obvious systematic variation in the general composition and structure of the plant communities that was correlated with the main changes in topography over the large area covered by each of the burns. To show these general trends, I plotted the structural characteristics for the shrub and herb layers against elevation for both burn areas, comparing north and south aspects using linear regression to show the trends (Mathsoft 1999).

2.2.3.2 *Tree regeneration*

To provide a general picture of conifer regeneration recruitment patterns at the burn sites, I grouped the cohort data for each burn into north and south aspects, and into high and low elevation categories. These elevation categories were separated at 2000 m in the Vermilion Pass burn, and at 2100 in the Rock Canyon Creek burn. I plotted the average number of seedlings and saplings per hectare for each species. To determine if these size cohort groups represented differences in ages, as opposed to competition effects, I grouped the age data for each species at a given location using box-plots and tested the data using Student's *t*-tests. Data were checked for homogeneity of variance and normality to determine if the assumptions of the test would be met. Where necessary, the data were log or square root transformed (Sokal and Rohlf 1995). In the case of transformed age values that grossly violated these assumptions, the non-parametric Wilcoxon rank sum method was used. The null hypothesis for these comparisons was that there was no difference between mean ages for each size cohort size class (alpha = 0.05). Statistical analyses were preformed using Splus statistical software (Mathsoft 2000).

2.2.3.3 *Conifer regeneration niches*

In high elevation forests, regeneration following disturbance is often delayed (Agee 1993). This can be related to poor germination or slow early growth due to unfavourable climatic conditions. However other factors, including pre-dispersal seed predation and irregular seed production, may also be important for species such as alpine larch and whitebark pine (Arno 1970, Lanner 1996, Appendix III). This means that not all areas suitable for regeneration of these conifers within recent burns would have necessarily received seed. I therefore took a more general plant community approach to identifying larch regeneration niche space. My rational was that enough time would have elapsed for the different microhabitats within the burn area to be distinctly characterised by the present post fire plant community and therefore might provide a key to identifying areas suitable for larch regeneration even if other factors had limited seed arrival. My first step was to use Two Way Indicator Species Analysis (TWINSPAN, Hill 1979) to classify the complete plant community data set (including the conifer cohorts) as a means of establishing floristic boundaries to the underlying environmental space in which recruiting alpine larch were found, or perhaps likely to be found, compared to that of the other conifer species. I used the TWINSPAN default options.

In a separate analysis I used the ordination method, Canonical Correspondence Analysis (CCA) to include the measured environmental variables described above with the same community dataset. This technique constrains the ordination axes to be linear combinations of the measured environmental variables (for details see ter Braak 1986). Species and plots are ordered along the axes in such a way that the relationship between these response variables and the measured environmental gradients is maximised in a small number of dimensions (ter Braak and Prentice 1988). To select the "best" environmental terms, I used the forward selection procedure in the CANOCO (ter Braak 1988) software to find the most important terms. I chose alpha = 0.05 as a criterion to reject terms for model inclusion.

I then combined the two analyses. To identify the environmental space associated with each of the conifer species from the plant community classification, I outlined the classification groups that contained a conifer seedling or sapling on the ordination biplot. I placed a rectangle of the smallest possible area around all of the species that were included in each of these conifer regeneration groups, representing the "community niche space" for each conifer. A rectangle was chosen for this niche space representation, because the main CCA axes are mutually orthogonal (ter Braak 1986).

2.2.3.4 The larch regeneration niche

To examine the regeneration niche of alpine larch directly, I modelled the larch seedling counts as a function of the measured environmental gradients using a multiple regression procedure. This analysis included the distance to a larch seed source, rather than the more general distance-to-forest-edge measurement. Otherwise, the predictor data set remained the same as in CCA. I used a Generalized Linear Model (GLM) that assumed the response data were drawn from a Poisson distribution, as the counts of the seedlings approximated this form. All the environmental variables were plotted against the seedling data to uncover any obvious relationships. I used smoothing splines in these plots to aid with this assessment and to look for non-linear relationships in the data. These smoothers are shown in plots of significant variables as a means of interpreting their effect, however, this was a visual assessment only. Possible interactions between environmental variables were explored using conditioning plots; these plots show the interaction between independent variables. The forward selection and residual error monitoring procedure described by Nicholls (1989) and O'Brien (1992) was used to determine the final model. As with the multivariate analysis, I chose alpha = 0.05 as a criteria to reject terms for model inclusion. These univariate analyses were completed using S Plus software (Mathsoft 2000). Correlation matrixes for all predictor variables are shown in Appendix V.

2.2.3.5 Spatial structure

Recent developments in the treatment of the spatial structure of data within statistical analyses have enabled researchers to measure the degree to which the variation in their data is correlated with changes in two dimensional space (Legendre 1993, Økland and Eilertsen 1994, Dale 1999). This is especially useful in ecological research, where there may be several orders of magnitude of scale under investigation. Now, previously unexplained variation can be tested to see if there is some underlying spatial structure. This may provide clues to identifying unmeasured environmental gradients (and the scale at which they occur) that are important in explaining the pattern in the response data.

Given the spatial structure of the study, it seemed important to determine the proportion of the explained variation that could be accounted for by the landscape and microsite level environmental variables in both the multivariate and univariate analyses. The plot's spatial co-ordinates were also used in these analyses to establish how much unexplained variation in the data was correlated with some undefined spatial gradient. I used the partial CCA feature in the CANOCO software to partition the explained variation in the analysis, following the method described by Borcard et al. (1992), Økland and Eilertsen (1994) and Palmer (1998). The set of terms for a cubic trend surface outlined in Borcard et al. (1992) is

$$z = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3. \qquad (1)$$

In this equation, z is the trend surface, b_i are the parameters, x is the east co-ordinate and y is the north co-ordinate of each plot. To select the "best" spatial terms, I used the forward selection procedure described above and excluded terms that were highly correlated with any previously fitted term. This was to prevent the spurious "arch" non-linear relationships that may occur between these polynomial terms and the response data (Palmer 1998). The spatial terms retained in the final analysis were

$$z = b_1x + b_2y + b_8xy^2. \qquad (2)$$

To determine the amount of variation accounted for by space alone, the environmental variables were introduced as a covariable data set, E, before the inclusion of the spatial terms from Equation 2 (data set S). The strictly spatial variation was calculated as "S given E", S|E. This involved dividing the sum of the partial canonical eigenvalues by the total inertia in the CCA analysis. The non-spatial environmental variation was found by swapping the data sets, and calculating $E|S$. The variation that was shared by both kinds of data, $E \cap S$, was calculated by subtraction from the total variation that the two data sets explained, i.e., $E \cup S - S|E - E|S = E \cap S$. To determine $E \cup S$, both data sets of explanatory variables were included together in a CCA to determine the sum of the complete canonical eigenvalues. The total unexplained variation was found by subtracting $E \cup S$ from the total inertia. To compare the amounts of variation explained by the microsite versus landscape gradients, the environmental data set was divided into two separate data sets and treated as just described.

In the GLM analysis of the larch seedlings, I followed Legendre's (1993) procedure on a single vector of response data. Conceptually, the analyses are the same, but in the univariate regression analysis, the r^2 values are used instead of eigenvalues. In the GLM analysis of spatial variation, none of the terms in Equation 1 were significant. Therefore, only the partitioning of the landscape and microsite variation in these GLM data is presented. The significant environmental variables were divided into a landscape data set, L, and a microsite data set, M. $L|M$ was calculated by firstly fitting M to the data as a covariable data set, followed by L. The unique M variation was determined in the reverse procedure. As in the multivariate analyses, the shared landscape and mircosite variation ($L \cap M$) was determined by fitting all of the environmental terms ($L \cup M$) and then calculating $L \cap M = L \cup M - L|M - M|L$. The unexplained variation was the difference between $L \cup M$ (i.e., the full model r^2) and 100%.

2.3 Results

2.3.1 General patterns of structure

The physiognomic structure of the regenerating vegetation reflected both the changes in topographic position and identity of the dominant species. This was most evident in the height of the shrub layer, where in Vermilion Pass it significantly declined with increasing elevation on both aspects (Figure 2.2). This change was due to the dominance of the taller lodgepole pine in the lower elevations. The boundary between the lodgepole pine community and those dominated by spruce, fir, and larch was most abrupt on the north aspect. Whereas, on the southern exposures, lodgepole pine and spruce gave way more gradually to shorter regeneration dominated by whitebark pine at higher elevations (Figure 2.2). At Rock Canyon Creek there was no consistent change in the height of the shrub canopy with either elevation or aspect; the average shrub height remained between 2 m and 4 m. Over the smaller elevation range sampled in that burn, the taller lodgepole pine was only a minor component (Figure 2.2). The tall shrub cover roughly followed these height trends. There were significant reductions in cover occurring over increasing elevation at Vermilion Pass, and no significant corresponding change at Rock Canyon Creek (Figure 2.3).

The low shrub cover responded somewhat differently. Although this part of the shrub layer also contained regenerating conifers, it was often dominated by broad-leafed shrub species. The most important of these were *Rhododendron albiflorum*, *Menziesia ferruginea*, and *Shepherdia canadensis*. *R. albiflorum* and *M. ferruginea* were more common on the northern aspects of each of the burns, where the low shrub cover tended to be greater (Figure 2.3). *S. canadensis* was more common on the southern aspects of the burn areas. The composition of the main species on the north aspects changed very little with elevation. Therefore, the significant decline in the low shrub cover with increasing

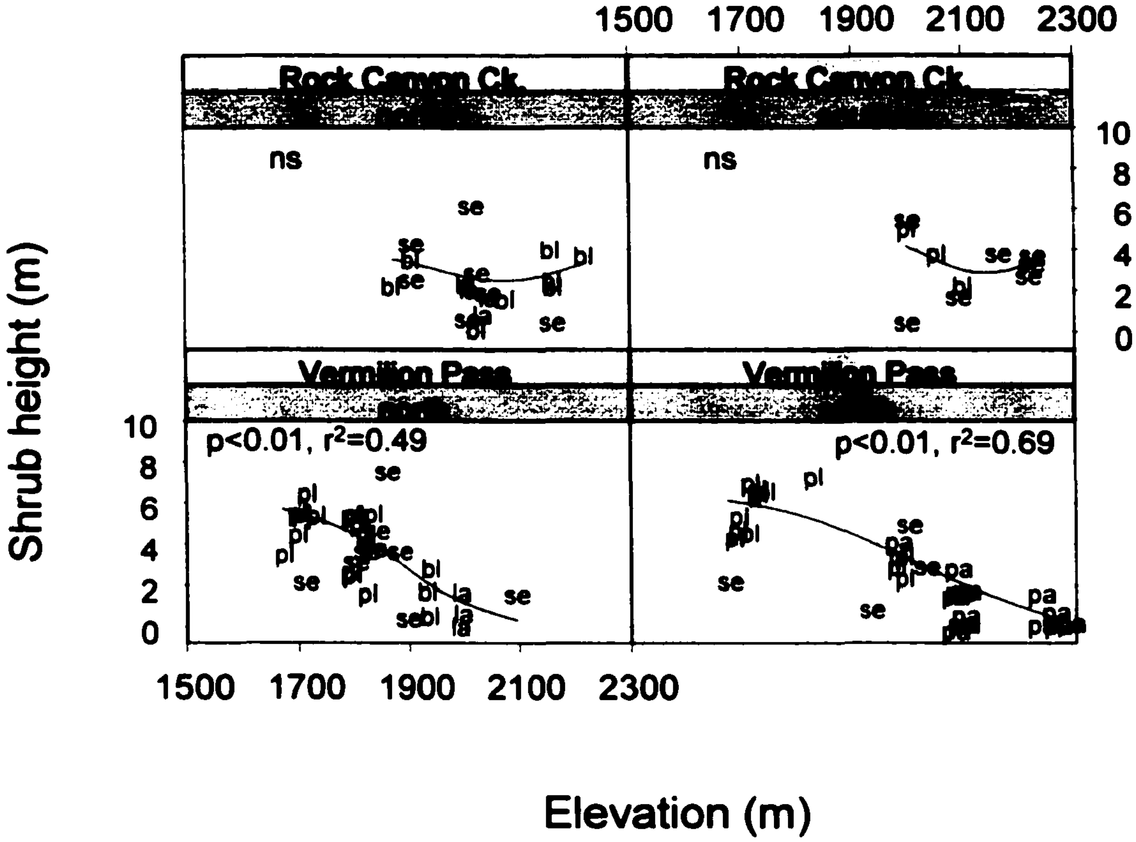


Figure 2.2: Relationship between elevation, aspect, and shrub height at both burn sites. Note the taller lodgepole pine at lower elevations at Vermilion Pass. The dominant species in each plot are shown as symbols. bl: fir, la: larch, pa: whitebark pine, pl: lodgepole pine, se: spruce. P and r^2 values are shown for regressions. ns: not significant. Fitted lines are locally weighted regression smoothers to aid with interpretation, but are independent from the tested model.

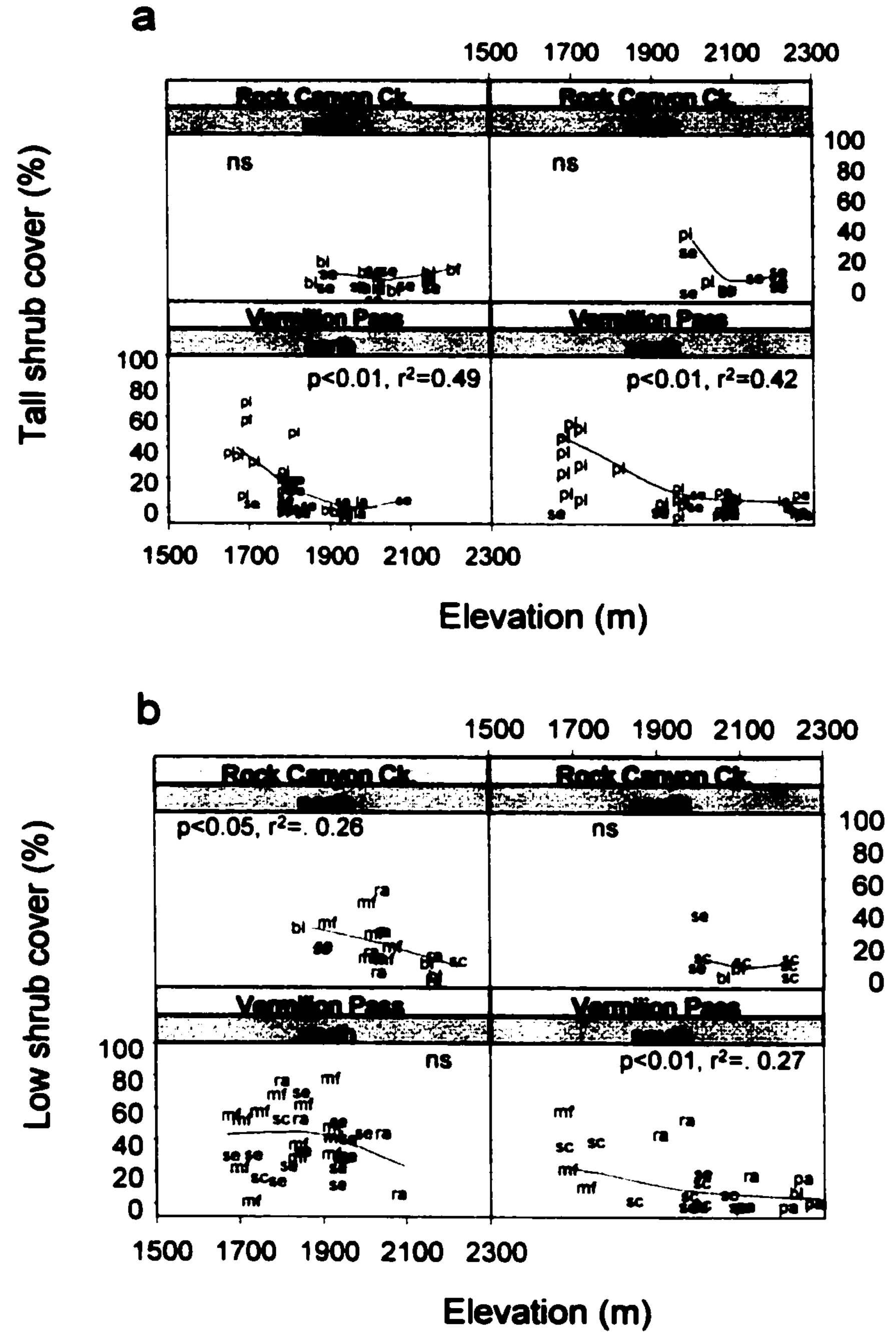


Figure 2.3: Relationship between elevation, aspect, and (a) tall shrub cover, and (b) low shrub cover at both burn sites. The dominant species in each plot are shown as symbols. bl: fir, la: larch, pa: whitebark pine, pl: lodgepole pine, se: spruce, mf: *Menziesia ferruginea*, ra: *Rhododendron albiflorum*, sc: *Shepherdia canadensis*. P and r^2values are shown for regressions. ns: not significant. Fitted lines are locally weighted regression smoothers to aid with interpretation, but are independent from the tested model.

elevation on the north aspect at Rock Canyon Creek was most likely related to slightly poorer soil conditions associated with steeper, higher ground at that site, as opposed to architectural changes associated with different species. The lower cover on the southern aspects reflects the warmer, drier conditions at these sites. The higher southern elevations were also generally steeper with poorer soil development. These effects are shown by the significant decline of lower shrub cover over the greater range of elevation sampled in Vermilion Pass (Figure 2.3).

The herb layer was dominated by *Vaccinium* species on the north aspects. *V. scoparium* was the most important species, followed by *V. membranaceum* (Figure 2.4). The lower southern slopes at Rock Canyon Creek supported a high cover of *Spirea betulifolia*. The dominant species at the higher elevations at this site were more diverse, the community included *Achillea millefolium*, *Hedysarum sulphurescens*, and *Juniperus communis*. This change in species composition also explained the significant decrease in the average herb layer height, as the mature *S. betulifolia* tend to be taller than the other herb layer species found at this site (Figure 2.4). On the southern slopes at Vermilion Pass the dominant lower elevation herb layer species included *Linnaea borealis*, *Epilobium angustifolium*, and *Erigeron peregrinus*. The herb layer cover increased significantly with elevation and became dominated by *V. scoparium*. This increase appeared to be correlated with the combined decreasing tall and low shrub cover in this location (Figure 2.3).

2.3.2 Conifer recruitment patterns

The distribution of the larch seedling and saplings at Vermilion Pass shows that the greatest density of recruitment occurred on the higher, northern aspects; although sparse recruitment occurred on all aspects and elevations (Figure 2.5). The cohort age data showed that the sapling groups were, on average, significantly older than the seedlings. Individuals of this older cohort started establishing at the higher locations within 3 years following the 29-year-old disturbance, but recruitment was delayed at the lower elevations (Figure 2.5). The fir and spruce cohorts showed a similar recruitment

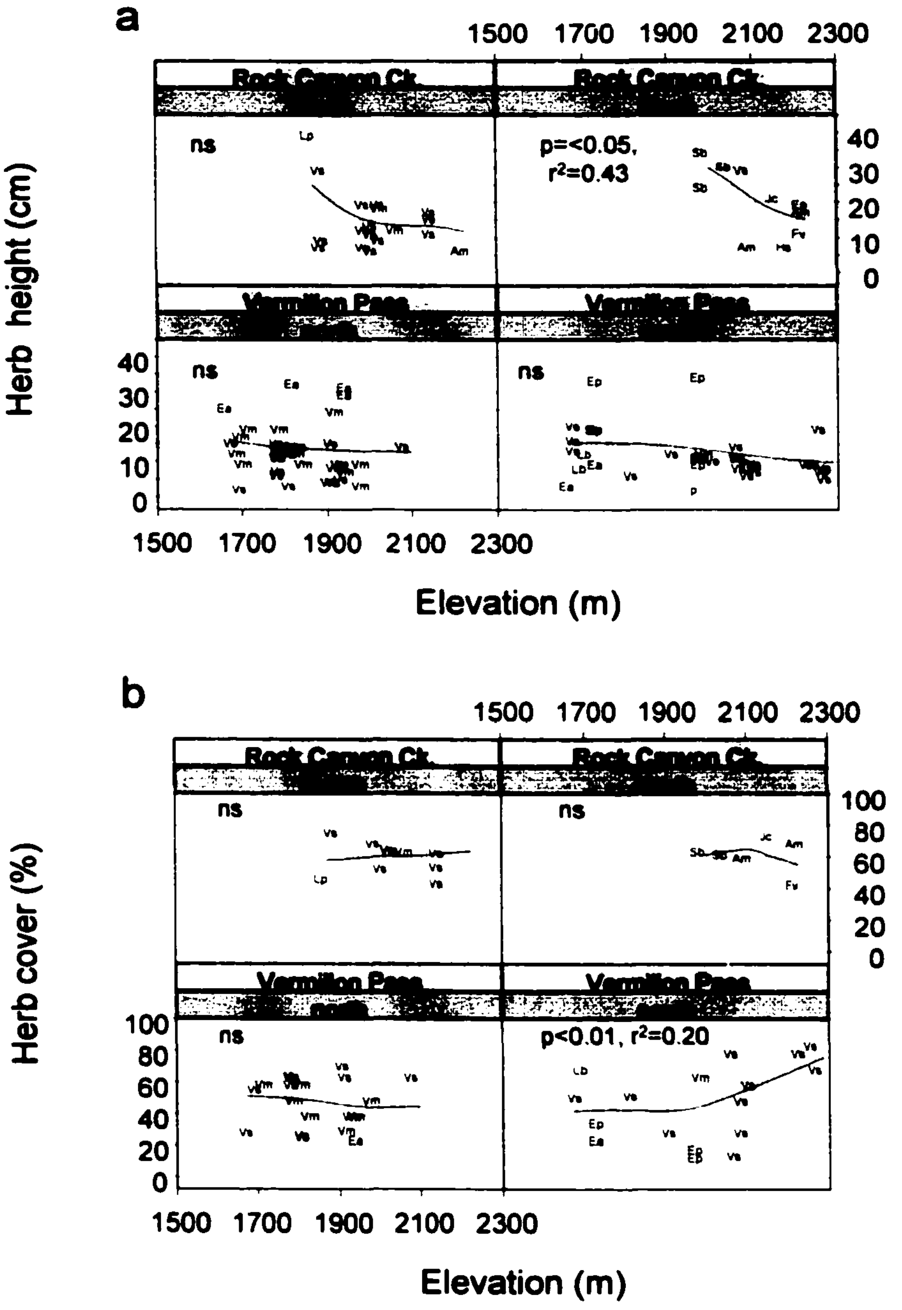


Figure 2.4: Relationship between elevation, aspect, and (a) herb height, and (b) herb cover at both burn sites. The dominant species are plotted as symbols. Am: *Achillea millefolium*, Ea: *Epilobium angustifolium*, Ep: *Erigeron peregrinus*, Fv: *Fragaria virginiana*, Hs: *Hedysarum sulphurescens*, Jc: *Juniperus communis*, Lb: *Linnaea borealis*, Sb: *Spirea betulifolia*, Vm: *Vaccinium membranaceum* Vs: *V. scoparium*. P and r^2values are shown for regressions. ns: not significant. Fitted lines are locally weighted regression smoothers to aid with interpretation, but are independent from the tested model.

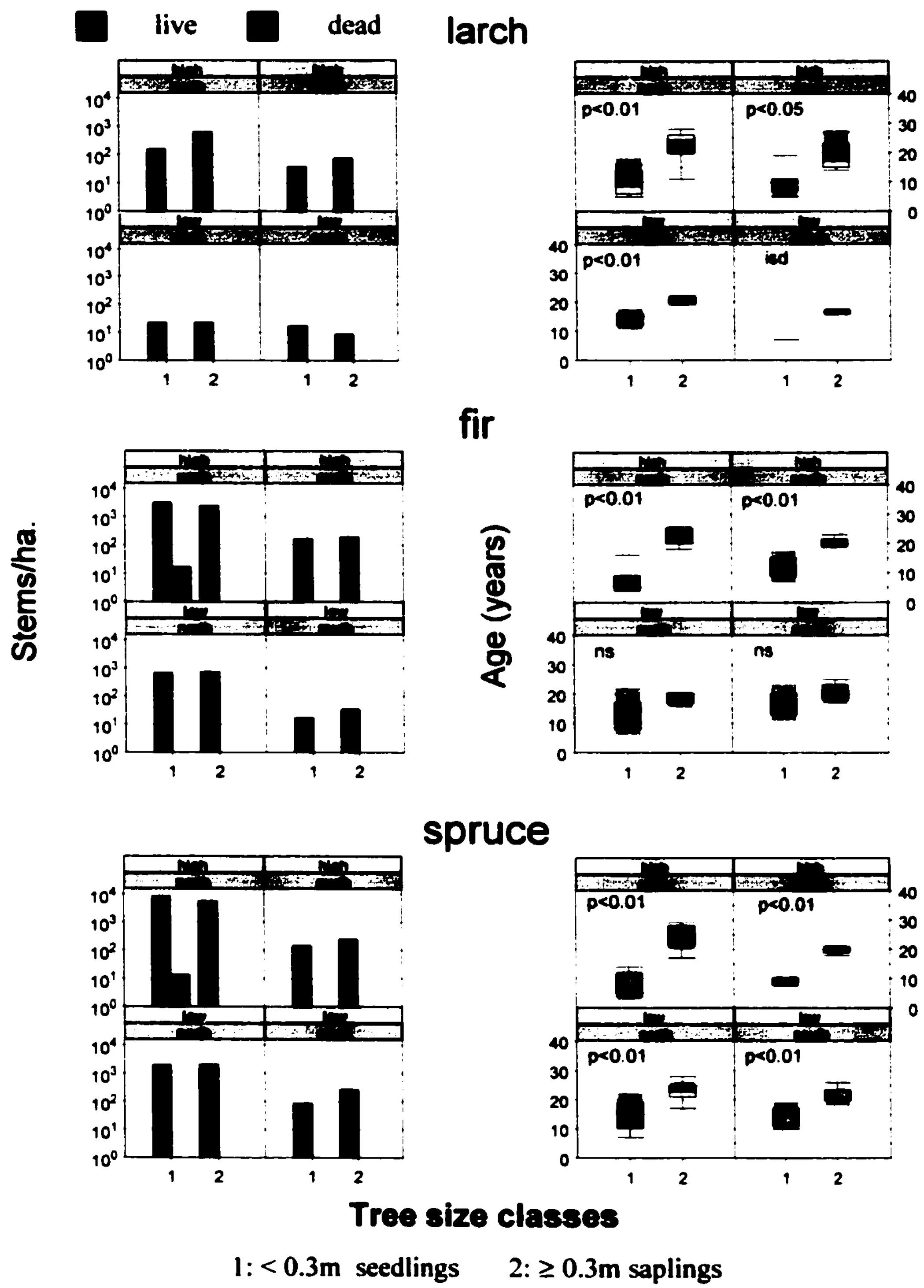


Figure 2.5: Cohort density and age estimates for larch, spruce, and fir over elevation and aspect at Vermillion Pass. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. P-values indicate the outcome of t-tests. ns: not significant. isd: insufficient data for analysis.

preference to the higher, northern areas at this site. However, these species generally occurred at much greater densities (note the logarithmic y-axes). There were no significant differences in the average ages of the fir cohort in the lower areas of the burn (Figure 2.5). On the south aspect it appeared that some of the smaller fir seedlings had arrived earlier and had experienced suppression, whereas, on the lower northern slopes, the sapling ages were younger, indicating that there may have been a delay in the initial recruitment.

The whitebark pine regeneration patterns over elevation were similar to that of the larch, but this species was more common on the high southern aspects (Figure 2.6). The age data for the sapling cohort showed that establishment started within 5 years of the disturbance. As the shrub height information suggested, the lodgepole pine recruitment at Vermilion Pass was greatest on southern aspects, at lower elevations. The sapling cohorts for this species also showed the only consistent mortality for any of the conifer species surveyed, indicating that stand thinning in the lower elevations was initiating (Figure 2.6). Recruitment initiation for lodgepole on the south aspects also started within 5 years of the disturbance, but appeared to be delayed on the northern aspects.

At Rock Canyon Creek, larch regeneration was restricted to the higher elevations, and almost exclusively to the northern slopes (Figure 2.7). The very small numbers of sapling sized larch that were found on the southern aspects were in low slope areas. The age data showed that recruitment on the north aspect occurred within 10 years following this 37 year old disturbance. The spruce and fir cohorts were again found in high densities on the northern aspects (Figure 2.7). The age data indicated that spruce was an early coloniser of the high elevations on both aspects, with some individuals appearing within only one to two years of the fire. The whitebark pine were only found in low densities at higher elevation on both aspects. The lack of a seedling cohort indicates that recruitment had not occurred in these locations for the last 20 years (Figure 2.8). Lodgepole pine was also reduced in abundance at Rock Canyon Creek. The exception was the slightly greater number of both seedlings and saplings found on the higher northern locations. The lack of lodgepole in the lower plots on the north aspect was likely due to locally cool temperatures from cold air drainage at this narrow valley bottom site.

2.3.3 Conifer regeneration niche definition

The TWINSPAN classification seems to split the conifer niche groups based on a moisture and light gradient (Figure 2.9). Most of the shrub and herb species in the upper part of the dendrogram are commonly found in areas of with greater soil moisture and/or canopy cover, whereas those in the lower groups, in most cases, are found in drier, more open locations. This pattern also correlated with the general change in aspect from north to south facing slopes.

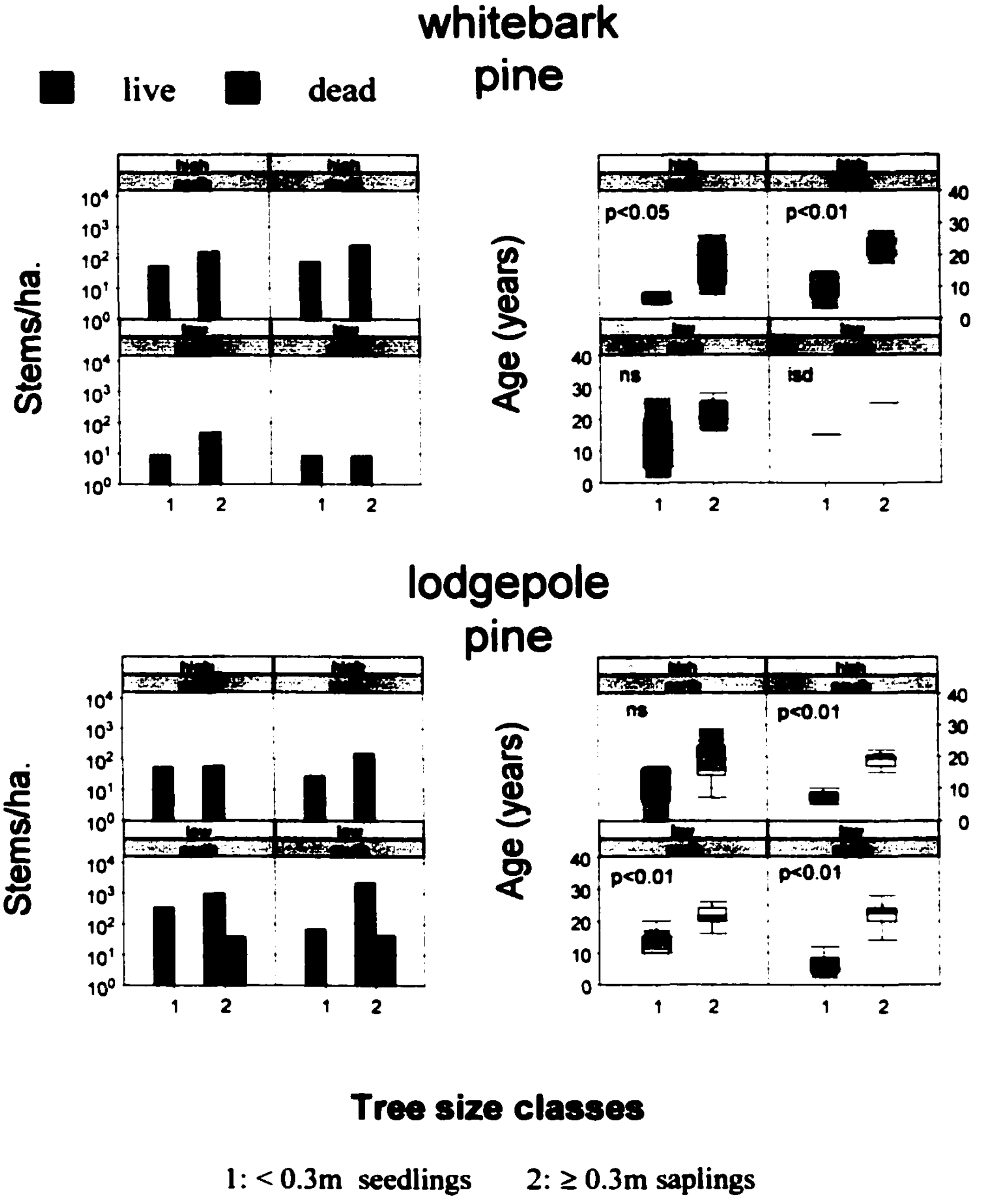


Figure 2.6: Cohort density and age estimates for whitebark and lodgepole pine over elevation and aspect at Vermillion Pass. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. P-values indicate the outcome of t-tests. ns: not significant. isd: insufficient data for analysis.

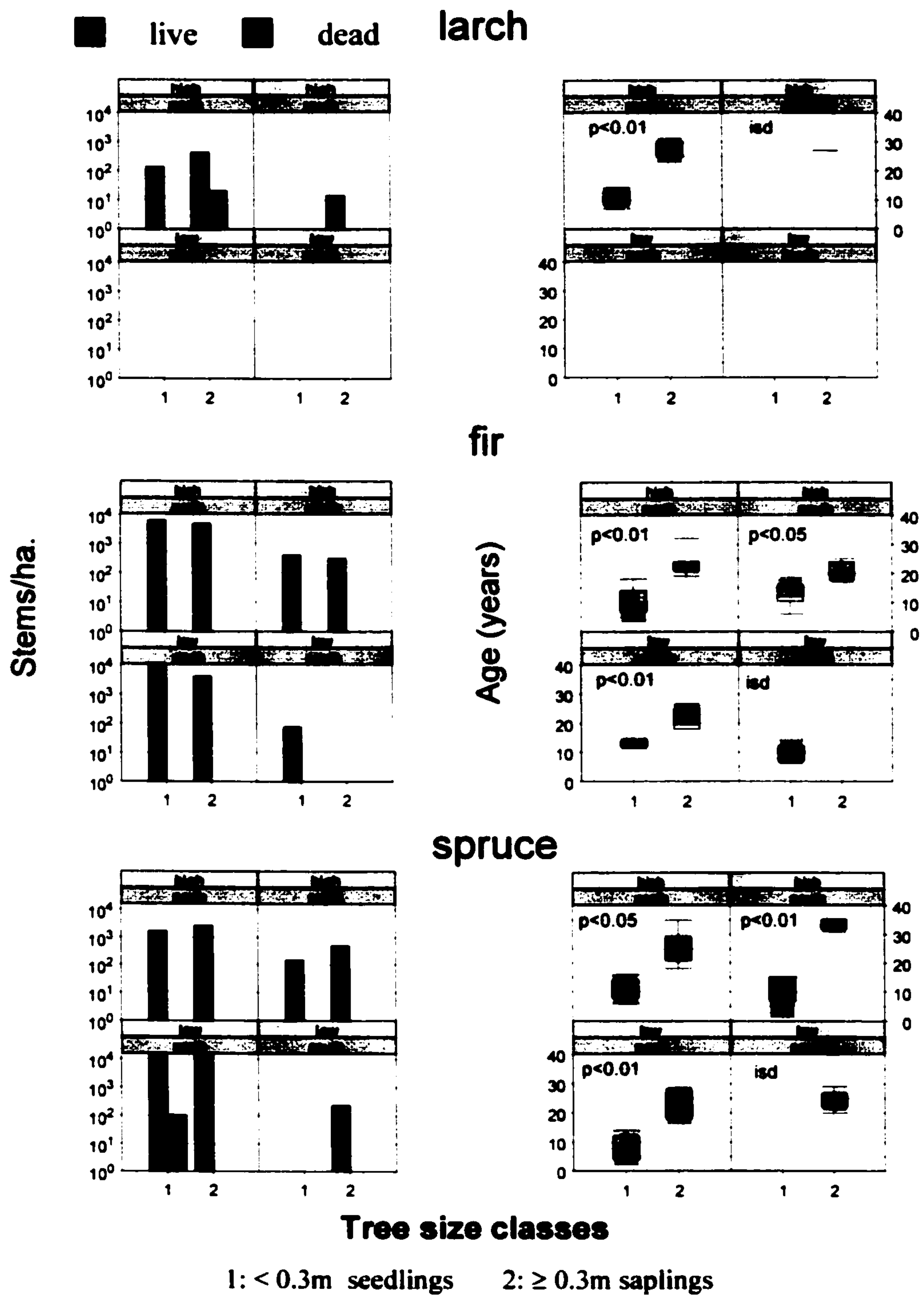


Figure 2.7: Cohort density and age estimates for larch, spruce, and fir over elevation and aspect at Rock Canyon Creek. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. P-values indicate the outcome of t-tests. ns: not significant. isd: insufficient data for analysis.

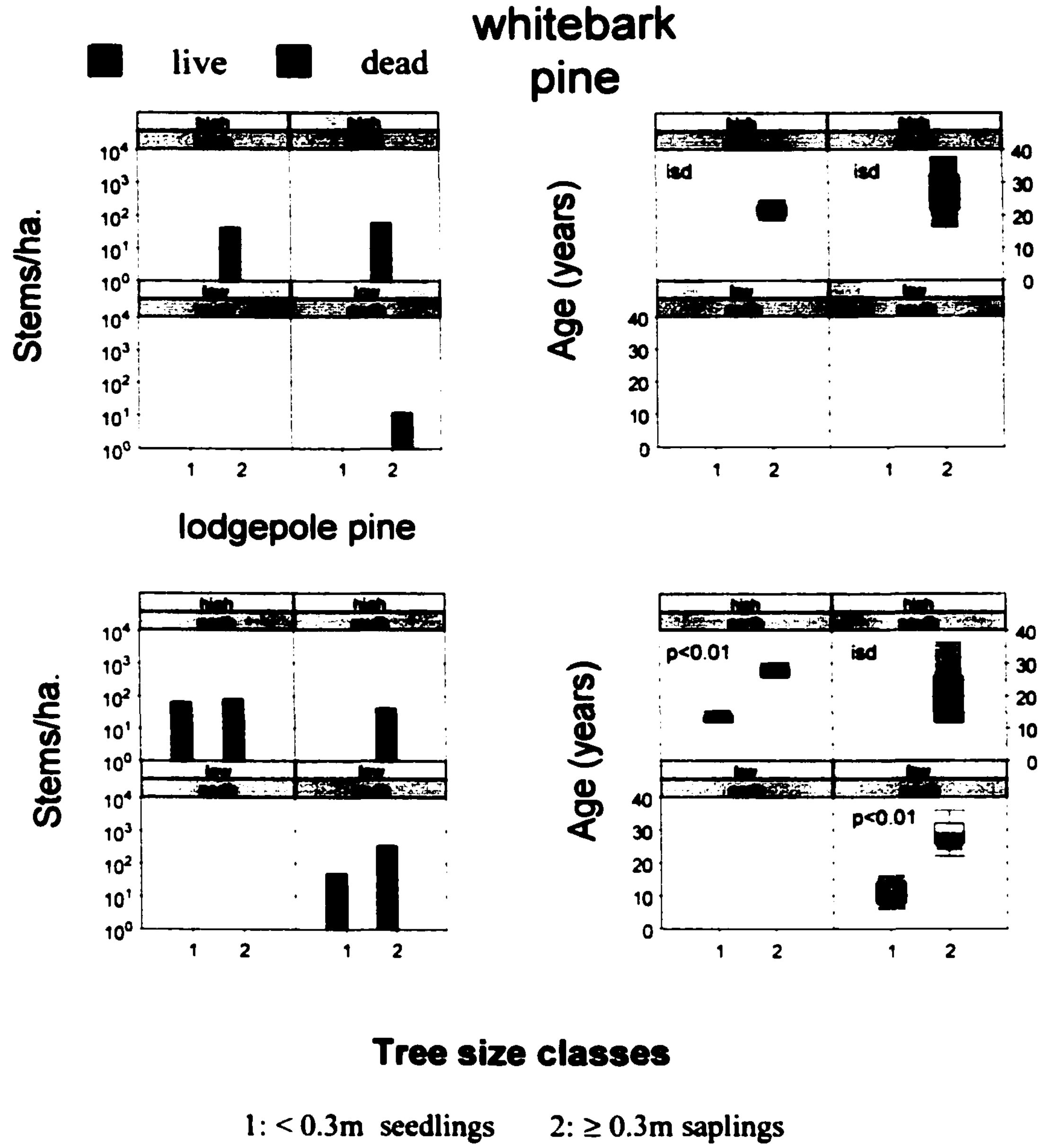


Figure 2.8: Cohort density and age estimates for whitebark and lodgepole pine over elevation and aspect at Rock Canyon Creek. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. P-values indicate the outcome of t-tests. ns: not significant. isd: insufficient data for analysis.

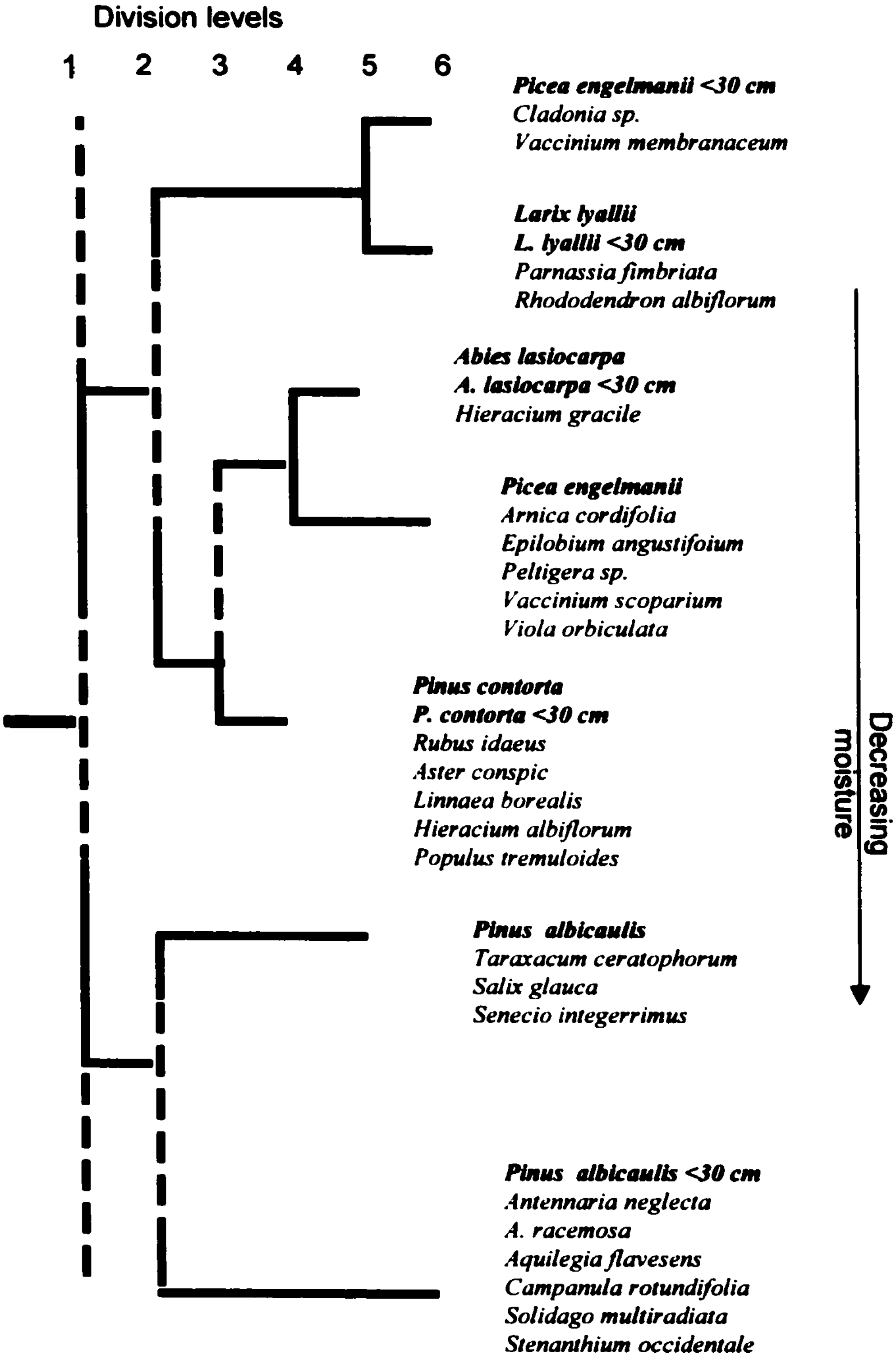


Figure 2.9: Dendrogram of conifer cohort species association groups from the TWINSPAN analysis on the complete plant community data set. The general trend in the species' organization is related to soil moisture and aspect. Note: the dashed lines indicate that more groups of species (with no conifers) exist in these areas of the figure than are shown.

The primary division of the dendrogram separates the larch group along with those for the spruce, fir and lodgepole pine, from the whitebark pine. Interestingly, the spruce and whitebark pine seedlings are split into separate groups from the sapling cohorts, suggesting that some modification of the micro-environment by the saplings and the species associated with these sapling groups makes the area under their influence less conducive for the smaller life stages of the same conifer species. The larch seedling/sapling group is most closely associated with spruce seedling group. This association between conifer cohort groups is also the strongest in the data, as these groups were the last to separate (division level 5, Figure 2.9).

The positions of the conifer groups in the ordination environmental space of Figure 2.10 confirm the general environmental preferences for these species, and the large scale regeneration patterns of the conifers noted above. In this biplot, the conifer seedling and sapling groups are spread out over the first CCA axis in a very similar way to their organisation in the TWINSPAN classification. On the right hand side of the diagram, the two large rectangular boxes outline the community niche for whitebark pine seedlings and saplings. These community niches are strongly influenced by the landscape level gradients of southerly aspects and higher elevation. The microsite gradients of low soil moisture, low shrub cover, and a high percentage of mineral soil are also important in describing the regeneration niche of this species (Figure 2.10).

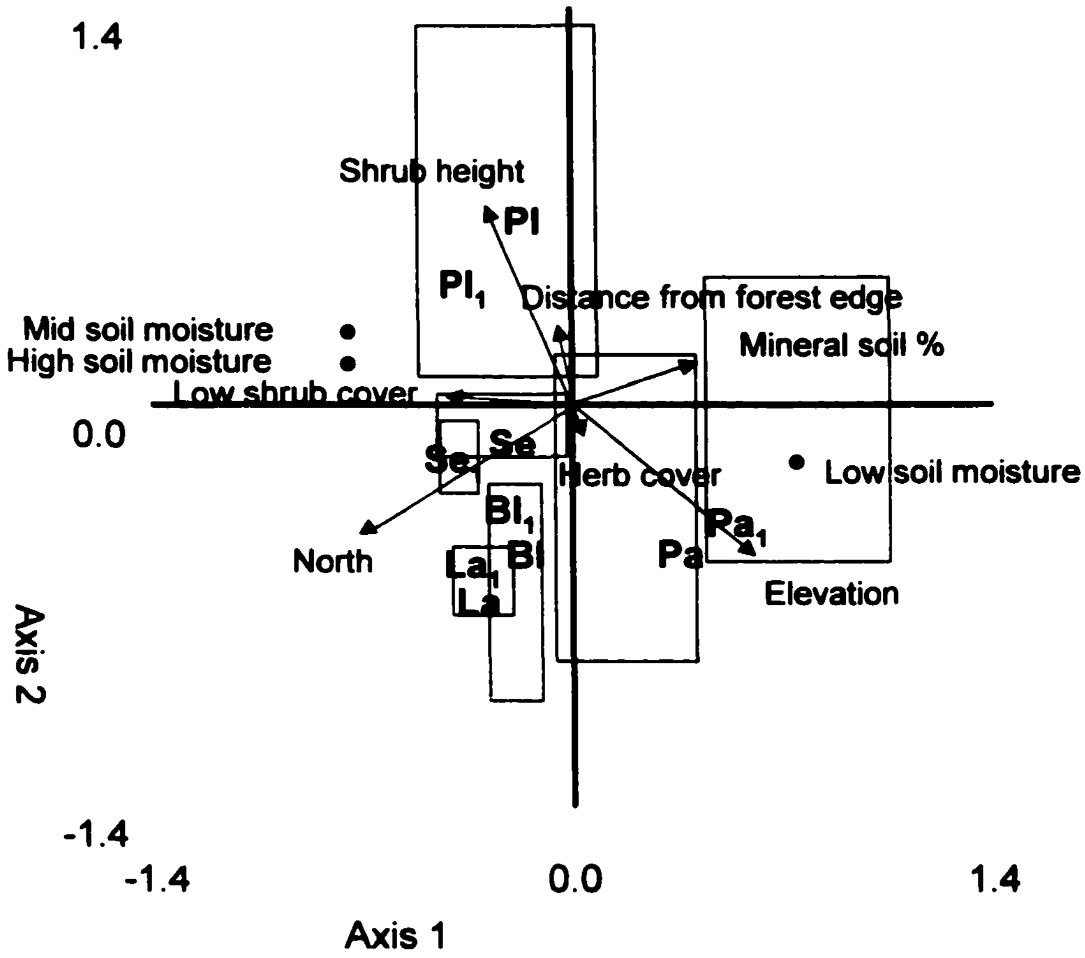


Figure 2.10: CCA biplot of conifer cohort niches and significant environmental variables. Boxes denote the "conifer community niche" defined by the vegetation community classification (see text for details). Only the location of the each conifer species' seedling and sapling cohorts is shown within these niche spaces. The labels for the rest of the plant species have been masked. **Bl/Bl1**: subalpine fir saplings/seedlings, **La/La1**: alpine larch saplings/seedlings, **Pa/Pa1**: whitebark pine saplings/seedlings, **Pl/Pl1**: lodgepole pine saplings/seedlings, **Se/Se1**: Engelmann spruce saplings/seedlings. **Note**: only the Engelmann spruce and whitebark pine have separate niches for saplings and seedling.

On the left hand side of Figure 2.10, all of the other niches show some degree of overlap on axis 1. Although the ordering is similar to that of the classification, the biplot shows a representation of the variation in environmental preferences of the species associated with each of the conifer cohorts. The lodgepole pine seedling/sapling niche and the Engelmann spruce sapling niche span the entire gradient range of the spruce seedling, larch seedling/sapling, and subalpine fir seedling/sapling niches. This overlap occurs primarily in areas of greater shrub cover and higher soil moisture. However, these niche spaces are differentiated over axis 2 by elevation, shrub layer height, distance from forest edge, and the amount of herb layer cover. The environmental gradients associated with axis 1 accounted for 10% of the explained species variance. Axis 2 explained an additional 7% of this variance.

The variation in the community data explained by the environmental gradients was 24.4% (i.e., C+D in Figure 2.11a). An additional 6.1% was accounted for by spatial structure not related to the measured environmental gradients. Only 2.9% of the measured environmental gradients could be explained by the spatial structure. Of the explained variation, 7.3% was described solely by the landscape gradients and 7.1% solely by the microsite gradients (Figure 2.11b). The remaining 9.9% of explained variance was shared between the landscape and microsite gradient groups.

2.3.4 Larch seedling model

Initial graphical exploration of the data indicated that distance to surviving seed source and low shrub cover had a non-linear relationship to the number of alpine larch seedlings (Figure 2.12). Therefore, I included the logarithm of the distance to surviving seed source and a second order polynomial of low shrub cover in the forward selection procedure. The model that best describes the data included both of these terms (Table 2.1).

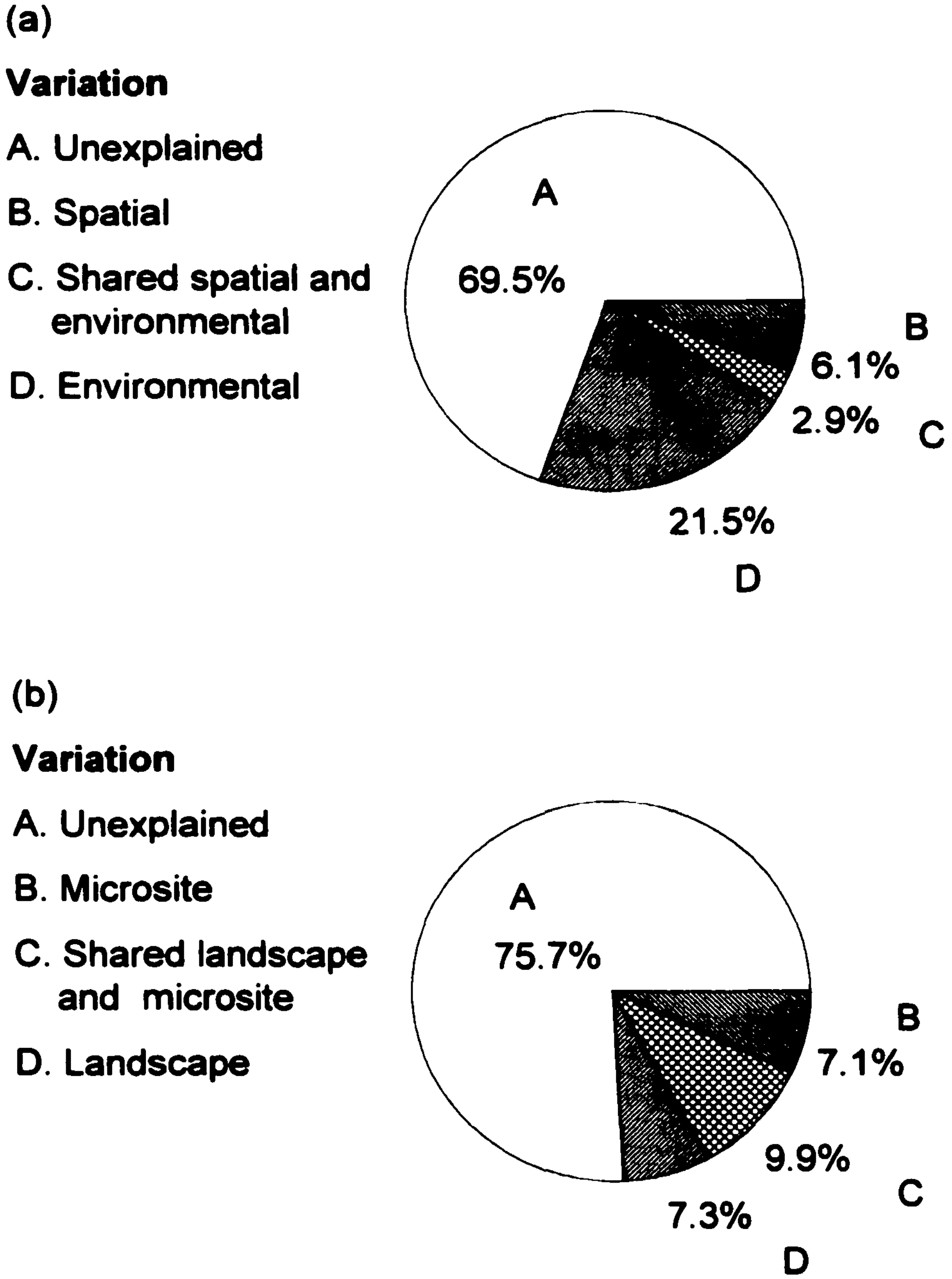


Figure 2.11: Community vegetation variation partitioned by (a) environmental and spatial gradients; and (b) by landscape level and locally acting gradients.

Table 2.1: Poisson model summary for alpine larch seedlings.

Model term	df	Term deviance	Residual df	Residual deviance	p-value (Chi^2)
Null model			101	216.7	0.00
log (distance to seed source)	1	78.8	100	137.9	0.00
*Low shrub %	2	53.3	98	84.6	0.00
Shrub height	1	10	97	74.6	0.00
Tall shrub %	1	5.2	96	69.4	0.02
Aspect gradient	1	6.5	95	62.9	0.01
Tall shrub % by aspect	1	4.5	94	58.3	0.03

*Fit as a 2nd order polynomial.

The log of distance to seed source was the most important gradient explaining larch seedling regeneration, accounting for a third of the null model deviance (Table 2.1). This effect is clearly visible at both sites, where density of individuals rapidly declined with increasing distance from the forest edge seed source (Figure 2.12a). The limit for larch seed dispersal in Rock Canyon Creek was about 100 m, and close to 300 m in Vermilion Pass. The quadratic relationship of seedling count and shrub cover explained nearly a quarter of the null model deviance (Table 2.1; Figure 2.12b). This curvilinear relationship is most evident in Vermilion Pass where the greatest amount of establishment occurred under about 40% shrub cover. At Rock Canyon Creek, only the first part of this trend is apparent, as there was generally less low shrub cover at this site and fewer samples.

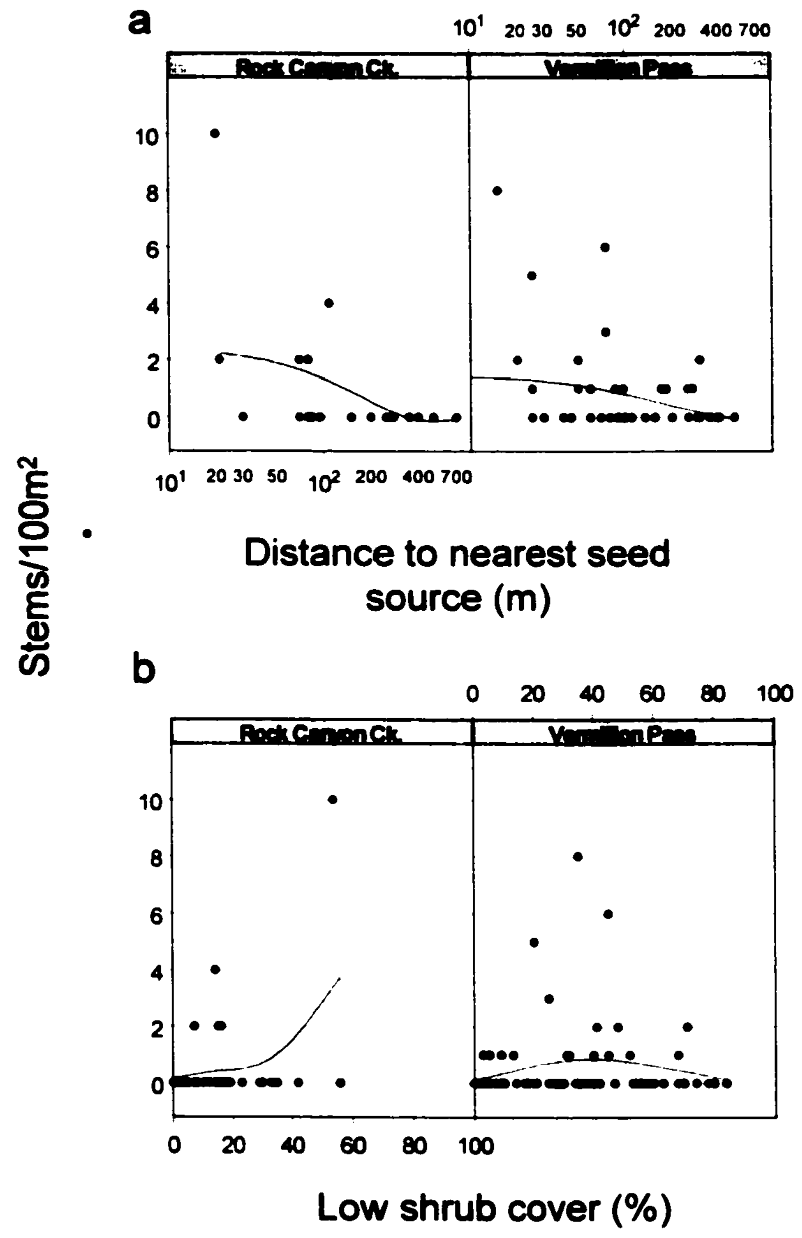


Figure 2.12: The relationship between (a) of distance to seed source (log scale) and (b) shrub cover on recruitment of the alpine larch seedlings at both burn sites. The fitted lines are cubic smoothing splines to aid with visual interpretation, but are independent of the statistical model.

It was also apparent that the majority of the larch seedling establishment occurred beneath shrubs that were shorter than 3 m (Table 2.1; Figure 2.13a). At Rock Canyon Creek, this was the shrub height limit, over which no recent recruitment occurred. At Vermilion pass, a small number of seedlings were found in areas where the surrounding conifer regeneration reached a height of 6 m. This corresponded to where lodgepole pine regeneration started to dominate the lower regions of the burns.

The amount of tall shrub cover present also was important in explaining seedling abundance. Although the cover and height of the taller vegetation appeared to be highly correlated ($r = 0.66$), their affect on larch recruitment was somewhat different. In general, there was less recruitment of seedling larch with greater tall shrub cover (Figure 2.13b). However, the significant interaction of tall shrub cover with aspect showed that while greatest amount of recruitment occurred on northern aspects with less than 10% cover, establishment on the southern aspects almost exclusively occurred where there was greater than 10% tall shrub cover (Figure 2.14). The only exception, a south easterly facing larch seedling plot with no tall shrub cover, was located on a relatively flat bench, on a generally steeper, slope (see arrow in Figure 2.14b).

The deviance explained by landscape gradients (distance to seed source and aspect) fitted to the univariate seedling data alone was 41.6%, compared to the 23.9% explained by the microsite gradients (tall and low shrub cover, shrub height) (Figure 2.15). The shared variation between these two sets of gradients was 5.5%. The final interaction term explained 2.1% of the null model deviance, giving a total explained deviance of 73.1%.

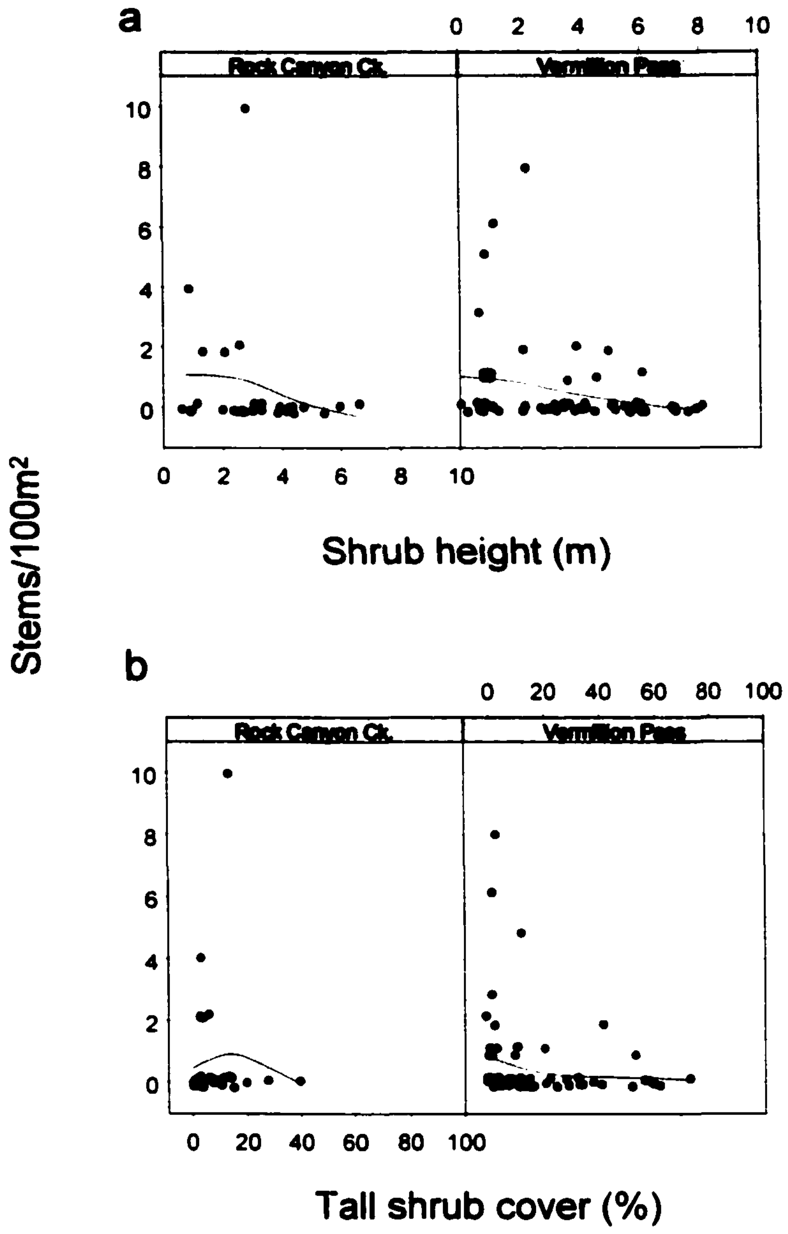


Figure 2.13: The relationship between (a) increasing shrub height and (b) increasing canopy cover on recruitment of the larch seedlings at both burn sites. The fitted lines are locally weighted regression smoothers to aid with visual interpretation, but are independent of the statistical model.

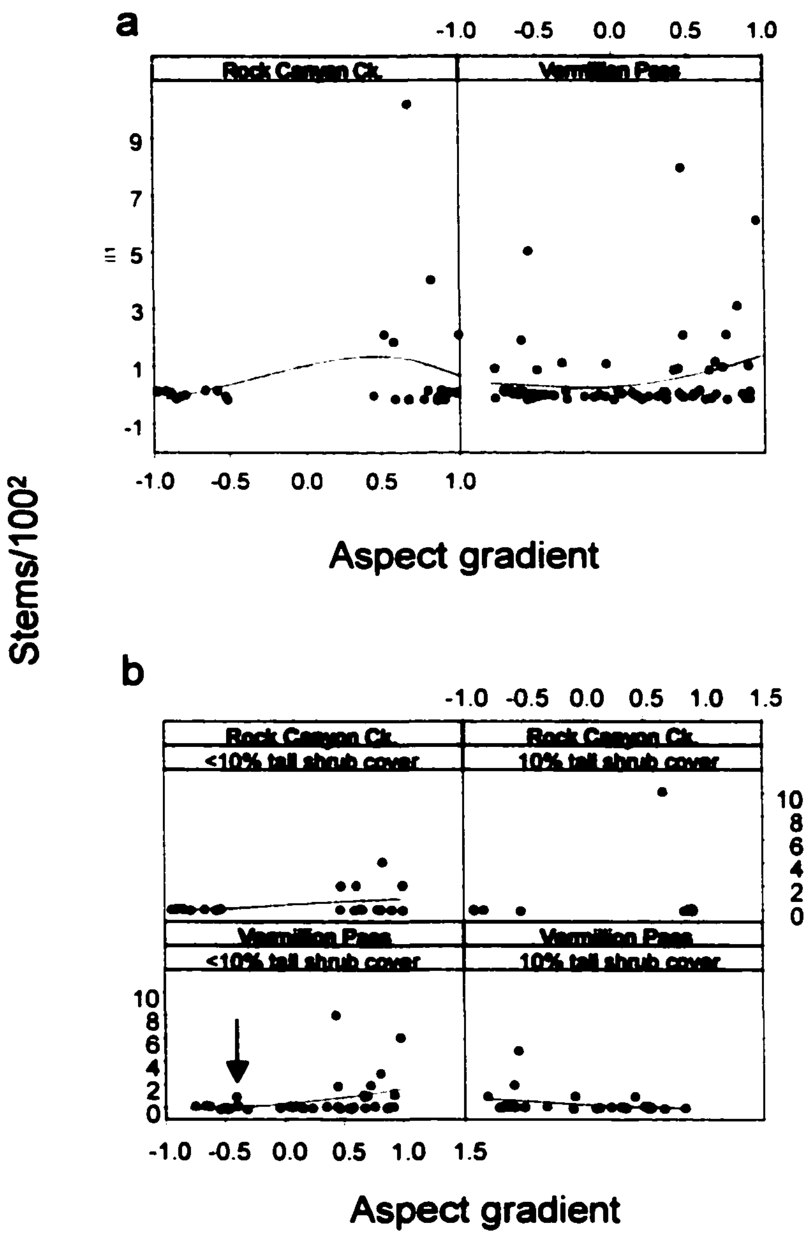


Figure 2.14: The relationship between (a) aspect and larch recruitment at both burn sites. The gradient is the difference between due south (-1) and due north (1). Note that east and west equal 0. (b) The interaction between aspect and tall shrub cover on larch seedling recruitment. The arrow identifies the only occurrence of a larch seedling under <10% cover on a south-facing slope. The fitted lines are cubic smoothing splines to aid with visual interpretation, but are independent of the statistical model.

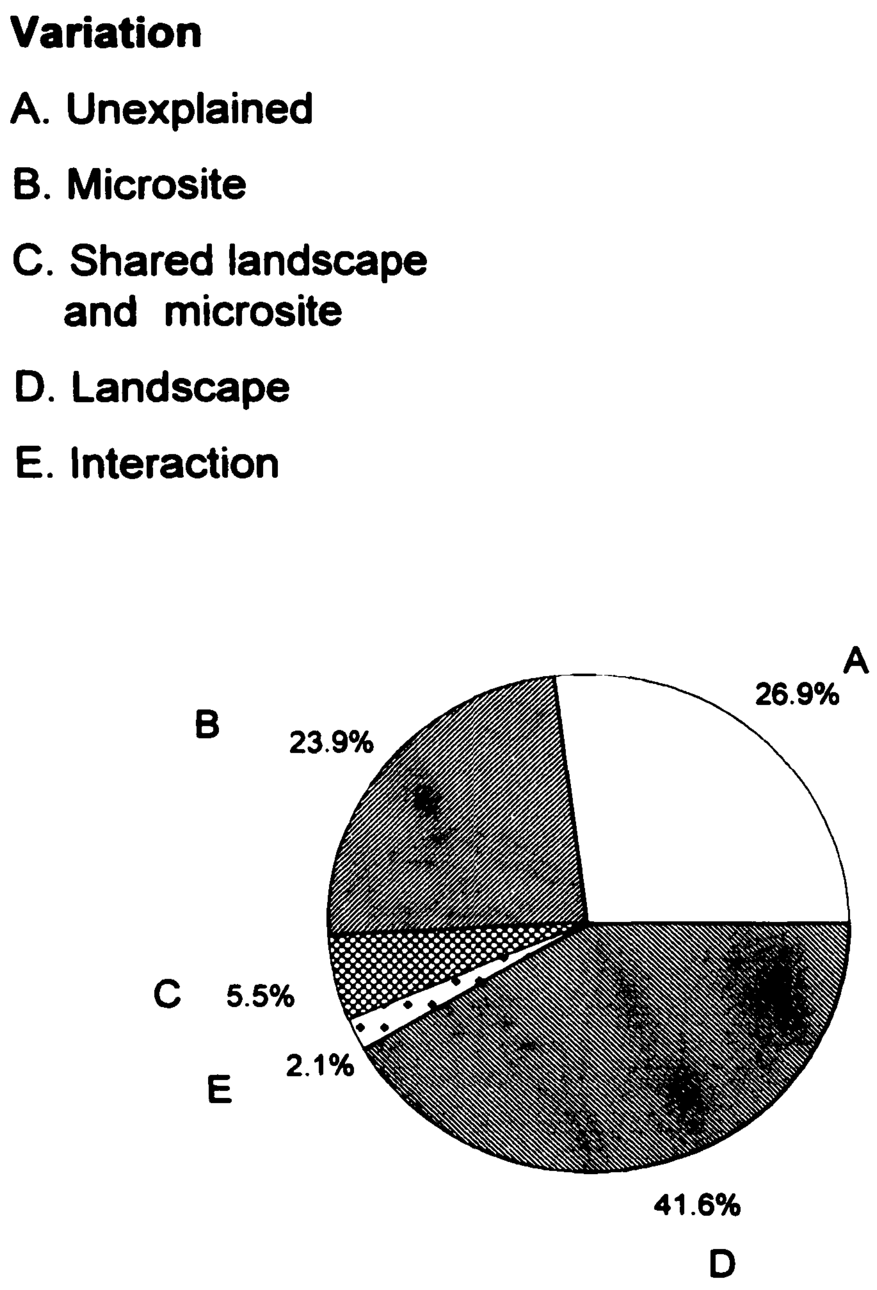


Figure 2.15: Alpine larch seedling GLM model variation partitioned by landscape level and locally acting environmental gradients.

2.4 Discussion

The regeneration of alpine larch following stand-replacing fire has never been considered important in the population biology of the species. In the only study examining the general ecology, Arno (1970) briefly described the occurrence of seral alpine larch stands of fire origin on the east slopes of the Canadian Rockies, between Crowsnest and Banff. However, this mode of regeneration was apparently not significant in the southern higher timberline areas of the species' distribution where Arno (1970) worked more intensively. The general conifer regeneration data for the two burns I studied (Figures 2.5-2.8) indicates that, although alpine larch is a minor component of the regenerating forest as a whole, in appropriate conditions, regeneration following fire is quite good. In these locations the species can dominate the local shrub community with superior height growth (Figure 2.2-2.3). This is an important revelation, because at this northern edge of the species' distribution a considerable proportion of the population is located in relatively dense Engelmann spruce – subalpine fir dominated forest, well below the more open timberline habitat with which "alpine" larch is commonly associated. To provide more insight into how these mixed stands may initially arise I will first discuss the results of the other conifers observed within the fires.

The separation of the whitebark pine regeneration niche from that of alpine larch and the other conifer niches over the moisture-light gradient described by axis 1 of the CCA indicates strong niche partitioning at this early life stage (Figure 2.10). This timberline pine species is thought to have co-evolved with the Clark's nut cracker (Tomback and Linhart 1990), which caches pine seeds just beneath the soil surface, typically on southern slopes (Stuart-Smith 1998). The birds appear to prefer caching sites where there are few mature trees. It has been suggested that fire is an important agent for providing the kinds of openings favoured by the nutcracker and hence, for the regeneration of the pine (Arno 1986). Interestingly in the present study, seedlings were also found in the areas of very low shrub cover, suggesting that even after the removal of the forest canopy, the preference of the bird is to cache seeds in the more open areas (Figure 2.10).

Lodgepole pine occurs over a wide range of environmental conditions throughout the Pacific Northwest from Alaska to the Midwest of the United States (Lotan and Critchfield 1990). This "generalist" behaviour is reflected in this study as the lodgepole pine regeneration niche includes the mesic part of the soil moisture gradient and overlaps the niches of the larch, spruce and fir (Figure 2.10). The lodgepole pine seedling and sapling community niche is found separated from the alpine larch and other conifer niches most strongly on the basis of shrub height, elevation, and a greater average distance from the forest edge. In this study, the tallest, most frequent "shrubs" at low elevations were the lodgepole pine saplings, thus the positive correlation with shrub layer height.

In the northern Rockies, lodgepole pine predominantly produces serotinous cones (Lotan and Perry 1983), which permit early germination following a fire, and with rapid initial growth, this species can establish several years before its competitors. In large burn areas, lodgepole pine regeneration may be found as a monoculture in the middle, if the tree or its cones were present before the fire (Turner et al. 1997). Although the age data for lodgepole pine in this study failed to consistently show lodgepole pine as the first coloniser (perhaps due to systematic error, i.e., boring the stems above the true root collar), this information suggests that the timing of seed dispersal, the size of disturbed area, and elevation are important dimensions in this species regeneration niche.

The preference of subalpine fir and Engelmann spruce for regeneration on northern aspects, where there is greater soil moisture, has been noted in other studies (Beil 1966, Alexander and Shepperd 1990, Alexander et al. 1990). Both species prefer shaded areas for seedling growth; with small spruce seedlings being especially sensitive to desiccation during hot dry periods (Knapp and Smith 1982, Alexander 1987). These environmental preferences are supported by the pattern of regeneration for these species in Figure 2.10, where the close association of both the spruce and fir seedling/sapling niches is on the north end of the aspect gradient and in the areas of greater soil moisture and shrub cover. The larch regeneration niche is also found in this environmental space. Previous work by Arno and Habeck (1972) confirms that alpine larch is typically found at high elevation on cool, moist, northern aspects. However, this species is considered very shade intolerant (Arno et al. 1995), and therefore understanding its association with greater shrub cover requires further clarification.

2.4.1 Larch regeneration: a facilitated response?

Richards (1981) studied the relationship between light intensity and net carbon assimilation for needles of alpine larch seedlings located near timberline. He found their light compensation point to be higher than needles of other timberline trees. In addition, he determined that relatively small increases in atmospheric vapour pressure deficits or short durations of soil drought drastically reduced the stomatal conductance, and therefore, net assimilation. On comparing climatological data from a lower subalpine forest site, Richards concluded that these factors largely constrained the occurrence of the species to the more open, and less atmospherically demanding timberline zone (i.e., where the vapour pressure deficit is less). Certainly, the removal of the forest canopy by wildfire means that establishing seedlings will likely have greater ambient light levels. The non-linear relationship between shrub cover and alpine larch seedling abundance described in Figure 2.12 suggests that the presence of shrub cover may play a facilitative role in avoiding problems associated with increased vapour pressure deficit.

Facilitation describes the beneficial modification of neighbourhood environmental conditions by previously established plants for the establishment of new arrivals (Clements 1916, Connell and Slatyer 1977). Although facilitation may occur through the provision or modification of any number of environmental gradients, the presence of some form of plant cover has been shown to provide cooler summer daytime temperatures and greater relative humidity at the air-soil interface than occurs in absence of cover (Larcher 1983). This is of particular importance to the young larch seedlings and may be another example of the importance of positive interactions in plant communities (cf. Bertness & Callaway 1994).

Holmgren et al. (1997) present a conceptual model of the growth response that an establishing plant population might exhibit when faced with the trade-off between competition and facilitation over interacting gradients such as light and moisture. The quadratic relationship between number of seedlings and shrub cover described by the smoothed line in Figure 2.12b strongly supports this type of trade-off model. The greater number of individuals found in the intermediate levels of shrub cover compared to both lower and higher levels suggest that the local environment created by intermediate cover is beneficial to larch seedling establishment.

This relationship was also indicated by the interaction between aspect and tall shrub cover (Figure 2.14), further supporting the idea that a moderated moisture environment is critical for larch regeneration in these burn areas. However, a question arises regarding the initial recruitment conditions immediately following the disturbance. Was there any surviving vegetation to facilitate the initial establishment of larch? Dubé's (1976) study of early plant succession in the Vermilion Pass fire sampled 12 stands on the northwest facing slopes. He found that shrub survival following the fire on this aspect was considerable. The combined mean for the herb-dwarf shrub and shrub cover was 16.2% (with a range of 6.6% - 30.8%), only 2-3 years following the disturbance.

There are no previously published reports documenting alpine larch seed dispersal. However, the rapidly declining abundance of seedlings, and the approximate maximum distance of 300 m from a forest edge seed source for seeding regeneration (Figure 2.12), corresponds well with the wind dispersal patterns of the morphologically similar western larch and Engelmann spruce seeds (McCaughey et al. 1986, Schmidt and Shearer 1990). Although tamarack (*Larix laricina* (Du Roi) K. Kock) seeds are lighter than alpine larch seeds, little seedling recruitment for tamarack is reported greater than 60 m from a parent tree (Brown et al. 1988, Johnston 1990).

Alpine larch, like Engelmann spruce, has thin bark, increasing the chance of mortality even in low intensity fires (Arno 1990). This limits the probability of mature individuals surviving these disturbance events and acting as seed trees (although see Barrett 1996).

The severity of both fires in the present study meant that there were no residual trees occurring with in the burns except near the watercourses in the valley bottoms. Based on these characteristics, and the importance of dispersal distance in the GLM model, the magnitude of disturbance can be seen as the most important axis in larch regeneration niche space. Given the distribution of the data in Figure 2.12a, I would expect to see the majority of alpine larch regeneration occurring within 100 m of the forest-edge seed source in other large disturbed areas, similar perhaps, to the pattern of Engelmann spruce regeneration described by Johnson and Miyanishi (1991).

2.4.2 Spatial structuring of the data

The results of the variance partitioning in both the CCA and GLM analyses suggest that there was relatively little spatially structured variation in the response data *at the scale in which space was accurately measured.* There were several sources of error in determining the exact location at which any given plant or gradient was measured. The first is related to the size of the plot compared to the scale of variability for environmental gradients within that sample plot space. For example, different plant species have been shown to respond to changes in soil moisture and nutrient gradients that occur over distances of much less than a metre (Svensson and Callaghan 1988, Bell et al. 1993). Given that my sample plots had a radius of 5.64 m and the only spatially referenced point was the plot centre, there was no way to assess the spatial structure that these kinds of small scale gradient fluctuations have on the measured plant response. The other type of error was related to geo-referencing the sample plot centres.

These problems all compound to create a lack of sensitivity in detecting the small scale plant response to equally small scale spatial heterogeneity in the environment. Therefore, only landscape gradients were likely to show up as spatially structured variables in the variance partitioning analyses performed here. This suggests that in the case of the multivariate plant community analysis, the unique spatially structured variation (Figure 2.11a) was related to some larger scale factor like burn intensity (Turner et al. 1997), or changes in general soil types (Galipeau et al.1997) that was not identified in my study.

These considerations may help explain why there were no significantly important spatial terms (unique or shared) structuring the larch GLM seedling data. Nearly a third of the explained variation in the data was accounted for by microsite gradients that have poor spatial representation. The landscape gradient, distance to seed source, which explained a large proportion of the variation in the data, was present not only at a number of different locations around the perimeter of the burns, but also on elevated adjacent cliffs and ridges. Strong winds associated summer storms, and more generally with locally occurring thermal differences (katabatic and anabatic wind; Barry 1992) may have lead to seed arriving from locations other than the nearest measured source, and help explain why the differences between the actual input of seed and the nearest spatially referenced seed source were poorly correlated.

2.4.3 The importance of landscape versus microsite gradients

In the conifer community niche analysis, there appeared to be a roughly equal participation in the species' organisation between the landscape and microsite gradients (Figure 2.11b). The large proportion of overlap in these gradient types suggests, however, that the two gradient groups were not independent. Most of the gradients that were measured in this study could be classified as indirect gradients (Austin 1980); scalars that act as surrogates for gradients that directly affect the growth or physiology of a species. For example, the landscape gradient between north and south aspect does not affect the establishment or growth of a plant directly, but it does control the amount of solar radiation that a given location receives, and the depth and duration of the snow pack, which in turn influences the summer moisture status of the soil. These latter factors a direct influence on plant establishment and growth. The microsite gradient of relative soil moisture is not a direct measure, but estimates moisture conditions related to aspect, soil depth and texture, and so on. The large overlap in the landscape and microsite gradients points to the underlying direct gradients that they share.

The partitioning of variance from the GLM seedling model indicates that the landscape gradient of distance to a seed source, can be seen as a major controlling factor in the establishment of the species. This conclusion is supported by the relatively small proportion of shared variance between the landscape and microsite gradients, and that the aspect gradient accounted for little of the model variance. However, this observation should not overshadow the important contribution of the smaller scale environmental gradients to the structure of the larch's regeneration niche, as these local gradients likely act as the ultimate filter as to whether recruitment occurs.

In summary, the within-stand environmental heterogeneity created by the coarse-scale fire disturbance studied here was sufficient to allow the establishment and initial development of a group of coniferous species. The physical structure of the vegetation present following fire appears to be an important influence on the subalpine distribution of alpine larch. This is shown by the occurrence of the species' regeneration up to 300m within burn areas where there is partial shrub cover, and the apparent facilitative nature of this shaded, moist environmental space. However, greater overlap in regeneration niche with Engelmann spruce and subalpine fir means greater competition as the forest ages, and as the microsite environmental conditions change. Further work is required to determine the recruitment strategy of alpine larch, given the full range of forest age and structure in this landscape.

2.5 Literature cited

Agee, J. K. 1990. The historical role of fire in Pacific Northwest forests. Pages 25-38 *in:* Walstad J. D., S. V. Radosevich, and D. V. Sandberg, editors. Natural and prescribed fires in Pacific Northwest forests. Oregon State University Press. Corvallis, Oregon, USA.

Agee. J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press. Washington, DC, USA.

Alaback, P. B. and Tappeiner II, J. C. 1991. Response of western hemlock (*Tsuga heterophylla*) and early huckleberry (*Vaccinium ovalifolium*) seedlings to forest windthrow. Canadian Journal of Forest Research. **21:** 534-539.

Alexander, R. R. 1987. Ecology, silviculture, and management of the Engelmann spruce-subalpine fir type in the Central and Southern Rocky Mountains. **Agricultural Handbook 659**. US Department of Agriculture, Forest Service. Washington DC, USA.

Alexander, R. R., Shearer, R. C., and Shepperd, W. D. 1990. *Abies lasiocarpa* (Hook) Nutt. Pages 60-70 *in:* Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC.

Alexander, R. R. and Shepperd, W. D. 1990. *Picea engelmannii* Parry ex Engelm. Pages 187-202 *in:* Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC.

Anonymous 1999. Canadian climate normals. Environment Canada URL: http://www.cmc.ec.gc.ca./climate/normals/ [2000]

Arno, S. F. 1970. Ecology of alpine larch in the Pacific Northwest. PhD thesis University of Montana, Missoula, MT, USA.

Arno, S. F. 1986. Whitebark pine cone crops - a diminishing source of wildlife food? Western Journal of Applied Forestry. **1:** 92-94.

Arno, S. F. 1990. Alpine Larch (*Larix lyallii* Parl). Pages 152-158 *in:* Burns R. M. and B. H. Honkola, editors. Silvics of North America. **Agricultural Handbook 654**. Forest Service, US Department of Agriculture. Washington, DC, USA.

Arno, S. F. and Habeck, J. R. 1972. Ecology of Alpine Larch (*Larix lyallii* Parl) in the Pacific Northwest. Ecological Monographs. **42:** 418-450.

Arno, S. F. and Sneck, S. 1977. A method of determining fire history in coniferous forests of the Mountain West. **INT-42**. USDA Forest Service. Ogden, UT, USA.

Arno, S. F., Worrall, J., and Carlson, C. E. 1995. *Larix Lyallii:* colonist of tree-line and talus sites. Pages 72-78 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and Management of Larix Forests: A Look Ahead. **GTR-INT-319.** US Department of Agriculture, Forest Service. Ogden, UT, USA.

Austin, M. P. 1980. Searching for a model for use in vegetation analysis. Vegetatio. **42:** 11-21.

Austin, M. P. and Smith, T. M. 1989. A new model for the continuum concept. Vegetatio. **83:** 35-47.

Barrett, S. W. 1996. The historic role of fire in Waterton Lakes National Park, Alberta. **KWL 30004**. Parks Canada contract report. Waterton, AB, Canada.

Barry, R. G. 1992. Mountain weather and climate. Routledge. New York, NY, USA.

Beil, C. E. 1966. An ecological study of the primary producer level of the subalpine spruce - fir ecosystem of Banff and Jasper National Parks, Alberta. M.Sc. thesis, University of Alberta, Edmonton, AB, Canada.

Bell, G., Lechowicz, M. J., Appenzeller, A., Chandler, M., DeBlois, E., Jackson, L., Mackenzie, B., Preziosi, R., Schallenberg, M., and Tinker, N. 1993. The spatial structure of the physical environment. Oecologia. **96:** 114-121.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. TREE. **9:** 191-193.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons. New York, NY, USA.

Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology. **73:** 1045-1055.

Braumandl, T. F. and Curran, M. P. 1996. A field guide for site identification and interpretation for the Nelson forest region. Crown Publications. Victoria, BC, Canada.

Brokaw, N. V. L. and Scheiner, S. M. 1989. Species composition in gaps and structure of a tropical forest. Ecology. **70:** 538-541.

Brown, K. R., Zobel, D. B., and Zasada, J. C. 1988. Seed dispersal, seedling emergence, early survival of *Larix laricina* (Du Roi) K. Koch in the Tanana Valley, Alaska. Canadian Journal of Forest Research. **18:** 306-314.

Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forest of the northern Rocky Mountains, USA. Oikos. **82:** 561-573.

Cameron-Duffy, D. and Meier, A. J. 1995. Do Appalachian herbaceous understories ever recover from clearcutting? Pages 190-195 *in:* Ehrenfeld D., editor. Reading from Conservation Biology: wildlife and forests. The Society for Conservation Biology and Blackwell Science, Inc. Cambridge, Mass, USA.

Clements, F. E. 1916. Plant succession. **242**. Carnegie Institution. Washington, DC, USA.

Connell, J. H. and Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist. **111:** 1119-1144.

Dale, M. R. T. 1999. Spatial pattern analysis in plant ecology. University Press. Cambridge, UK.

Day, R. J. 1972. Stand structure, succession and use of southern Alberta's Rocky Mountain forest. Ecology. **53:** 427-478.

Denslow, J. S. 1985. Disturbance-mediated coexistence of species. Pages 307-323 *in:* Pickett S. T. A. and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press. Orlando, USA.

Dubé, D. E. 1976. Early plant succession following a 1968 wildfire in the subalpine zone of the Vermilion Pass, Kootenay National Park. M.Sc. thesis, University of Alberta. Edmonton, AB, Canada.

Ecoregions Working Group Canada Committee on Ecological Land Classification 1989. Ecoclimatic regions of Canada: first approximation. **Ecological land classification series No 23**. Sustainable Development Branch, Canadian Wildlife Service, Conservation and Protection. Ottawa, ON, Canada.

Galipeau, C., Kneeshaw, D., and Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after the fire. Canadian Journal of Forest Research. **27:** 139-147.

Grabherr, G., Gottfried, M., and Pauli, H. 1994. Climate effects on mountain plants. Nature. **369:** 448.

Grubb, P. 1977. The maintenance of species-richness in the plant communities: the importance of the regeneration niche. Biological Review. **52:** 107-145.

Harper, J. L. 1977. Population biology of plants. Academic Press. London, UK.

Heinemann, K., Kitzberger, T., and Veblen, T. T. 2000. Influences of gap microheterogeneity on the regeneration of *Nothofagus pumilio* in a xeric old-growth forest of northwestern Patagonia, Argentina. Canadian Journal of Forest Research. **30:** 25-31.

Hill, M. O. 1979. TWINSPAN: a fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes . Ecology and Systematics, Cornell University, Ithaca, NY, USA.

Holmgren, M., Scheffer, M., and Huston, M. A. 1997. The interplay of facilitation and competition in plant communities. Ecology. **78:** 1966-1975.

Holt, R. F. 2000. An ecological foundation for a proposed terrestrial ecosystem restoration program. Pandion Ecological Research Ltd. Nelson, BC, Canada.

Johnson, E. A. 1992. Fire and vegetation dynamics. Cambridge University Press. Cambridge, UK.

Johnson, E. A. and Fryer, G. I. 1989. Population dynamics in lodgepole pine-Engelmann spruce forests. Ecology. **70:** 1335-1345.

Johnson, E. A. and Miyanishi, K. 1991. Fire and population dynamics of lodgepole pine and Engelmann spruce forests in the southern Canadian Rockies. Pages 77-91 *in:* Nakagoshi N. and F. B. Golley, editors. Coniferous forest ecology from an international perspective. Academic Publishing. The Netherlands.

Johnston, W. F. 1990. *Larix laricina* (Du Roi) K Koch Tamarack. Pages 141-151 *in:* Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC, USA.

Knapp, A. K. and Smith, W. K. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Canadian Journal of Botany. **60:** 2753-2761.

Lacelle, L. E. H. 1990. Biophysical resources of the East Kootenay area: soils. **Wildlife Technical Monograph TM-1**. Wildlife Branch, Habitat Inventory Section, BC Ministry of Environment. Victoria, BC, Canada.

Lanner, R. M. 1996. Made for each other: a symbiosis of birds and pines. Oxford University Press. New York, NY, USA.

Larcher, W. 1983. Physiological plant ecology. Springer-Verlag. Berlin.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology. **74:** 1659-1673.

Lertzman, K. P. 1992. Patterns of gap-phase replacement in a subalpine, old growth forest. Ecology. 657-669.

Lertzman, K., Fall, J., and Dorner, B. 1998. Three kinds of heterogeneity in fire regimes: at the crossroads of fire history and landscape ecology. Northwest Science. **72:** 4-23.

Lotan, J. E. and Critchfield, W. B. 1990. Pinus contorta Dougl ex Loud. Pages 302-315 *in:* Burns R. M. and B. H. Honkala, Technical coordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC.

Lotan, J. E. and Parry, D. A. 1983. Ecology and regeneration of lodgepole pine. **Agricultural Handbook 606**. US Department of Agriculture, Forest Service. Washington DC, USA.

Mathsoft 1999. S-Plus 2000 guide to statistics. **1:** Data Analysis Products Division, Mathsoft. Seattle, WA, USA.

Mathsoft 2000. S-Plus 2000 Professional Release 2. Data Analysis Products Division, Mathsoft, Seattle, WA, USA.

McCaughey, W. W., Schmidt, W. C., and Shearer, R. C. 1986. Seed-dispersal characteristics of conifers in the inland mountain west. Pages: 50-62 *in:* Shearer R. C., Compiler. Proceedings - conifer tree seed in the inland mountain west symposium, Missoula, Montana, August 5-6, 1985. **General Technical Report INT-203**. United States Department of Agriculture, Forest Service. Ogden, UT, USA.

Miller, C. and Urban, D. L. 1999. Interactions between forest heterogeneity and surface fire regimes in the southern Sierra Nevada. Canadian Journal of Forest Research. **29:** 202-212.

Morrison, D. A., Le Brocque, A. F., and Clarke, P. J. 1995. An assessment of some improved techniques for estimating the abundance (frequency) of sedentary organisms. Vegetatio. **120:** 131-145.

Nicholls, A. 1989. How to make biological surveys go further with generalised linear models. Biological Conservation. **50:** 51-75.

O'Brien, L. 1992. Introducing quantitative geography: measurement, methods and generalised linear models. Rutledge. London, UK.

Økland, R. H. and Eilertsen, O. 1994. Canonical Correspondence Analysis with variation partitioning: some comments and an application. Journal of Vegetation Science. **5:** 177-126.

Palmer, M. 1998. The ordination web page . Available at: http://wwwokstateedu/artsci/botany/varparhtml [1999]

Pyne, S. J. 1984. Introduction to wildland fire: fire management in the United States. John Wiley & Sons. New York, NY, USA.

Richards, J. H. 1981. Ecophysiology of a deciduous timberline tree, *Larix lyallii* Parl. PhD thesis, Department of Botany, University of Alberta. Edmonton, Alberta.

Romme, W. H. and Knight, D. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology. **62:** 319-329.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology. **62:** 1041-1051.

Schmidt, W. C. and Shearer, R. C. 1990. *Larix occidentalis* Nutt Western Larch. Pages 160-172 *in:* Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **654**. US Department of Agriculture, Forest Service. Washington, DC.

Shugart, H. H., Bonan, G. B., and Rastetter, E. B. 1988. Niche theory and community organization. Canadian Journal of Botany. **66:** 2634-2639.

Sokal, R. R. and Rohlf, J. F. 1995. Biometry. W H Freeman and Company. New York, NY, USA.

Stuart-Smith, J. 1998. Conservation of whitebark pine in the Canadian Rockies: blister rust and population genetics. M.Sc. thesis University of Alberta. Edmonton, AB, Canada.

Svensson, B. M. and Callaghan, T. V. 1988. Small-scale vegetation pattern related to the growth of *Lycopodium annotinum* and variations in its micro-environment. Vegetatio. **76:** 167-177.

Tande, G. F. 1979. Fire history and vegetation pattern of coniferous forest in Jasper National Park, Alberta. Canadian Journal of Botany. **57:** 1912-1931.

ter Braak, C. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology. **67:** 1167-1179.

ter Braak, C. J. 1988. CANOCO: a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis and redundancy analysis (version 31). Microcomputer Power, Ithaca, NY, USA.

ter Braak, C. J. and Prentice, I. C. 1988. A theory of gradient analysis. Advances in Ecological Research. **18:** 271-317.

Tomback, D. F. and Linhart, Y. B. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology. **4:** 185-219.

Turner, M. G., Romme, W. H., Gardner, R. H., and Hargrove, W. W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs. **67:** 411-433.

Veblen, T. T., Hadley, K. S., and Reid, M. 1991. Disturbance and stand development of a Colorado subalpine forest. Journal of Biogeography. **18:** 707-716.

Walker, B. D., Taylor, W. S., and Allan, D. T. 1984. Chapter II - soils. Pages 33-42 *in:* Achuff P. L., W. D. Holland, G. M. Coen, and K. Van Tighem, editors. Ecological land classification of Kootenay National Park, British Columbia. **M-84-10**. Alberta Institute of Pedology, University of Alberta. Edmonton, AB, Canada.

White, M. A. and Vankat, J. L. 1993. Middle and high elevation coniferous forest communities of the North Rim region of Grand Canyon National Park, Arizona, USA. Vegetatio. **109:** 161-174.

Wilson, B. C. 1997. The ecology of alpine larch in the northern Rocky Mountains. Cordillera. **3:** 8-11.

Wilson, B. C. and Stuart-Smith, G. J. 2000. Whitebark pine conservation for the Canadian Rocky Mountain National Parks. **KNP03-00**. Cordilleran Ecological Research. Winlaw, BC, Canada.

CHAPTER 3: STRUCTURE OF OLDER SUBALPINE FORESTS: IS THERE A PLACE FOR ALPINE LARCH?

3.1 Introduction

In the northern Rocky Mountains, Engelmann spruce (*Picea engelmannii* Parry.) and subalpine fir (*Abies lasiocarpa* (Hook) Nutt) form the dominant high elevation forests (Daubenmire 1943, Beil 1966, Alexander 1987). These two species replace the lower elevation lodgepole pine (*Pinus contorta* Dougl. *var. latifolia* Engelm.) and white spruce (*Picea glauca* (Moench) Voss) forests between about 1400 and 1800 m, and then generally remain the most common tree species up to timberline (Achuff 1982). However, on northern aspects, alpine larch (*Larix lyallii* Parl.) co-occur with these two high elevation generalists, although larch is restricted to a narrower range of environmental conditions (Arno 1970).

The deciduous alpine larch is generally considered a resistant timberline species, given its ability to withstand winter desiccation and other physical damage from the severe winter environment (Arno and Habeck 1972, Richards 1981). However, the species' ability to compete effectively in the more dense subalpine forest has been in question, given its higher moisture and light requirements, compared to that of the spruce and fir (Richards 1981, Arno 1990). Nevertheless, there are a number of areas where the species has been observed at much lower elevations than its conspicuous timberline habitat. Arno (1970) described several instances were alpine larch occurred on talus slopes at elevations as low as 1500 m, apparently where seeds were transported by down slope winds, or avalanches fortuitously. Alpine larch has also been observed as an early seral species, appearing below timberline in subalpine areas recently disturbed by fire (Arno 1970, Arno et al. 1995, Chapter 2). In all these observed distributions, larch was found in apparently "low competition" environments.

Less well understood is the persistence of alpine larch in older subalpine forest stands at the northern edge of its continental distribution. In the Canadian Rocky Mountain National Parks of Banff, Kootenay, and Yoho, alpine larch has been observed as a component of well established spruce-fir forest down to the transition with lodgepole pine (Arno 1970, Wilson 1997). This indicates that the realised niche for the species is broader than the niche space characterised by the more open timberline or early seral subalpine habitat, and may be linked to some measure of forest structure.

Generally, there is an elevation gradient in forest structure from the closed, tall montane forest to the more open, shorter timberline forests (Tranquillini 1979). However, the physical structure of subalpine forest is dependent on a variety of interacting factors. These include the frequency, magnitude, and intensity of the dominant disturbance type(s) that make up the local disturbance regime, and the subsequent forest development (Day 1972, Sprugle 1976, Oliver 1991,Veblen et al. 1991, Agee 1993). Geographic site characteristics, such as the aspect, slope, soil development, soil and air temperature, wind exposure, summer precipitation, and the depth and persistence of the winter snow pack are also important (Daubenmire 1974, Arno and Hammerly 1984, Hansen-Bristow 1986). These factors not only directly influence the environmental gradients affecting the growing vegetation, but also help to characterise the given disturbance regimes (Romme and Knight 1981).

Two different examples of this type of disturbance - structural interaction are pertinent for the north facing Engelmann spruce – subalpine fir vegetation types under discussion. These forests are described as having a low frequency, high intensity fire regime where, on average, the cooler, more moist subalpine conditions limit the spread of lightening ignition events to relatively infrequent large scale disturbances (Tande 1979, Agee 1990). This type of disturbance creates large open areas where most of the above-ground vegetative structure is removed, dramatically changing both the quantity and quality of available light, moisture, and nutrients (Dubé 1976). Typically, fire frequency for these forests is highly variable; estimated from 100 years to greater than 400 years (Tande 1979, Agee 1993, Barrett 1996, Rogeau 1996). As the upper end of this range exceeds the average longevity of both species, regeneration in older stands is facilitated by finer scale gap disturbance (Veblen 1986, Aplet et al. 1988, Veblen et al. 1991). Here, the changes to environmental gradients are subtler. The removal of one or more canopy individuals creates a break in the overstory. Understory vegetation, including conifer seeds and seedlings, are then able to use the increases in nutrients and changes in other environmental gradients to grow.

This information highlights a key point about a general mechanism of succession: vegetation acts as both a complex, or indirect environmental gradient (Whittaker 1972, Austin and Smith 1989), and as a response variable. The existing forest structure creates a kind of dynamic filter that regulates the local environmental gradients through competition. This, in turn, affects the opportunities for different plant populations to establish, regenerate, or recruit to a dominant structural form (Horn 1976, Connell and Slatyer 1977, van der Valk 1992). To understand better the population, or niche dynamics of alpine larch over a larger landscape scale, it is necessary to explore more fully the species' relationship with disturbance and subalpine forest structure.

From an applied land management perspective this has important implications. Disturbance and the resulting forest structure are now actively managed throughout Canadian federally and provincially administered lands by fire suppression, fire prescription, logging, and associated silvicultural practices (CHPC 1994, Ministry of Forests 2001). Furthermore, rapidly changing global climatic conditions will alter the rates at which plant species grow, reproduce, and disperse (Grabherr et al. 1994, Prentice 1992, Graumlich 1994). To conserve species, such as alpine larch, effectively we not only need specific details regarding the species' life history and ecophysiology, but also information that links the distribution of the species to variables, such as physiognomic forest structure, that managers can easily measure in the field or from remotely sensed data (Wilson 1998). This information can then be used to develop both parameters for predictive models (Smith et al. 1992, Keane et al. 1996), and targets for adaptive management prescriptions (Wilson and Stuart-Smith 2000).

3.1.1 Objectives

The objective of this Chapter is to describe the realised niche of alpine larch in maturing and older subalpine forests as a function of the present stand structural characteristics. There were three questions that I wanted to answer:

1. How does the age of the forest affect the size/age distribution of alpine larch compared to that of the other tree species?
2. Are there identifiable forest structural features, and/or plant species that are correlated with the establishment of alpine larch? And if so,
3. Do these factors limit the subalpine distribution of this species?

3.2 Methods

3.2.1 Study location and site selection

The study area was located on the continental divide formed by the southern Canadian Rockies in Banff National Park (Figure 3.1). I established four research sites, each covering subalpine elevations between approximately 2000 m and 2200 m on the southern side of the Bow Valley between Banff and Lake Louise (approximately 51°N, 116°W). This area lies in the subalpine southern cordilleran ecoclimatic region (EWGCCELC 1989). The weather is characterised by cool summers and cold winters, but there are, occasionally, high pressure systems that settle in this region of the Rockies that create prolonged hot, dry, forest fire conditions in the summers (Johnson and Miyanishi 1991). Data from the nearest weather station in Banff, Alberta show a mean maximum air temperature in July of 22.1° C, and a mean maximum temperature in January of -5° C. The average yearly precipitation in Banff is 468.0 mm, with the greatest precipitation occurring in the summer between May and August (Anonymous 1999).

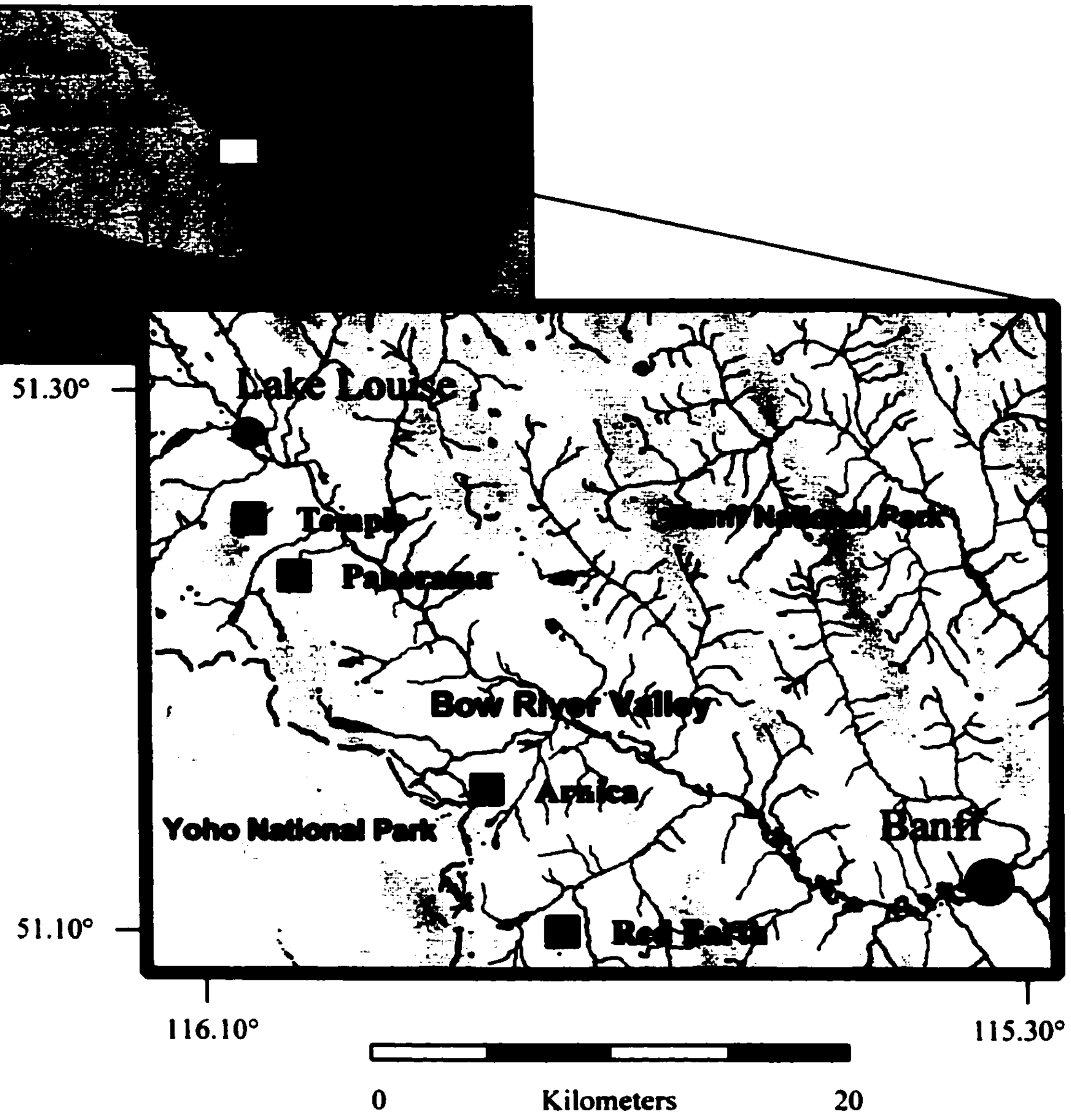


Figure 3.1: Maturing and old forest sites, Banff National Park, Alberta.

The stands were chosen to represent two forest developmental stages. Panorama and Temple were the maturing forest stands with estimated stand origin dates of 1840 and 1850 respectively (Rogeau and Gilbride 1994). In these stands, the dominant canopy trees were recruited from a stand replacing fire event and very little fine scale gap disturbance had taken place. The two older forest stands, Arnica and Red Earth, had estimated stand ages of greater than 300 years. Considerable downed woody debris in various states of decay resulting from fine scale gap disturbance characterised these sites. To limit the amount of variation in forest structure caused by topography, the stands were all located on north-facing aspects, with relatively uniform slopes (Table 3.1). Soils at all sites were comprised of moderate to well drained brunisols of glacial till origin (Walker et al. 1982).

3.2.2 Data collection

I stratified these selected stands over the elevation range in which alpine larch of any size was present. The lowest sampling areas were located around 2000 metres in all of the sampled stands (Table 3.1) where typically only a few mature individuals were found. This elevation was also roughly the upper limit of lodgepole pine in each of the stands. The upper sampling areas for the maturing forests were located near the highest end of the contiguous stand - i.e., the obvious burn area boundary. In the case of the older forest stands, no obvious boundary existed, and so I located the upper transects close to the elevation of the younger stands. Intermediate sampling locations in each of the stands were chosen close to the mean elevation of the upper and lower transect locations (Table 3.1).

Table 3.1: General site characteristics.

Site (stage)	Transect	Elevation (m)	Slope (%) (mean)	Aspect
Arnica (old)	upper	2170	12.3	NNE
	middle	2070	14.2	NNW
	lower	1980	25.2	N
Red earth (old)	upper	2150	16.6	N
	middle	2070	21.1	N
	lower	2000	42.7	N
Temple (mature)	upper	2200	31.8	NE
	middle	2100	28.8	NE
	lower	1960	21.6	NE
Panorama (mature)	upper	2150	26.8	NNE
	middle	2050	26.3	NNE
	lower	2000	31.6	NNE

I placed 10 sampling plots in each of these elevation strata by first generating a set of random distances from a geographically referenced starting point along a traverse. Circular 100m^2 sample plots were defined using a 5.64 m measuring cord attached to a pole placed at the marked plot centre.

3.2.2.1 Forest structural characteristics

I recognised five distinct forest structural layers present within the surveyed stands. These where: (1) mature forest canopy: trees ≥ 10 m; (2) tall shrubs: woody species ≥2 m, and <10 m; (3) low shrubs: woody species ≥30 cm, and <2 m; (4) herbs: all woody species <30 cm and any sized forbs or grasses; (5) Forest floor: terrestrial bryophytes and lichens, rocks, decaying wood, organic matter, and mineral soil.

True canopy cover and tall shrub cover (hereafter "canopy cover") were estimated with a convex densiometer from the four cardinal points of each plot. The measurements were taken standing at the edge of the plot reading the densiometer value while facing toward the plot centre. The meter was held level at 1 m above the ground. I performed a calibration of the measured percent cover values to the actual light attenuation experienced under a range of forest canopy (Appendix I). This test indicated that there was nearly a directly proportional relationship between these values over a large range of the data. Low shrub cover was estimated by drawing the plot cord toward each cardinal direction and determining the average proportion of intersection with the underlying or overtopping shrubs. This line intercept procedure (Bonham 1989) was also used to determine the percent cover of the herb layer, and the percent cover of the forest floor components. To complete the structural description of the community, I measured the average height of the shrub and herb layers from four randomly chosen locations within each plot. Average canopy heights were determined from the tree population information described below.

To provide a more general picture of the tree species' influence surrounding the plot, I estimated each tree species' standing basal area. This was performed by measuring basal area at the plot cardinal points using a Bitterlich gauge with a sight width of 1 cm and an eye-to-sight distance of 25 cm (Mueller-Dombios and Ellenberg 1974). The average values (m^2/ha) were then calculated for each plot location. I also measured the distance to the nearest seed bearing adult tree for each species.

3.2.2.2 Tree population structure.

To determine the tree population structure, I identified and measured the height of each tree within the sample plot. The very dense juvenile subalpine fir were recorded in smaller sets of plots depending on their density. These data were then classified into four size cohorts based on the above-ground vegetation layer definitions provided above. This was done for both live and dead individuals.

To provide an estimate of the age of each cohort found on a given transect, I collected increment cores, and also destructively sampled individuals from the size range of each species. Trees that were greater than approximately 3 m tall were bored approximately 30 cm above the ground. Complete disk samples from individuals smaller than this were taken by cutting the stem at the root collar. Both increment cores and disks were mounted on wooden holders and either sanded with successively finer sandpaper following Arno and Sneck (1977), and/or lightly planed using a razor blade depending on the quality of the wood. The numbers of annual growth rings were counted on the prepared samples under a dissecting microscope in the lab.

3.2.2.3 Understory vegetation composition.

To document the local plant community and to characterize independently the environmental influence at each plot, I chose to record the presence and 'importance' of all vascular plant species that were present in geometrically increasing zones within each 100m^2 plot (Morrison et al.1995). Using this method, the occurrence of a species was only recorded once, the first time it was encountered, searching from the smallest zone around the centre of the plot outwards. An importance score was assigned to the species depending on the size of zone it is first found in (the greater area searched, the less importance assigned). This method provides not only frequency data, but also a quantitative estimate of relative species abundance when scores are averaged for a given area (see Morrison et al. 1995 for details, Wilson and Stuart-Smith 2000). Appendix II presents the details of this method.

3.2.3 Data analysis

3.2.3.1 Tree population and stand structural characteristics.

I plotted the frequency distribution of the average number of trees per hectare in each species' size class to examine the population patterns found at each site transect. These graphical displays provide information about whether a population was comprised of mostly similar sized cohorts that may have recruited from the original stand replacing disturbance event, or of continuously recruiting individuals that arose in absence of major disturbances since that time. The dead cohort information backs up these patterns, and may indicate when a size specific mortality agent has just started operating on a population. These inferences rely on the size of the trees being directly related to the trees' age (Harper 1977).

I used box-plots to group the age data for each species found on a given transect into cohort classes to compare directly with the size frequency distributions. I used one-way analysis of variance (ANOVA) to determine if the ages of the size cohort classes present for a tree species on given transect were different. Data were checked for homogeneity of variance and normality to determine if the assumptions of the test would be met. Where necessary, the data were log or square root transformed (Sokal and Rohlf 1995). I plotted the 95 % confidence interval above each box as a method to determine where any detected differences lay. In the case of transformed age values that grossly violated these assumptions, the non-parametric Kruskal-Wallis rank sum method was used. The null hypothesis for these comparisons was that there was no difference between mean ages for each cohort size class (alpha = 0.05). Statistical analyses were preformed using Splus statistical software (Mathsoft 2000).

I also used boxplots and ANOVA to provide general inference regarding the change in forest layer cover and height with elevation at each site. I followed the same data checking, transformation, and difference detection procedures outlined above. The null hypotheses for these comparisons were that there was no difference between means for each transect elevation. I then compared these results to the patterns of cohort recruitment and mortality as part of my exploratory analysis.

3.2.3.2 Determination of forest structural niche.

To provide a more detailed examination of the relationships between physiognomic forest strata and that of the cohort individuals present, I used Direct Gradient Analysis (DGA) (Whittaker 1978, ter Braak and Prentice 1988) to explore simultaneously the forest structural and tree cohort data. I used three separate DGA approaches to determine what forest structural features described the realised niche of alpine larch compared to that of the other conifers.

First, I used the multivariate ordination method, Canonical Correspondence Analysis (CCA; ter Braak 1986) to look at the response of all of the cohorts of the subalpine tree species to the measured stand structural and environmental site description variables (Table 3.2). This technique constrains the ordination axes to be linear combinations of the measured variables. Species and plots are ordered along the axes in such a way that the relationship between these response variables and the measured environmental variables is maximised in fewer dimensions (ter Braak and Prentice 1988). The output from this analysis is a two dimensional "biplot" diagram that indicates the strength of association species have with each of the included variables (see Jongman et al. 1995 for details). Thus the relative position species take up with respect to one another in this "environmental space" can be viewed as a representation of the centre of their respective realised niche space (Austin 1985).

Table 3.2: Description of site and stand structure variables.

Variable name	data type	number of levels	unit of measurement/level names
Site description variables			
Location	discrete	4	Panorama, Temple, Arnica, Red Earth
Forest development stage	discrete	2	development stage
Transect elevation	discrete	3	lower, middle, upper
Stand structural variables			
Slope of plot area	continuous	na	percent slope
Canopy height	continuous	na	height, m
Tall shrub height	continuous	na	height, m
Low shrub height	continuous	na	height, cm
Herb height	continuous	na	height, cm
Canopy cover	continuous	na	percent cover
Shrub cover	continuous	na	percent cover
Herb cover	continuous	na	percent cover
Bryoid cover	continuous	na	percent cover
Organic matter cover	continuous	na	percent cover
Rock cover	continuous	na	percent cover
Mineral soil cover	continuous	na	percent cover
Decaying wood	continuous	na	percent cover
Duff depth	continuous	na	depth, cm
Distance to conifer seed tree	continuous	na	distance, m
Total live basal area of each conifer	continuous	na	m^2/ha.
Total dead basal area of each conifer	continuous	na	m^2/ha.

In this analysis I included the tree species' cohorts as individual species, or "pseudo-species" to see if there was any partitioning of the species, or of the separate cohorts by the measured predictor terms. To select the "best" environmental terms (i.e., those that explain the greatest variance), I used the forward selection procedure in the CANOCO (ter Braak 1988) software. I chose alpha = 0.05 as a criteria to reject terms for model inclusion.

Second, I ran a CCA analysis using the understory vascular plant community data and only included the tree species' cohorts passively. In this analysis, I wanted first, to confirm independently any species-environment pattern found in the tree species' cohort analysis by testing the prediction that the same pattern of association would be found between the environmental data and the understory vascular species. Although it would be less likely that the older, larger tree cohort pattern of organisation over the environmental gradients would be followed by the understory species, it seemed reasonable to expect that cohorts that formed part of the understory plant community would be influenced by similar environmental factors. Thus, I hoped the analysis would provide not only confirmation of the tree species' environmental regeneration niche, but also identify an understory "regeneration community" associated with the tree species' younger individuals. To limit the effect of rare species, I excluded species in the analysis that were found in less than 10% of the plots.

The other objective in identifying plant species associated with any resulting conifer cohort pattern was to help identify "latent" environmental gradients associated with larch regeneration that were not specified by the predictor variables included in environmental ordination (Austin 1985). To examine this objectively, I classified the understory and cohort data using TWINSPAN (a hierarchical polythetic divisive classification program; Hill 1979) and then directly compared the classification divisions with the grouping of species in the CCA ordination. Goldsmith et al. (1986) provide a discussion on the merits of different classification methods. I limited the influence of the conifer cohorts in the TWINSPAN analysis by excluding them from forming indicator species in the program iteration. I also set the maximum number of divisions at three as an attempt to avoid spurious lower level groupings.

Finally, to explore more closely the regeneration niche of alpine larch and the spruce and fir, I used univariate multiple regression to model the occurrence of the individual seedling cohorts of each species as a function of the measured stand structural and site characteristics. This was to provide a more in-depth assessment of the relationships and possible interactions between these predictor habitat variables and the dependent seedling data. Where the response data were not normally distributed or easily transformed, a generalised linear modelling (GLM) approach was taken (Crosbie and Hinch 1985, Nichols 1989, Lindsey 1995, Mathsoft 1999).

I used a forward selection and residual examination procedure described by Nichols (1989) to select the most parsimonious set of predictor variables for each species regeneration niche model. I chose alpha = 0.05 as a criteria to reject terms for model inclusion. In these univariate analyses, I included the dummy variable for transect elevation as blocking factor before starting the variable selection process. I did this because I was interested in how stand structure alone influenced the given cohort response and had determined from the stand structure and multivariate results below that elevation strongly covaried with many of the structural predictor variables.

Prior to these analyses, I visually explored the data to determine if there were non-linear relationships between the response and predictor variables that may have been better described by polynomial or logarithmic transformations of the predictor. I also identified and confirmed the accuracy of any outlying observations in the dataset at this time. Correlation matrixes for all predictor variables are shown in Appendix V.

3.3 Results

3.3.1 Tree population and forest structure

3.3.1.1 Mature forest sites

The cohort size-frequency distributions and the associated age estimates at both Panorama and Temple indicated that each of the three tree species have experienced continuous recruitment at the upper and middle elevations since the stand replacing fire events in the 19th century (Figures 3.2-3.5). However, at the lower transect locations, the smallest alpine larch seedling cohort was not present. The shape of the cohort distribution for alpine larch at the Panorama middle and upper transects showed greater numbers of both sapling and subcanopy trees (Figure 3.2).

The age estimates for these cohorts suggest that this more productive period of recruitment took place across these parts of the stand approximately 50 to 100 years ago and then diminished (Figure 3.3). At the lower transect location, the intermediate larch size classes were reduced and no seedlings were present. In comparison, subalpine fir and, to a lesser extent, Engelmann spruce showed a dramatic increase in frequency between the largest and the smallest cohorts over all elevations (Figure 3.2). The fir seedling cohorts reached their maximum density at the lower Panorama transect elevation (78 560 stems/ha.). The spruce seedlings reached a maximum density at the middle transect location at that site (2 930 stems/ha.). These high seedling densities correspond to locally high basal area values for these tree species (Table 3.3).

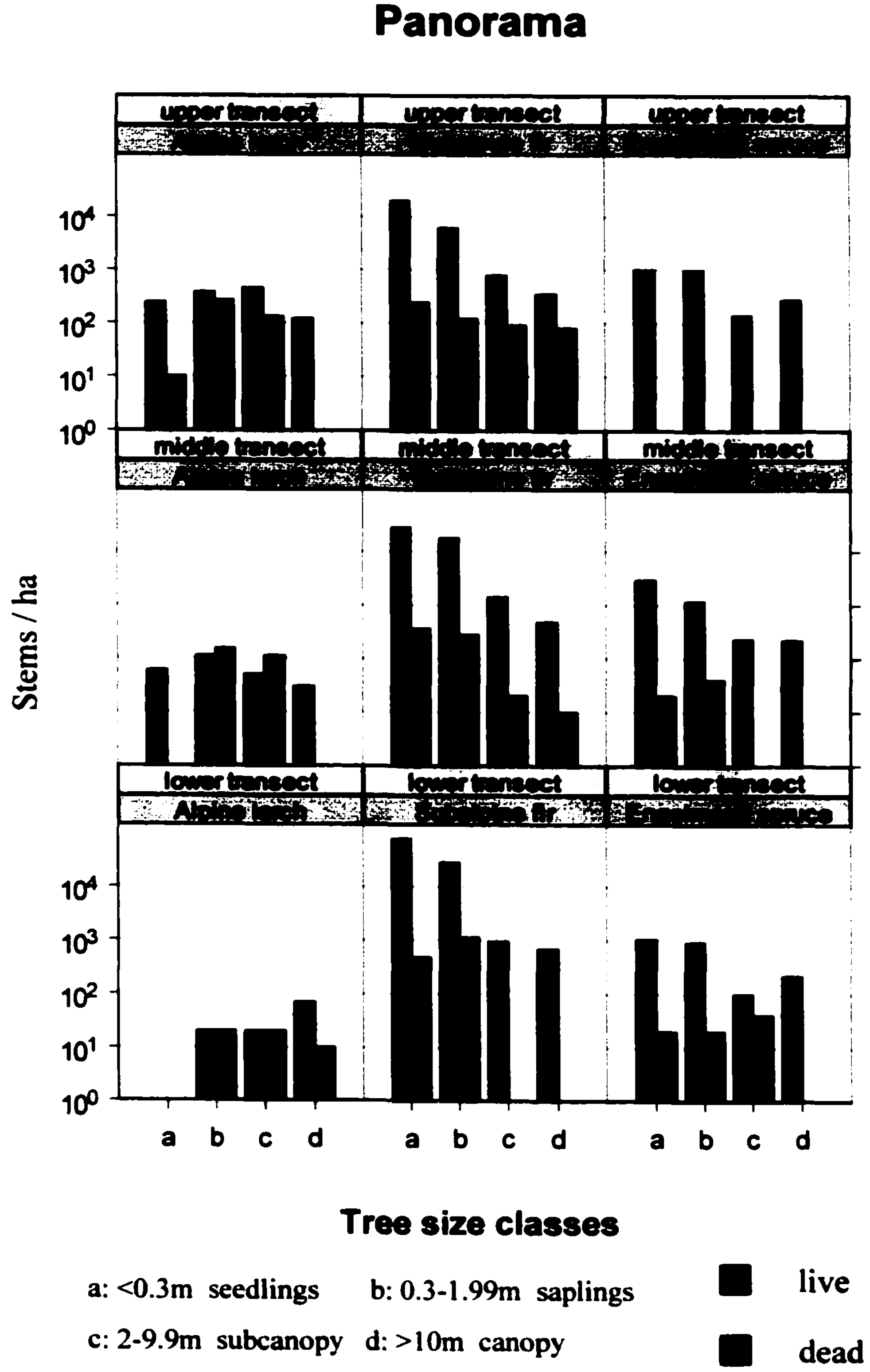


Figure 3.2: Tree species' cohort size-frequency distributions for live and standing dead stems at Panorama. Note the stems per hectare y-axis is a logarithmic scale.

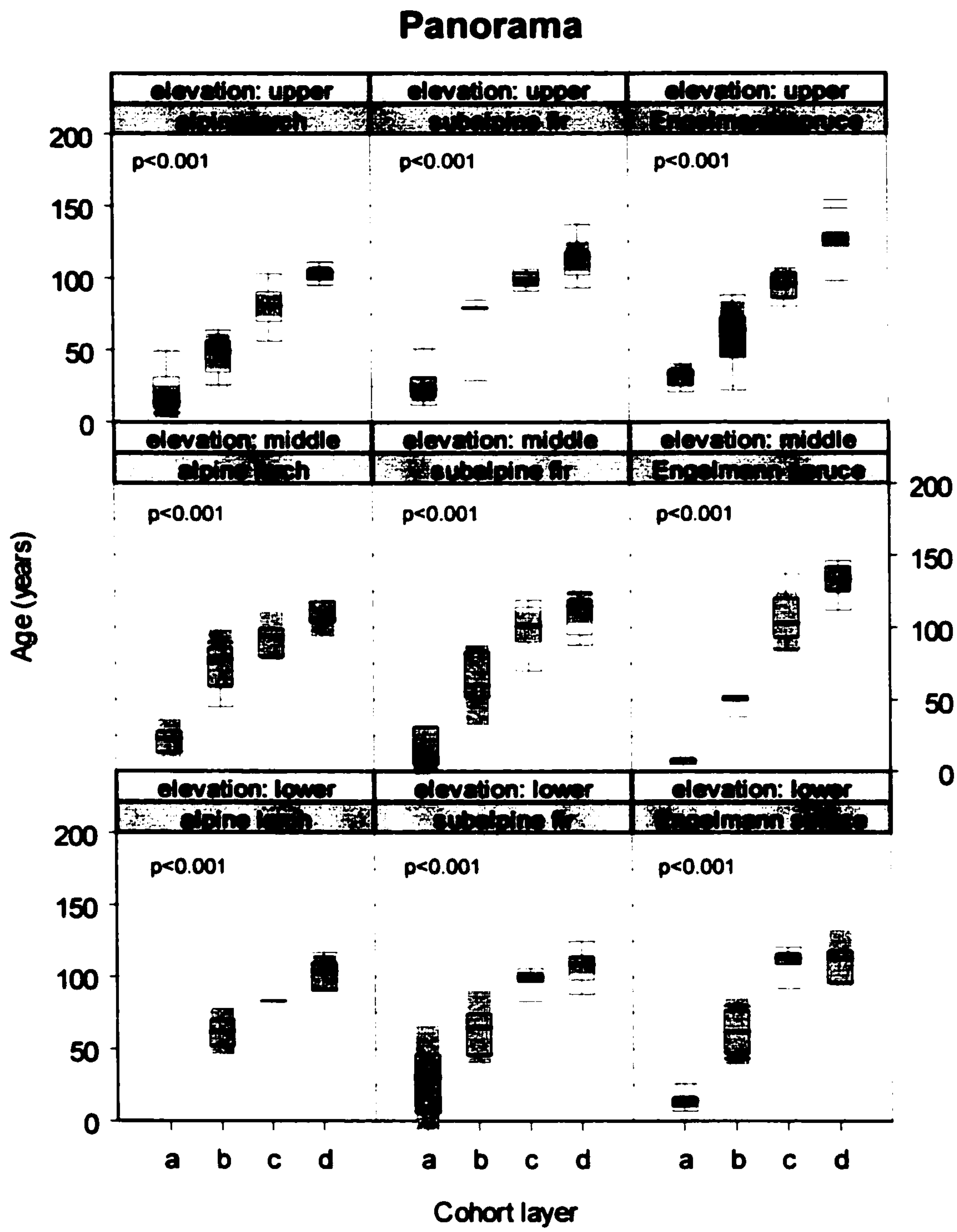


Figure 3.3: Cohort age estimates for Panorama (Fig. 3.2). The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. P-values indicate the outcome of one-way analysis of variance.

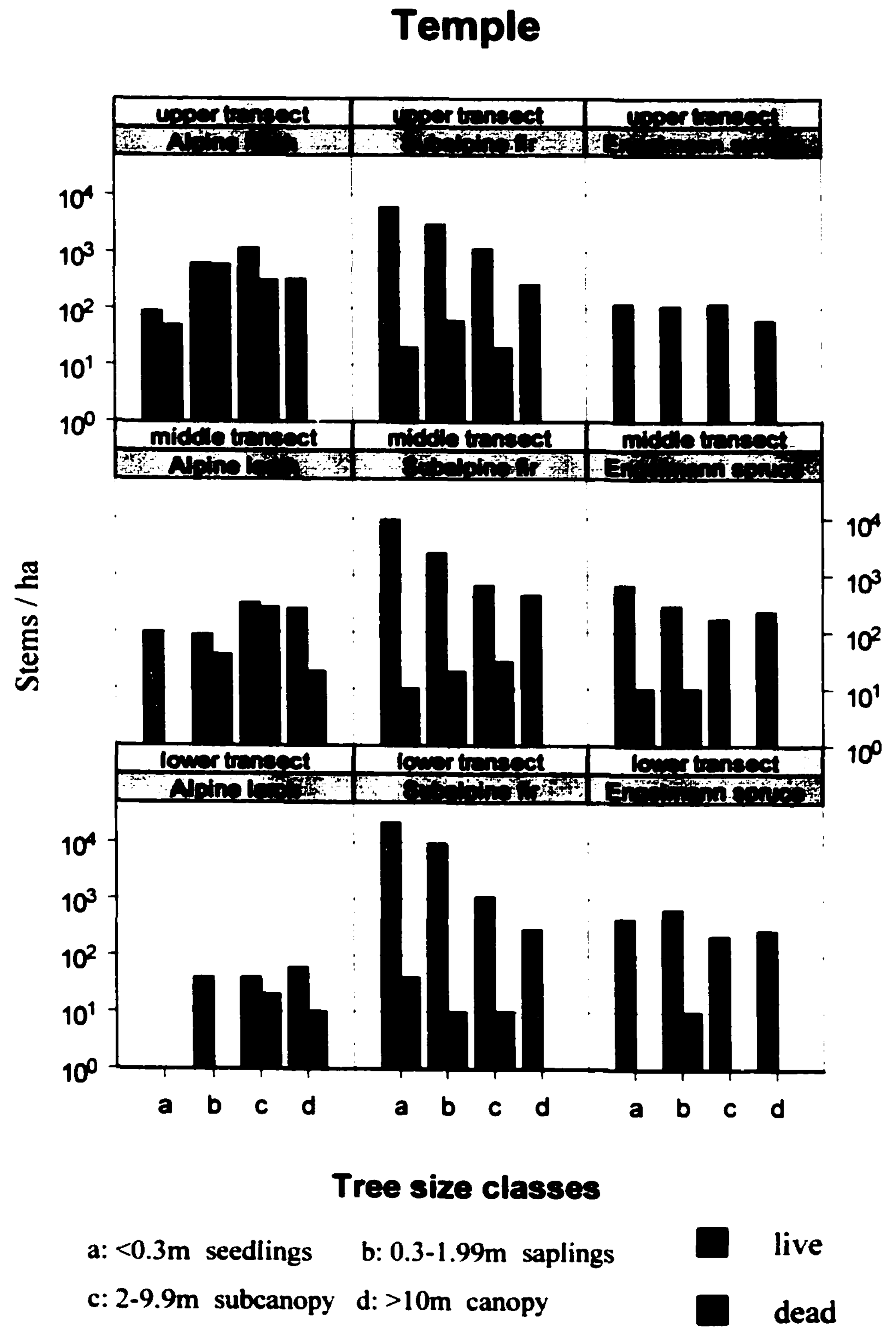


Figure 3.4: Tree species' cohort size-frequency distributions for live and standing dead stems at Temple. Note the stems per hectare y-axis is a logarithmic scale.

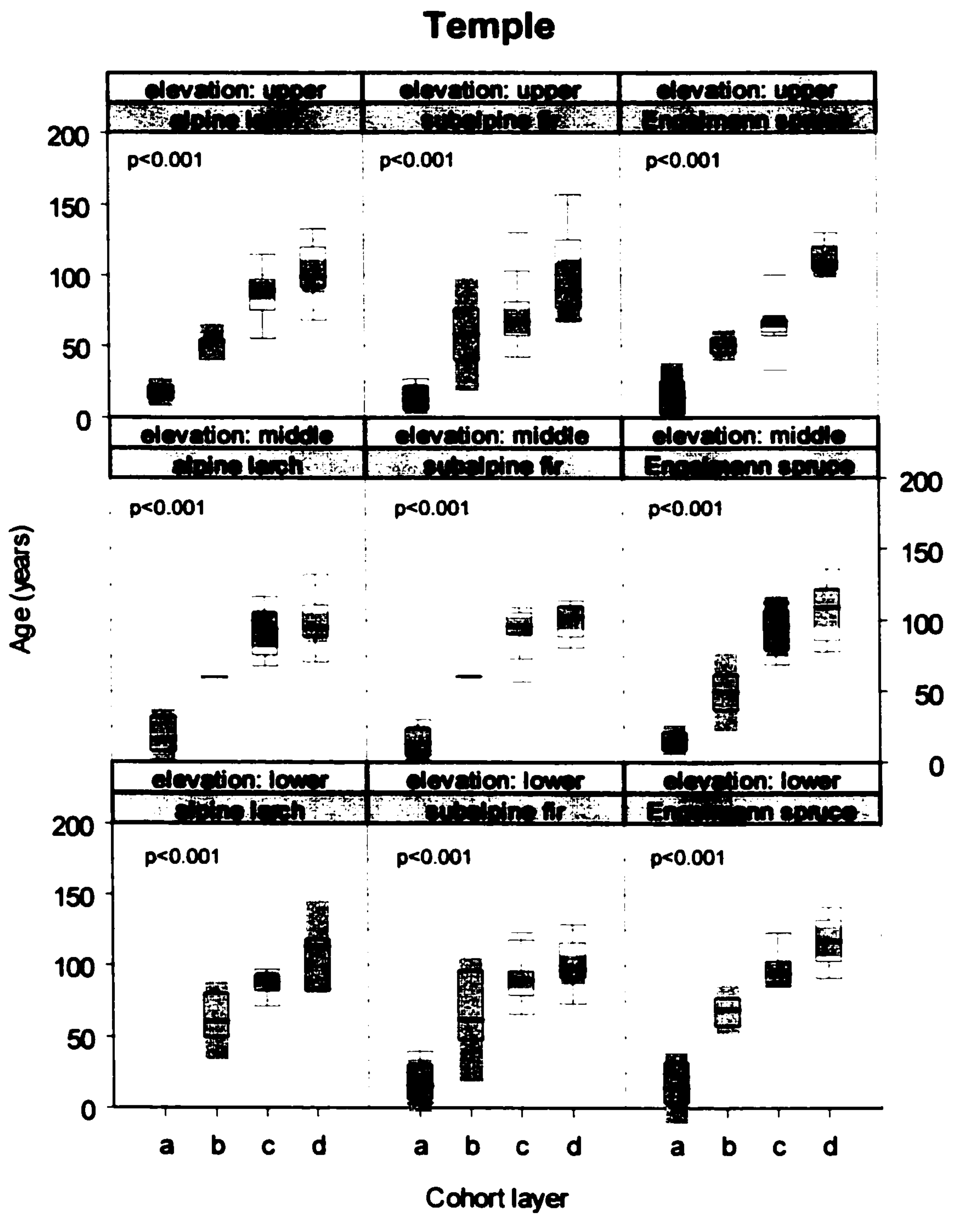


Figure 3.5: Cohort age estimates for Temple (Fig. 3.4). The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. P-values indicate the outcome of one-way analysis of variance.

Table 3.3: Live and dead basal area estimates for all tree species in each site.

Stand	transect	Live basal area (m^2/ha)						Dead basal area (m^2/ha)					
		La	Bl	Se	Pa	Pl	Total	La	Bl	Se	Pa	Pl	Total
Temple	upper	17.5	12.6	7.9	0.0	0.1	38.1	0.2	0.0	0.0	0.0	0.0	0.0
	middle	13.3	14.7	12.4	0.0	0.4	40.8	2.8	1.3	0.8	0.0	0.4	2.5
	lower	1.6	14.4	17.2	0.0	0.3	33.5	0.2	0.0	0.1	0.0	0.0	0.1
Panorama	upper	5.3	14.3	12.9	0.0	0.3	32.8	0.2	1.3	0.0	0.0	0.0	1.3
	middle	1.3	19.5	21.0	0.1	0.2	42.1	0.3	0.4	0.0	0.0	0.0	0.4
	lower	1.6	20.1	17.8	0.0	0.3	39.8	0.7	0.0	0.0	0.0	0.0	0.0
Arnica	upper	3.0	32.5	8.0	0.0	0.0	43.4	0.1	6.1	0.0	0.0	0.0	6.1
	middle	6.6	8.2	23.1	0.0	0.5	38.3	0.7	3.4	1.6	0.0	0.0	5.0
	lower	1.6	25.5	16.7	0.6	0.6	45.0	0.1	2.8	3.0	0.0	0.8	6.6
Red Earth	upper	10.3	12.0	16.6	0.0	0.0	38.9	3.1	4.4	0.4	0.0	0.0	4.8
	middle	6.3	22.1	21.4	0.0	0.0	49.8	0.6	5.7	2.3	0.0	0.0	8.0
	lower	0.8	25.1	19.6	0.0	0.0	45.5	0.3	6.3	2.5	0.0	0.0	8.8

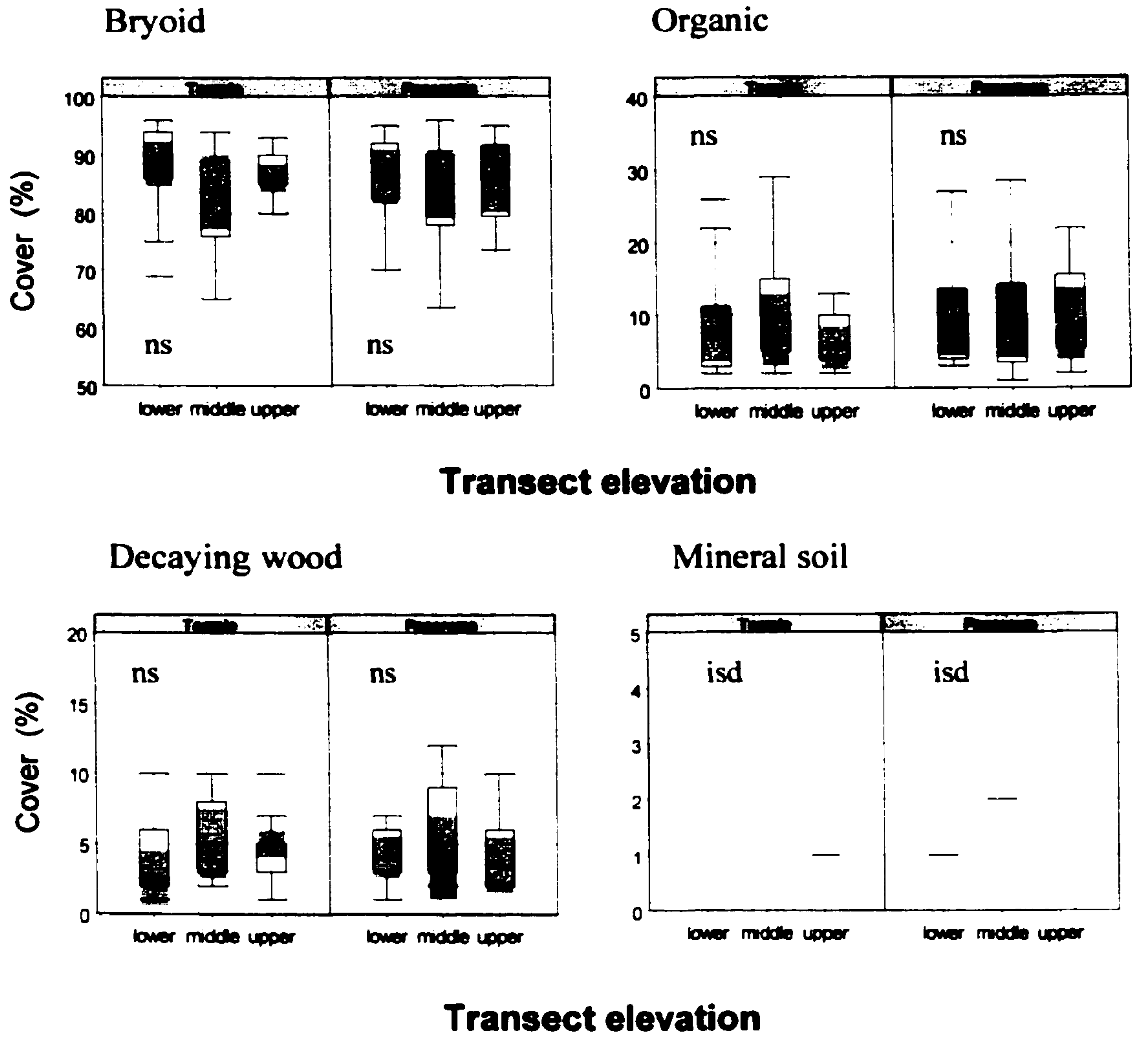
La: alpine larch; Bl: subalpine fir; Se: Engelmann spruce; Pa: whitebark pine; Pl: lodgepole pine.

The shapes of the recruitment distributions that occurred at the Temple site were similar, although the density of the species cohorts changed (Figure 3.4). There were greater densities of alpine larch in all of the cohort classes, except the seedlings, at the upper and middle areas of the stand, and an overall reduction in the numbers of fir and spruce seedlings compared to Panorama. This is also reflected in the basal area values, although oddly, there were fewer larch seedlings for a high larch basal area (Table 3.3). The increase in the larger larch cohort density was likely due the relatively close proximity and high density of veteran trees that were on the elevated adjacent mountain side and acted as a seed source above what would be expected from the adults found at the edge of the burn.

The dramatic differences in density of the seedling cohorts for the fir and spruce, compared to that of larch at these sites, may have been due to a difference in the availability of seed. The correlation of high seedling densities to locally high basal area estimates for the spruce and fir - but not the larch, may be a product of differences in species life history or predispersal predation (see Discussion). Another possibility was that the spruce and fir were much better at establishing on the available forest floor substrate that was present at these sites. However, this is unlikely considering that there were no significant differences between the levels of these at either site (Figure 3.6), yet there were large differences in densities of established seedlings.

The low numbers of canopy "d" class larch in the lower areas of both Panorama and Temple (70 stems/ha. and 60 stems/ha. respectively; Figures 3.2 and 3.4) also likely reflected the influence of available seed. Both lower transect locations were more than 200 m from an older forest edge that contained older seed trees. As indicated in Chapter 2, very few alpine larch seeds are likely to be dispersed greater than this distance in openings created by recent stand replacing fire.

The mortality patterns for the two maturing stands indicated a greater proportional loss of predominantly sapling and subcanopy larch cohorts compared to the spruce and fir (Figures 3.2 and 3.4). The subalpine fir cohort mortality appeared to be largely explained by the differences in the densities of the live cohorts at the two sites, although, the lower seedling mortality in the higher two transects at Temple indicated better survivorship at that site. The spruce cohorts experienced relatively little mortality except for the middle and lower elevations at Panorama, where attrition in the smaller cohorts may have been related to competition from the elevated numbers of fir. The spruce also experienced no canopy mortality at either site, while both the larch and fir canopy cohorts showed some thinning. Much of these mortality patterns for larch, and those patterns of the live larch cohort distributions at these sites, are correlated with the structural changes in the above-ground forest strata.



Bryoid

Organic

Decaying wood

Mineral soil

Figure 3.6: Forest floor constituents in the maturing forest. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. Single horizontal lines indicate one observation. P-values indicate the outcome of one-way analysis of variance between transect elevations. ns: not significant. isd: insufficient data for analysis.

In both of the maturing sites, shrub cover significantly increased between the upper and lower transect locations (Figure 3.7). Canopy cover also increased between the upper and lower elevations, but only significantly so at Panorama (Figure 3.7). Also, the height of the canopy tree layer increased significantly between the upper and lower elevations at both sites (Figure 3.8). Looking at the average heights of the individual tree species for these different elevations shows that both the spruce and the fir overtopped the mature larch at lower elevation (Table 3.4). As all of the tree species' canopy cohorts at lower elevation were roughly the same age, the mortality experienced by the mature larch, of which there was no obvious pathogen, was due most likely to competition.

Table 3.4: Average canopy class (d) tree height at the maturing sites.

Site	Transect elevation	alpine larch	subalpine fir	Engelmann spruce
			height (m)	
Temple	lower	13.8	14.8	17.6
	middle	11.9	12.9	13.9
	upper	11.6	11.1	11.8
Panorama	lower	12.5	14.6	15.3
	middle	11	13.5	14.4
	upper	11.5	12	13.1

3.3.1.2 Old forest sites

The frequency distribution patterns of the alpine larch cohorts at both of the old forest sites were different to that of the maturing forest. At Arnica, there were no seedlings or saplings at the lower transect location (Figure 3.9). There were also greater numbers of trees in the smaller larch seedling and sapling classes compared to the larger tree cohorts in the middle and upper transect locations. Red Earth differed in several ways. At this site, there were no live larch of any size at the lower transect location, and like Arnica, there were greater stem numbers in the seedling and sapling cohorts compared to the larger trees at the upper transect (Figure 3.10). However, there were declining stem numbers in the seedling and saplings at the middle elevation. For the other conifers, the changes between the forest stages were less pronounced.

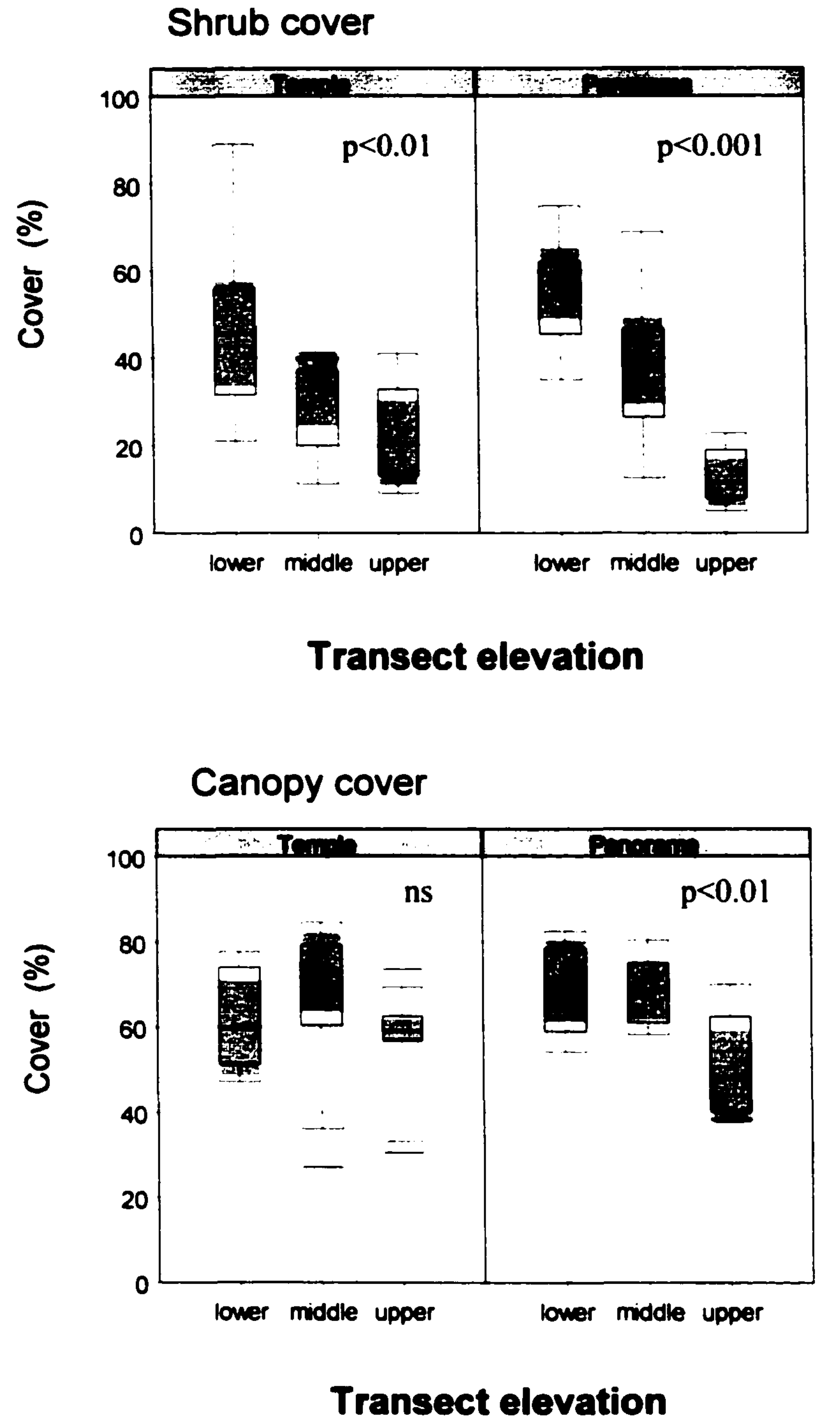


Figure 3.7: Shrub and canopy cover differences between transect locations in maturing forest. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. Single horizontal lines indicate one observation. P-values indicate the outcome of one-way analysis of variance.

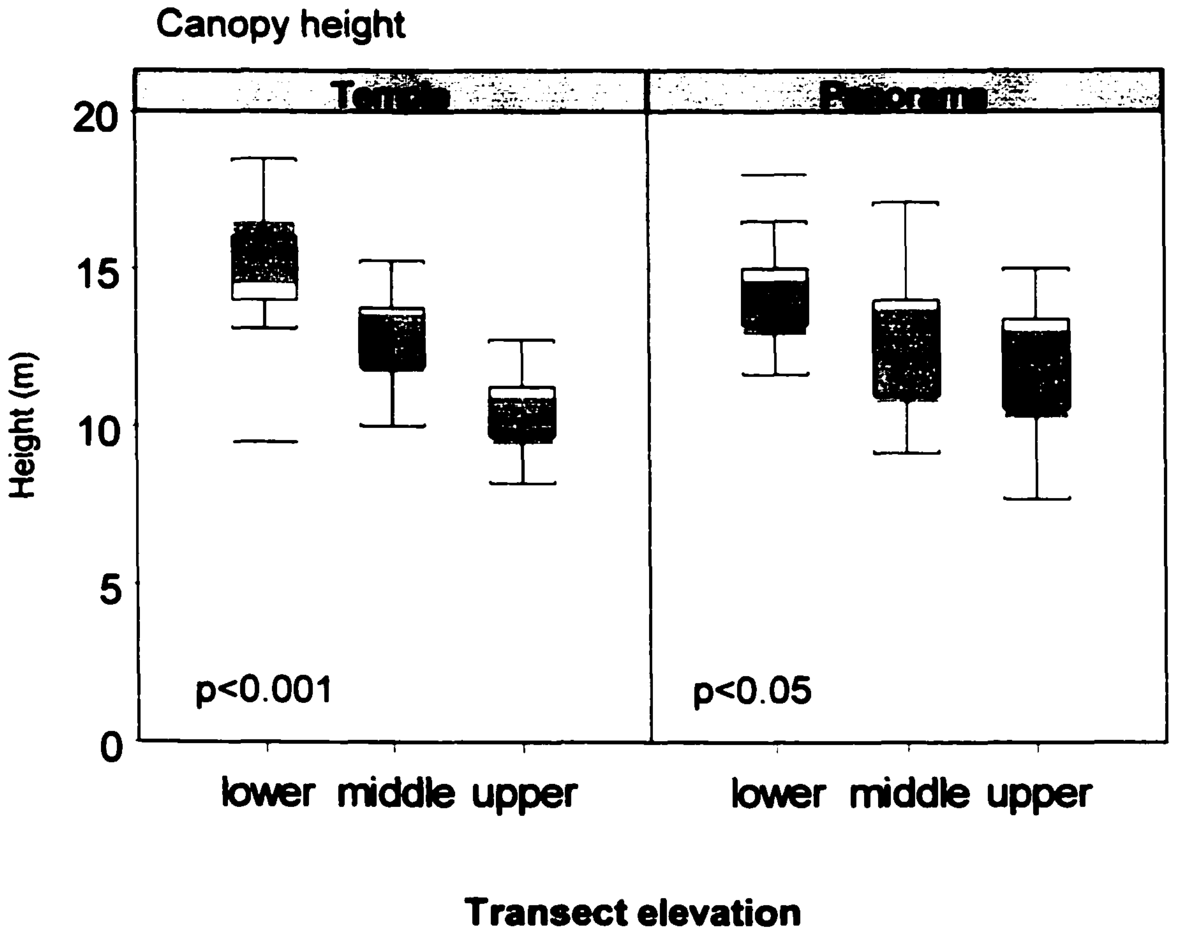


Figure 3.8: Canopy height differences between transect locations in maturing forest. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. Single horizontal lines indicate one observation. P-values indicate the outcome of one-way analysis of variance.

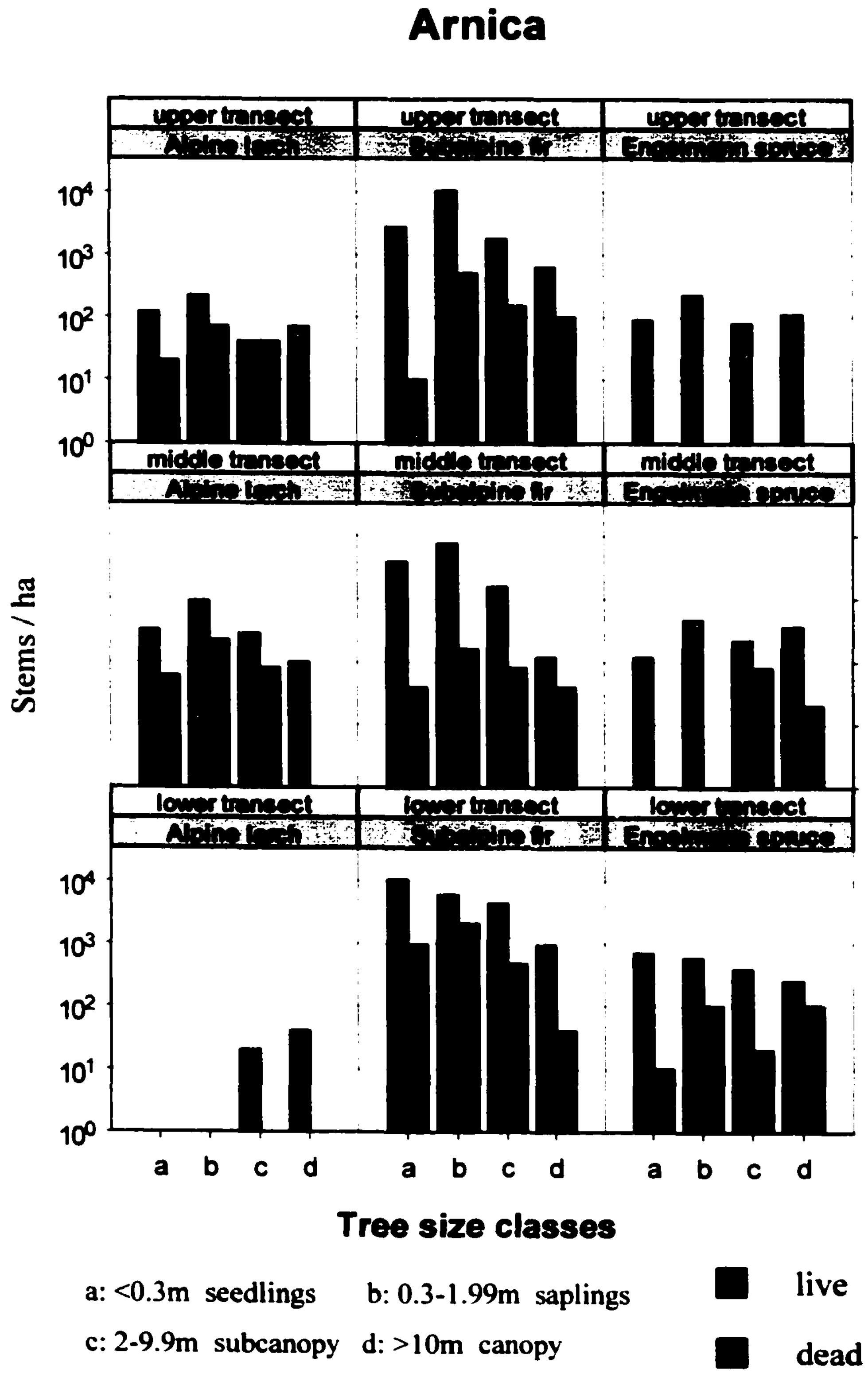


Figure 3.9: Tree species' cohort size-frequency distributions for live and standing dead stems at Arnica. Note the stems per hectare y-axis is a logarithmic scale.

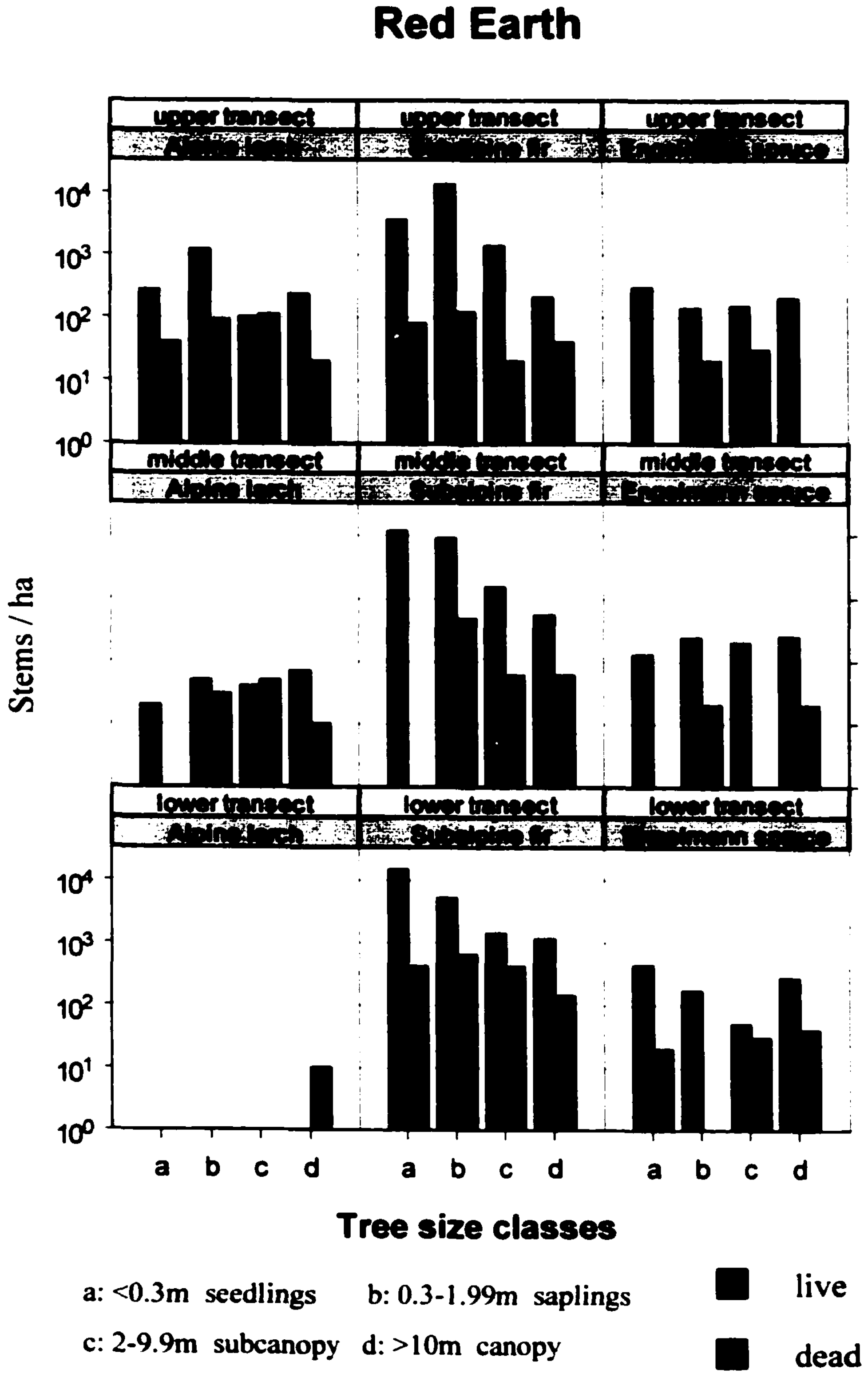


Figure 3.10: Tree species' cohort size-frequency distributions for live and standing dead stems at Red Earth. Note the stems per hectare y-axis is a logarithmic scale.

There were slightly fewer subalpine fir seedlings in both the middle and upper elevations at Arnica compared to similar elevations in the maturing forest (Figure 3.9), but this only occurred at the upper transect at Red Earth (Figure 3.10). Engelmann spruce similarly showed a decrease in the numbers of individuals in the smaller cohort sizes in the higher elevations at Arnica, and at the middle elevation at Red Earth.

The cohort mortality patterns were also somewhat different between forest stages. Larch mortality changed the least of the tree species with proportionally fewer standing dead saplings in the middle and upper transect elevations in the older sites (Figure 3.9 and 3.10). Subalpine fir mortality was generally greater in all of the cohorts at the lower transects. There was also consistent mortality of fir canopy class individuals in all locations. The spruce mortality was still relatively sporadic, although there were some dead standing canopy cohorts found in the middle and lower transect elevations at both Arnica and Red Earth. The exception was the lower transect at Arnica where there was spruce mortality in every cohort size (Figure 3.9).

Comparing the present vertical strata cover values of the different transect locations at the old forest sites provided some insight into the larch cohort frequency patterns. The shrub and canopy cover at both of the older sites was significantly greater at the lower elevation compared to the upper elevation (Figure 3.11). The canopy cover values at the lower transect elevations were considerably greater than those measured in the maturing stands (Figure 3.7), and, in combination with the greater old forest shrub cover values, correlated well with the diminished presence of larch in the old forest low elevations described above. Also, the combination of relatively dense shrub and canopy cover in the middle transect at Red Earth might help explain the reduced number of larch in the seedling and sapling cohort classes found at that site. Conversely, both the shrub and canopy cover values at the Arnica middle transect were not significantly different from those of the upper elevation (Figure 3.11). This helps explain the greater numbers of smaller cohorts at this elevation compared to the similar transect at Red Earth. The average canopy heights also aided in interpreting the changes in the larch cohort frequencies.

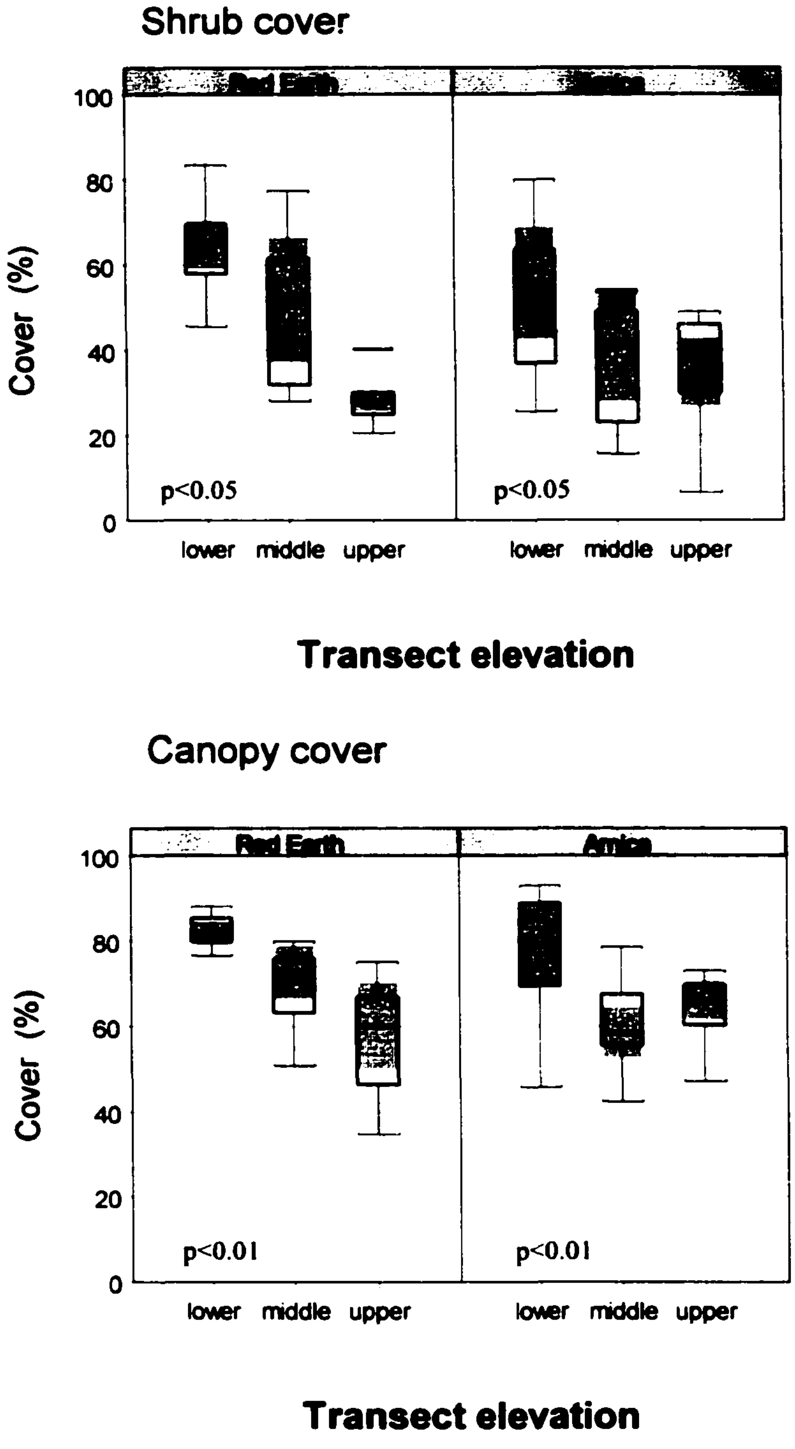


Figure 3.11: Shrub and canopy cover differences between elevations at the old forest sites. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. Single horizontal lines indicate one observation. P-values indicate the outcome of one-way analysis of variance.

At Red Earth, the average canopy height was significantly greater at the lower elevation compared to the upper and middle transect elevations (Figure 3.12). The average species' heights of the canopy cohort at this site indicated that the larch might have been completely out-competed by spruce and fir at the lower elevation (Table 3.5). At Arnica, the canopy height at the middle transect was significantly less than both the lower and upper transect canopy heights (Figure 3.12). Correlated with this shorter canopy height were the greatest numbers of canopy and subcanopy larch found at this site. The individual species' height differences at Arnica in the lower transect, where some larger larch individuals remained, were comparable to those in the maturing stands where there were also canopy "d" class larch present (compare Table 3.4 and 3.5).

Table 3.5: Average canopy class (d) tree height at the old sites.

Site	Transect elevation	alpine larch	subalpine fir height (m)	Engelmann spruce
Red Earth	lower	11.5 (dead)	15.6	21.5
	middle	17.1	13.8	17.9
	upper	12.5	12.4	15
Arnica	lower	14.5	13.7	16.1
	middle	14.2	15	13.1
	upper	15.3	13.8	15.5

The age data for the larch cohorts provided some useful chronology of the recruitment of the species in these older sites. The absence of the smaller larch seedling and sapling cohorts from the lower transect at Arnica indicated that the conditions for larch recruitment in that area had not been suitable for approximately 240 years, the age of the youngest larch aged at that site (Figure 3.13). Similarly, the dead canopy individuals present in the lower transect at Red Earth indicated that conditions at that site had not been suitable for at least the same length of time, given the average age (256 years) of the canopy cohort from the middle transect location (Figure 3.14). Heart rot prevented ageing the dead individuals at the lower transect.

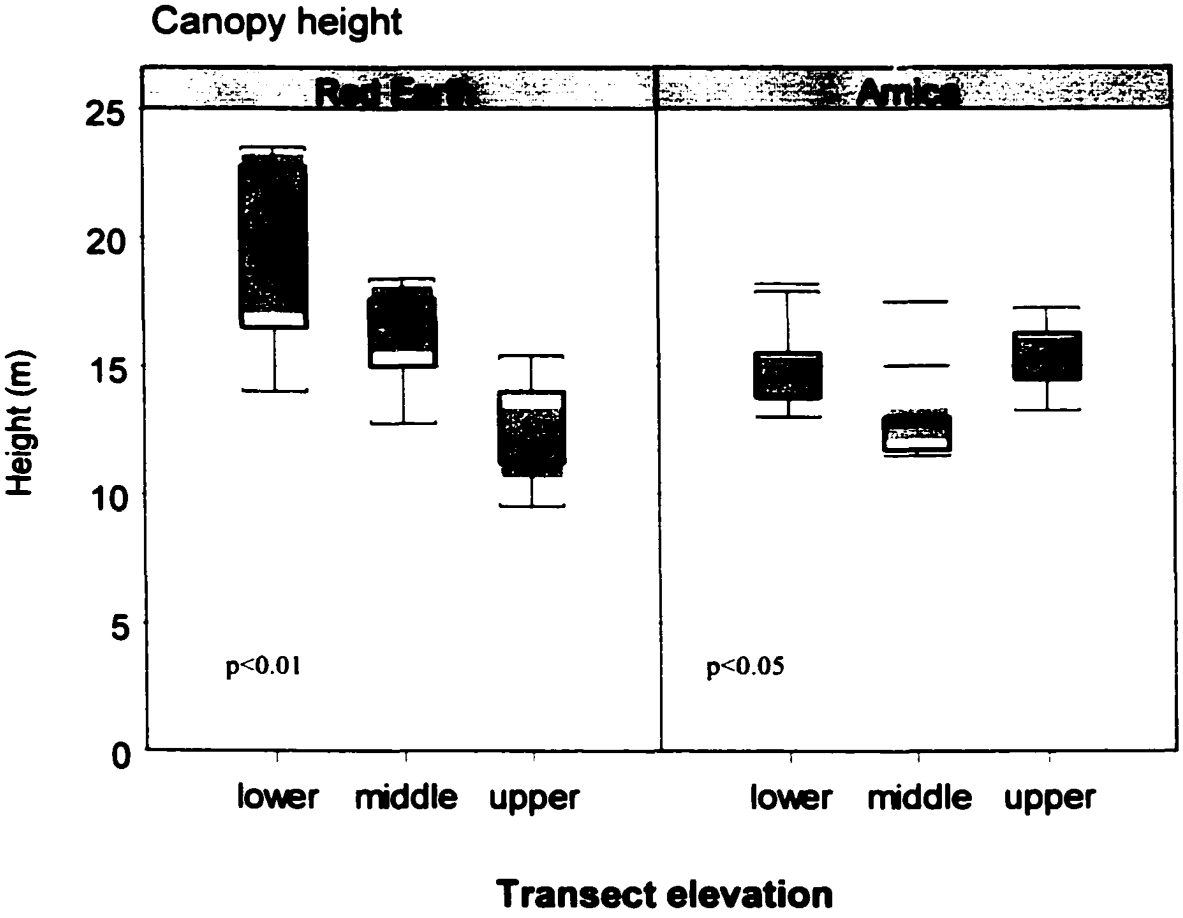


Figure 3.12: Canopy height differences between elevations in old forest. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. Single horizontal lines indicate one observation. P-values indicate the outcome of one-way analysis of variance.

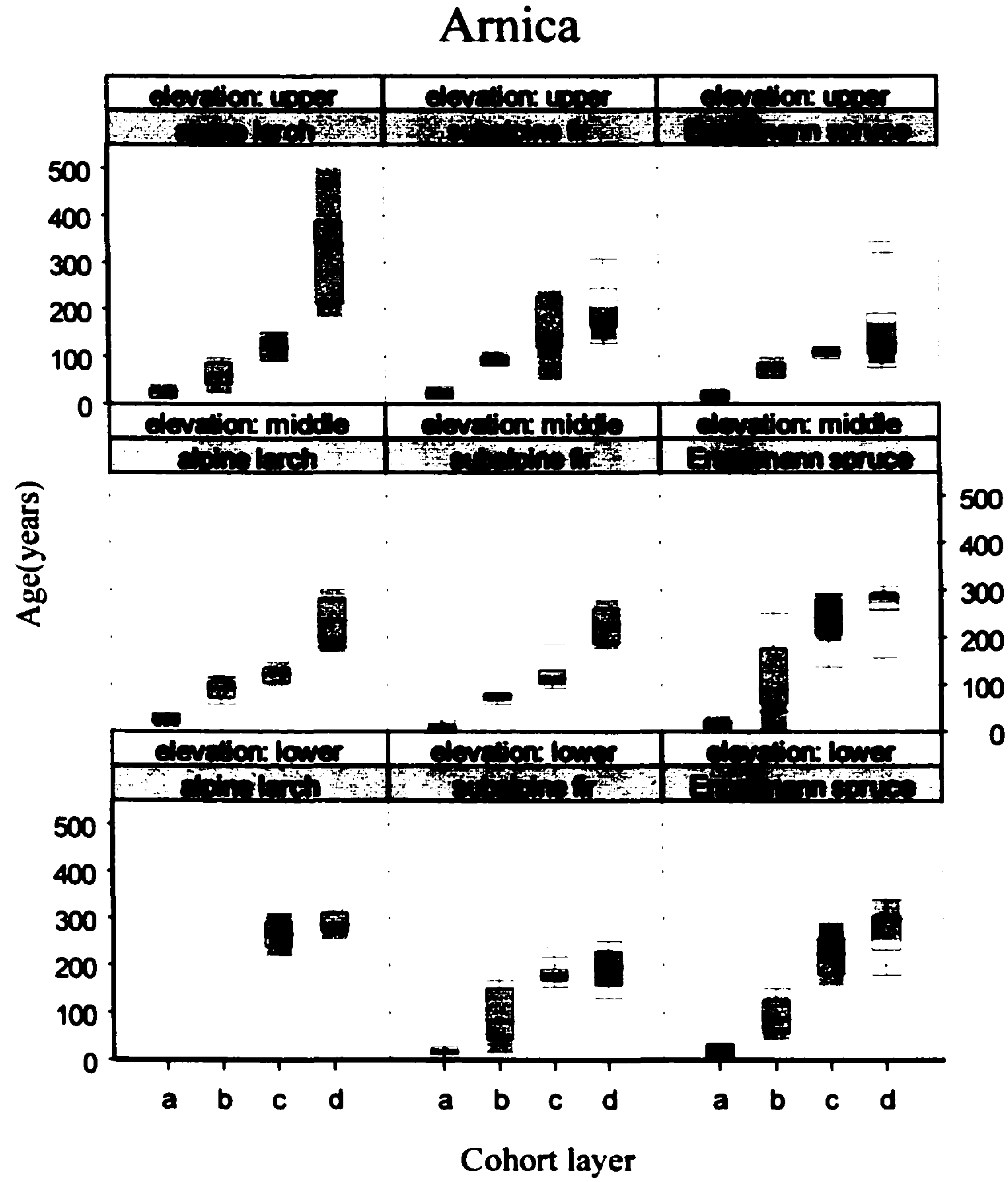


Figure 3.13: Cohort age estimates for Arnica. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. Single horizontal lines indicate one observation. P-values indicate the outcome of one-way analysis of variance.

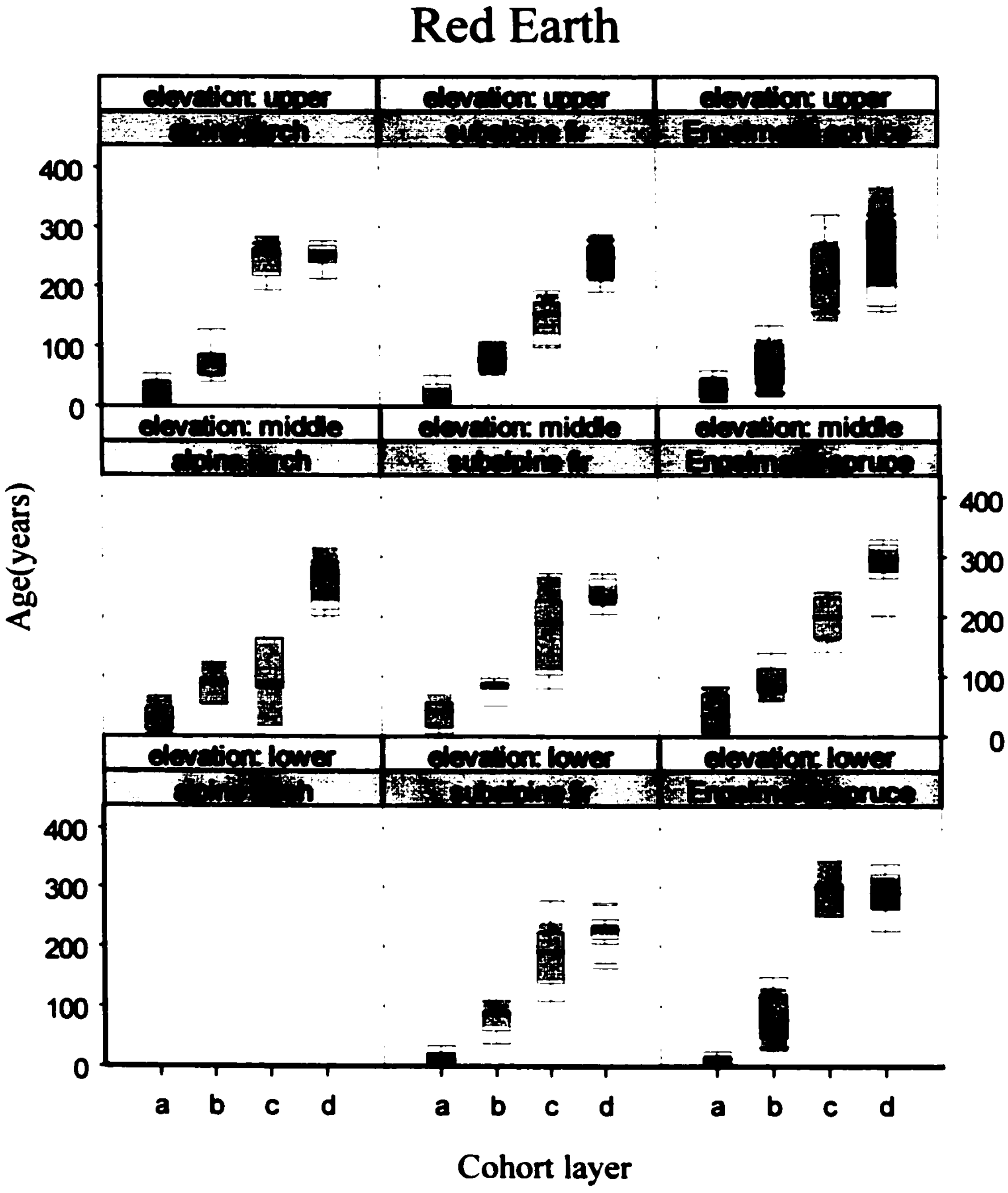


Figure 3.14: Cohort age estimates for Red Earth. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. Single horizontal lines indicate one observation. P-values indicate the outcome of one-way analysis of variance.

There were also some large gaps between the age distributions of the living cohorts of predominantly the larch and spruce at both sites (Figure 3.13). In Arnica, these differences indicate that recruitment may have diminished, or ceased after the first 150 to 200 years, and then reinitiated roughly 50 years later. A similar pattern occurred at Red Earth, except the length of regeneration delay was more variable (Figure 3.14). However, caution is needed in evaluating these patterns. A major problem with the age data was the low numbers of ages that were obtained due to the poor quality of the heart wood in the majority of the older trees encountered.

3.3.2 Determination of forest structural niche.

3.3.2.1 Multivariate analyses.

The ordination of only the conifer cohorts supports many of the structure – cohort correlations noted above. All of the larch cohort classes are separated along the first axis of the biplot from those of the relatively undifferentiated spruce and fir near the origin (Figure 3.15). The larch seedling and sapling cohorts were the furthest out and were most strongly separated by a negative correlation with canopy cover, and to a lesser extent by shrub cover. These two cohorts were also strongly correlated with higher elevation. All of the larch cohorts were equally associated with areas of lower average canopy height. This primary axis explained 19% of the variation in the pseudo-species data. The low eigenvalue of 0.8 is likely a reflection of both the poor separation of the spruce and fir cohorts over the measured descriptor variables and the overall small number of "species" in the analysis. The weak separation of the cohorts over axis 2 explains only an extra 2 % of the variation in the data (eigenvalue = 0.01), but confirms that more small larch were found in the older forest stands.

The separation of alpine larch cohorts from those of the Engelmann spruce and subalpine fir was also a feature in the ordination of the understory vascular vegetation data (Figure 3.16). Here, the passive conifer cohorts were arranged in a similar pattern. The species most closely associated with the larch cohorts were spread out to the right, along axis 1 of the biplot (eigenvalue = 0.22). The constrained environmental axes and centroids most correlated with this pattern were higher elevation, greater basal area of alpine larch and

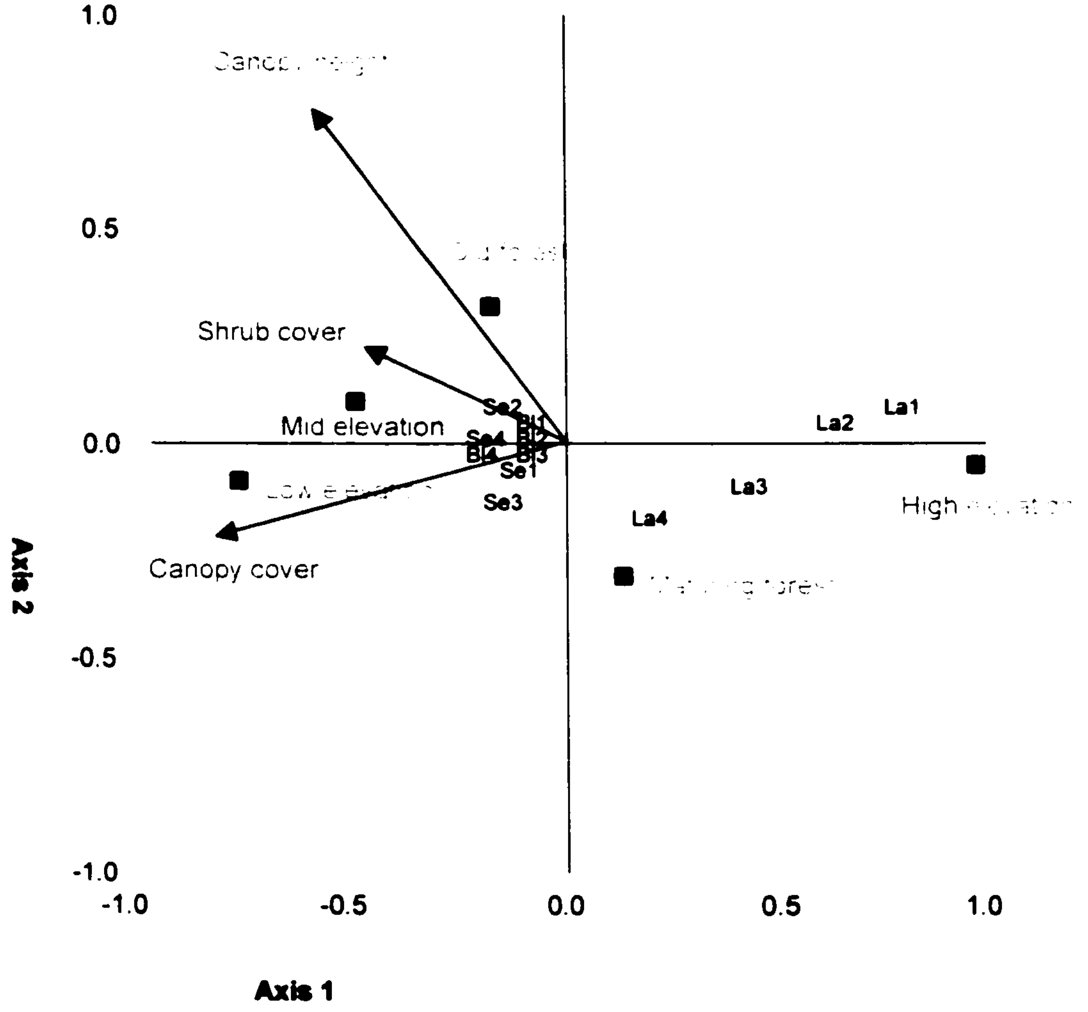


Figure 3.15: CCA biplot of the conifer cohort psuedo-species showing the separation of larch cohorts from those of the spruce and fir. La1-La4 are the seedling to canopy alpine larch cohorts. Bl1-Bl4 are the subalpine fir. Se1-Se4 are the Engelmann spruce. The arrows indicate the direction of the continuous environmental axes. The gray squares represent the discrete centroids.

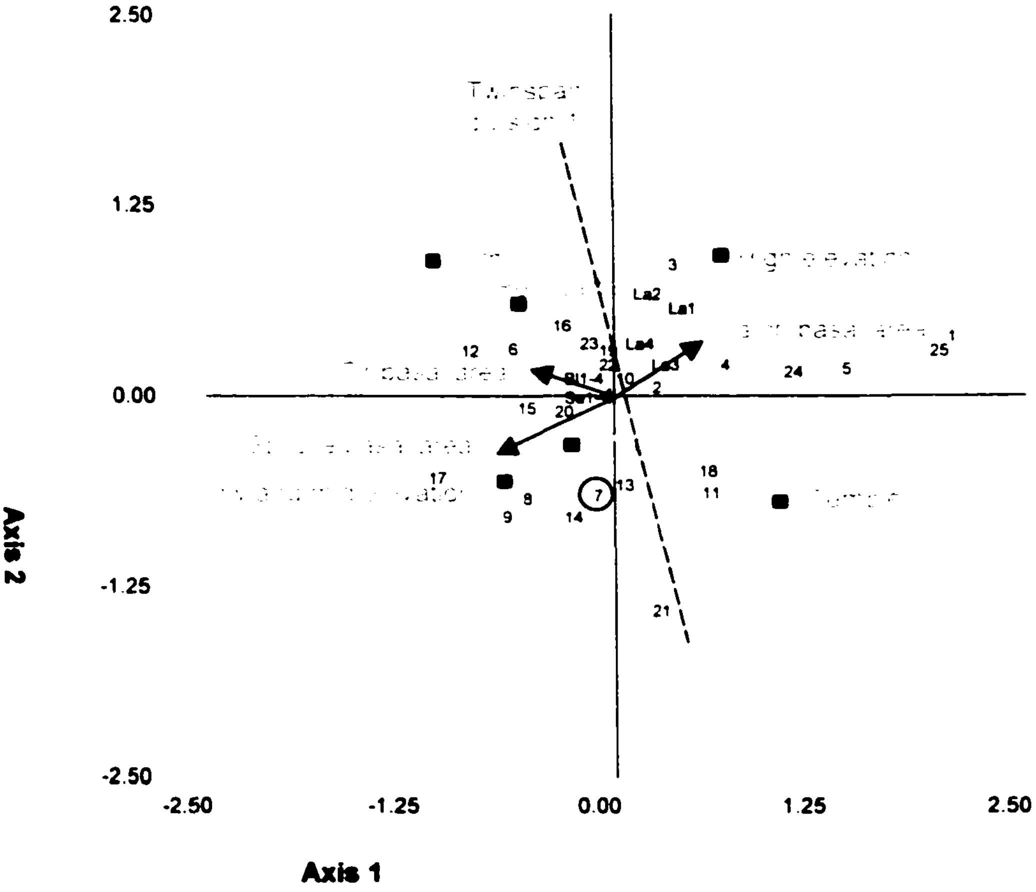
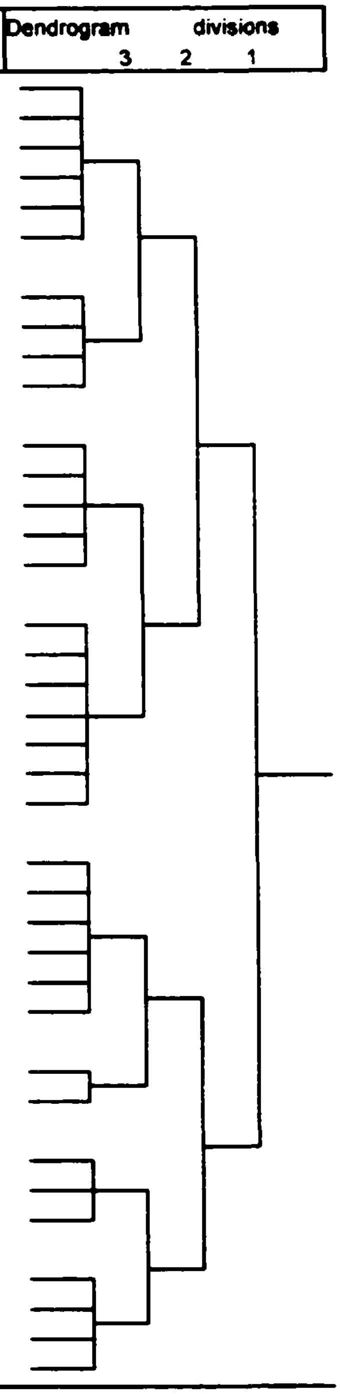


Figure 3.16: CCA biplot of passive tree cohorts derived from the ordination of the vascular vegetation showing the separate larch cohort group from the other conifers. The environmental predictors explain 14% of the variation in the species data. The numbered species are identified in Table 3.4. Circles surrounding species' numbers indicate a misclassification by the TWINSPAN analysis. The dashed line through the ordination represents the best fit (i.e., the least misclassification of species) for the primary TWINSPAN division from Table 3.4. La1-La4 are the seedling to canopy alpine larch cohorts. Bl1-Bl4 are the subalpine fir. Se1-Se4 are the Engelmann spruce. The arrows indicate the direction of the continuous environmental axes. The gray squares represent the discrete elevation or site centroids.

Table 3.6: Classification of understory vascular plants and conifer cohorts for all sites and elevations. The dendogram to the right shows the species groupings based on the TWINSPAN results where only three division levels were specified (the first division is the most important). Highlighted species are found in all sites.

Species number	Species name	Average site importance scores			
		Arnica	Red Earth	Temple	Panorama
8	*Erigeron peregrinus*	0.07	0.00	0.00	1.07
9	*Goodyera oblongifolia*	0.00	0.03	0.00	0.30
12	***Ledum groenlandicum***	**2.00**	**0.27**	**0.20**	**0.07**
15	***Menziesia ferruginea***	**3.40**	**2.40**	**1.63**	**1.03**
16	*Orthilia secunda*	0.80	0.03	0.07	0.37
17	*Parnassia fimbriata*	0.40	0.00	0.00	0.03
6	*Empetrum nigrum*	2.73	0.20	0.00	1.93
13	***Listera cordata***	**0.33**	**0.23**	**0.70**	**0.03**
14	*Lycopodium annotinum*	0.00	0.37	0.67	1.13
21	*Sorbus sitchensis*	0.00	0.00	0.50	0.13
20	***Rhododendron albiflorum***	**2.37**	**4.47**	**4.17**	**2.60**
	Bl4				
	Se2				
	Se3				
	Se4				
19	***Phyllodoce empetriformis***	**4.07**	**5.03**	**7.53**	**5.73**
22	***Vaccinium membranaceum***	**6.33**	**4.83**	**8.03**	**8.43**
23	***Vaccinium scoparium***	**7.57**	**9.00**	**6.43**	**9.60**
	Bl1				
	Bl2				
	Bl3				
	Se1				
3	*Luzula piperi*	0.00	0.03	0.00	0.00
4	***Cassiope mertensiana***	**0.90**	**0.33**	**2.23**	**1.20**
10	***Hieracium gracile***	**0.07**	**0.03**	**0.07**	**0.80**
	La1				
	La2				
	La3				
2	***Arnica cordifolia***	**2.17**	**0.97**	**6.97**	**4.90**
	La4				
7	*Epilobium angustifolium*	0.33	0.00	0.57	0.23
11	*Juniperus communis*	0.00	0.00	0.10	0.40
18	***Pedicularis bracteosa***	**0.40**	**0.03**	**2.97**	**0.40**
1	*Antennaria lanata*	0.00	0.00	0.43	0.00
5	*Castilleja raupii*	0.03	0.00	0.47	0.00
24	*Vahlodea atropurpurea*	0.00	0.10	0.00	0.27
25	*Viola orbiculata*	0.00	0.00	0.80	0.00



the decreasing basal area of Engelmann spruce and subalpine fir. The primary division of the understory species and the conifer cohorts in the independent TWINSPAN classification (Table 3.6) corresponds very well with the species and tree cohort separation over those environmental gradients associated with axis 1 in the understory species biplot. The only misclassification was *Epilobium angustifolium* (sp. number 7), which was found to the left of the division line (Figure 3.16). However, the second and third dendrogram group division appeared to provide little extra useful information, and have been omitted from the biplot.

The maturing site of Temple was also influential in the axis 1 species separation (Figure 3.16). However, this appeared largely due to the occurrence of *Viola orbiculata*, *Castilleja raupii*, and *Antennaria lanata* that were found only at that site (Table 3.6). A more robust representation of the understory community patterns associated with axis 1 was found by focusing attention on the species that occurred in all of the sites (highlighted in Table 3.6). The higher elevations, where all ages of alpine larch were found, were characterised by a moist heath association (*Cassiope mertensiana*, *Pedicularis bracteosa*, *Hieracium gracile*, *and Arnica cordifolia*). Whereas, the lower elevations, where greatest densities of canopy spruce and fir were found, were characterised by a taller shrub community dominated by *Menziesia ferruginea*, *Rhododendron albiflorum*, and *Ledum groenlandicum*.

There was also a group of transition species that were associated with most of the smaller cohorts of the spruce and fir (*Phyllodoce empetriformis*, *Vaccinium membranaceum*, and *V. scoparium*; Table 3.6). These were species that were found in relatively high density across all of the sites and elevations. This is indicated in Figure 3.16 by the close proximity of these species to the origin of the biplot.

Elevation was still the most important variable explaining variation in the pattern over the weaker axis 2 of the biplot (eigenvalue = 0.1). However, this axis highlights the separation of the maturing and older sites, compared to the individual site differences (Figure 3.16). The only clear qualitative species differences between the old and maturing sites were the presence of *Juniperus communis* and *Sorbus sitchensis* in both of the maturing sites (Table 3.6). However, there were also unambiguous quantitative differences between the forest stages. Greater abundance of *M. ferruginea* and *L. groenlandicum* occurred in each of the old sites. Similarly, greater abundance of *V. membranaceum, Lycopodium annotinum, Phyllodoce empetriformis, C. mertensiana* and *Arnica cordifolia* were found in both of the maturing sites compared to the old.

3.3.2.2 Univariate seedling modelling.

The conifer seedling univariate analysis provided more detailed information on the kinds of stand conditions that were necessary for each species' seedling recruitment.

3.3.2.2.1 Alpine larch

The best alpine larch seedling niche model included 5 terms aside from elevation, and one interaction (Table 3.7). As the counts of larch seedlings over the whole data set contained many zeros and low numbers, the data were not easily transformed to conform to a normal distribution. I therefore generalised the linear model using a log link function and specified a Poisson error distribution. Because the fitted model dispersion parameter was slightly under-dispersed (0.8 compared to 1.0) and some irregularities were present in the residuals, I also checked the final model terms' significance using the less restrictive quasi-likelihood estimation (Mathsoft 1999). The full model (including elevation) explained 72% of the null model deviance; whereas, the structural model (excluding elevation) explained just over half (53%) of the partial model deviance.

Table 3.7: Alpine larch seedling niche model.

Model term	df	Deviance explained	Residual df	Residual deviance	p-value (Chi^2)
Null model			119	318.65	
Transect elevation	2	125.33	117	193.32	0.00
Subalpine fir basal area	1	62.81	116	130.50	0.00
Canopy cover	1	10.04	115	120.46	0.00
Canopy height	1	15.50	114	104.96	0.00
Forest stage	1	7.24	113	97.72	0.00
Shrub cover	1	3.77	112	93.95	0.03
Forest stage by canopy cover	1	3.82	111	90.13	0.03

The elevation variable that I fit first to partial out the effects of this complex gradient was highly significant and explained over a third of the variance in the model. Figure 3.17a clearly shows this pattern previously observed in cohort frequency distributions, where no seedlings were found in the lower elevation transects. This Figure also illustrates the significant larch seedling-forest stage relationship, the fourth term in the model, showing greater overall numbers of seedlings in the older forest sites. However, subalpine fir basal area was the most important explanatory variable in the model with the effect of elevation removed. Seedling recruitment was greatly curtailed in areas with greater than 20 m^2 per hectare of live subalpine fir (Figure 3.17b).

It would also appear that this negative correlation was not due to competition for light. This was evident (1) due to the fact that subalpine fir basal area was poorly correlated with canopy cover ($r = 0.47$) relative to the total basal area-canopy cover correlation ($r = 0.60$), and (2) because canopy cover was also a significant variable in the model (Table 3.7). The negative influence of canopy cover on seedling recruitment is clearly shown in Figure 3.18a, where few seedlings appear in regions above 70% cover. The height of the local canopy surrounding each plot accounted for the second greatest reduction in deviance from the partial model (i.e., after fitting elevation). However, this term was significant in the model only following the fitting of the previous predictors. The plot of seedlings against canopy height (Figure 3.18b) shows that there was only an obvious continuous reduction in seedlings at Red Earth where there was the greatest range of canopy heights. However, local canopy height may act as more of an abrupt limit, as larch seedlings were not found in any plot with a canopy height greater than 17.5 m.

Shrub cover explained the least deviance in the data (Table 3.7), yet Figure 3.19a shows that no seedlings were present at cover values greater than 50%. The final larch seedling model term was the interaction between canopy and forest stage (Table 3.7). The interaction between these terms is shown in Figure 3.19b (and also apparent in Figure 3.18a) where the slope of the fitted smoother indicates that for any given percent canopy cover, more larch seedlings can be expected in older forest compared to younger forest.

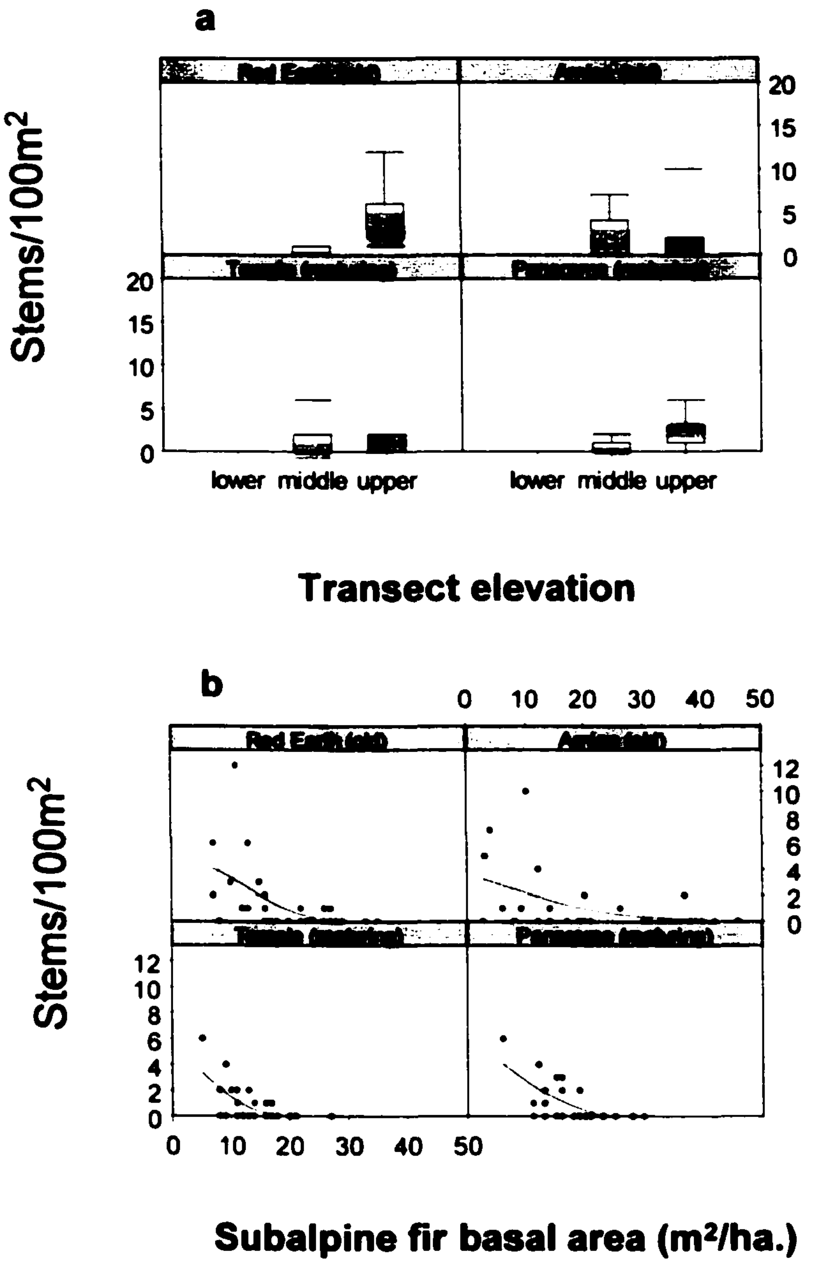


Figure 3.17: Response of alpine larch seedlings to (a) transect elevation and (b) basal area of subalpine fir. Fitted lines are cubic smoothing splines to aid with visual interpretation, but are independent of the statistical model.

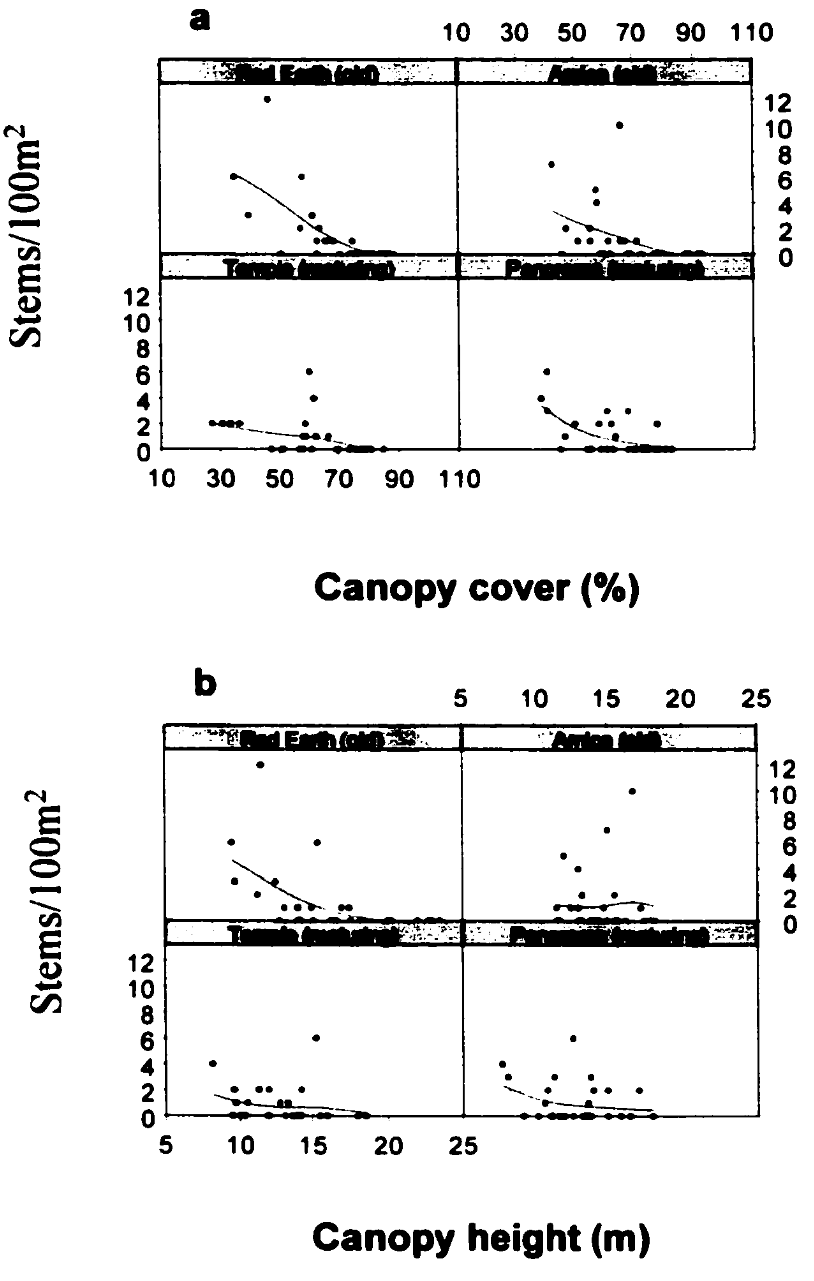


Figure 3.18: Response of alpine larch seedlings to (a) canopy cover, and (b) canopy height. Fitted lines are cubic smoothing splines to aid with visual interpretation, but are independent of the statistical model.

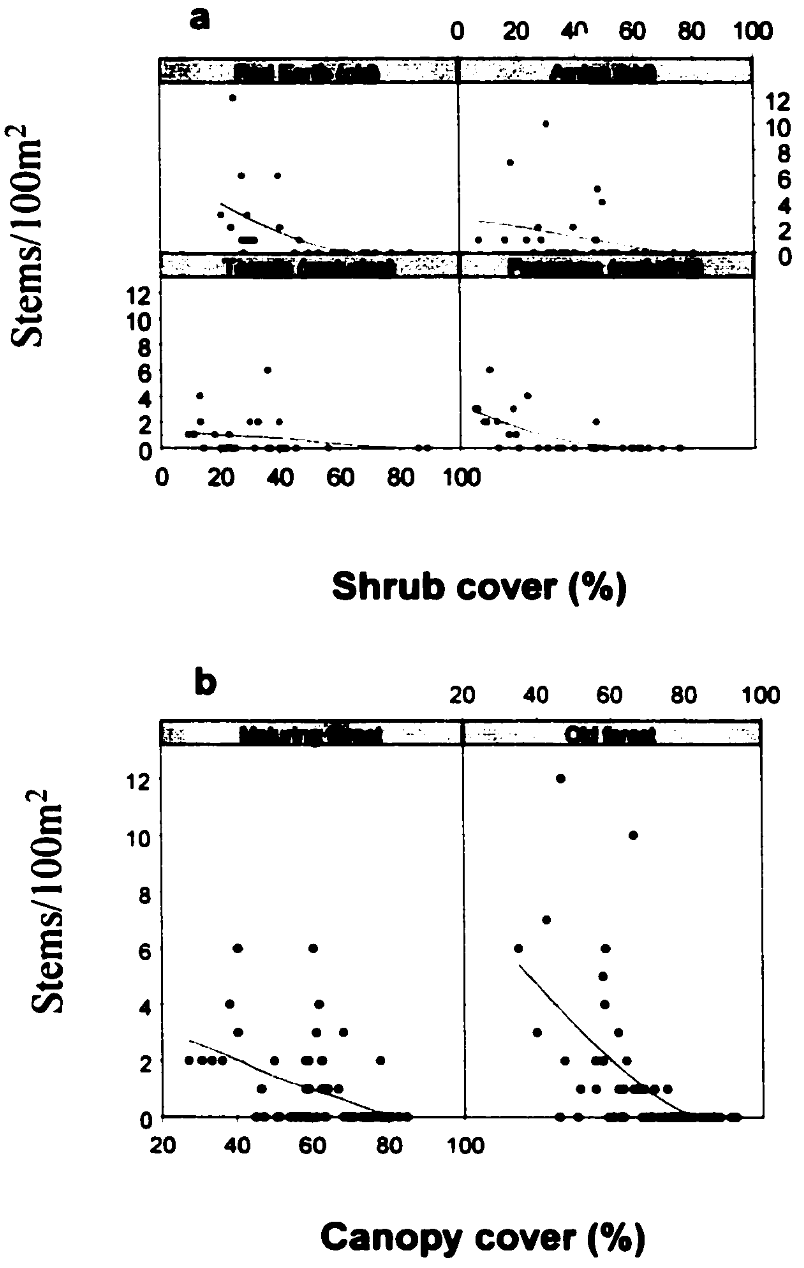


Figure 3.19: Response of alpine larch seedlings to (a) shrub cover, and to (b) the interaction between forest developmental stage and canopy cover. Fitted lines are cubic smoothing splines to aid with visual interpretation, but are independent of the statistical model.

3.3.2.2.2 Engelmann spruce

The best fit model for the spruce seedling data contained four terms after fitting the elevation dummy variable (Table 3.8). Like the larch data, the spruce seedling counts had many zeros and low numbers, so I again used the GLM approach described above for the larch seedling model. The full model described 50% of the null model deviance, and the structural model accounted for 47% of the partial model deviance.

Table 3.8: Engelmann spruce seedling niche model.

Model term	df	Deviance explained	Residual df	Residual Deviance	p-value (Chi^2)
Null model			119	676.10	
Transect elevation	2	39.74	117	636.36	0.00
Site location	3	140.72	114	495.63	0.00
Decaying wood	1	64.43	113	431.20	0.00
Total tree basal area	1	59.72	112	371.49	0.00
Canopy height	1	34.20	111	337.29	0.00

Although elevation was a significant covariable in the analysis, it accounted for little of the variation in the spruce seedling data. Figure 3.20 indicates that on average slightly greater seedling recruitment occurs lower in the stands. By far the most important variable in the model was site location, explaining 22% of the partial model deviance (Table 3.8). The strength of this term can be largely explained by the greater numbers of seedlings found at Panorama (Figure 3.20). Spruce seedling numbers also appeared to increase with greater availability of decaying wood on the forest floor. This was also most evident at Panorama, and to a lesser degree in both of the older sites (Figure 3.21a). However at these sites, this increasing trend appeared to be dependent on outliers in the data where the percentage of decaying wood exceeded that available in the maturing sites.

The strength of the negative relationship between total tree species basal area and spruce seedling abundance was also clearly aided by the previous inclusion of the site location variable in the model (Figure 3.21b, Table 3.8). In all sites, except Temple, there was a downward trend in seedling abundance where total basal area exceeded approximately 45 m^2 per hectare. At Temple the trend appeared to start much earlier, however, a single

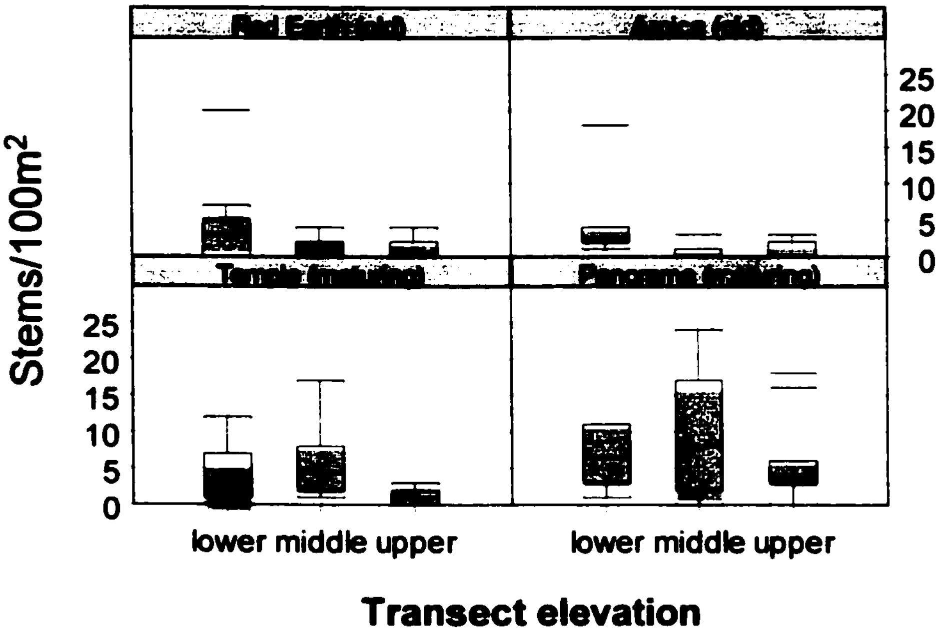


Figure 3.20: Response of Engelmann spruce seedlings to elevation and location. Note the greater abundance of seedlings in the lower and middle transects compared to the upper.

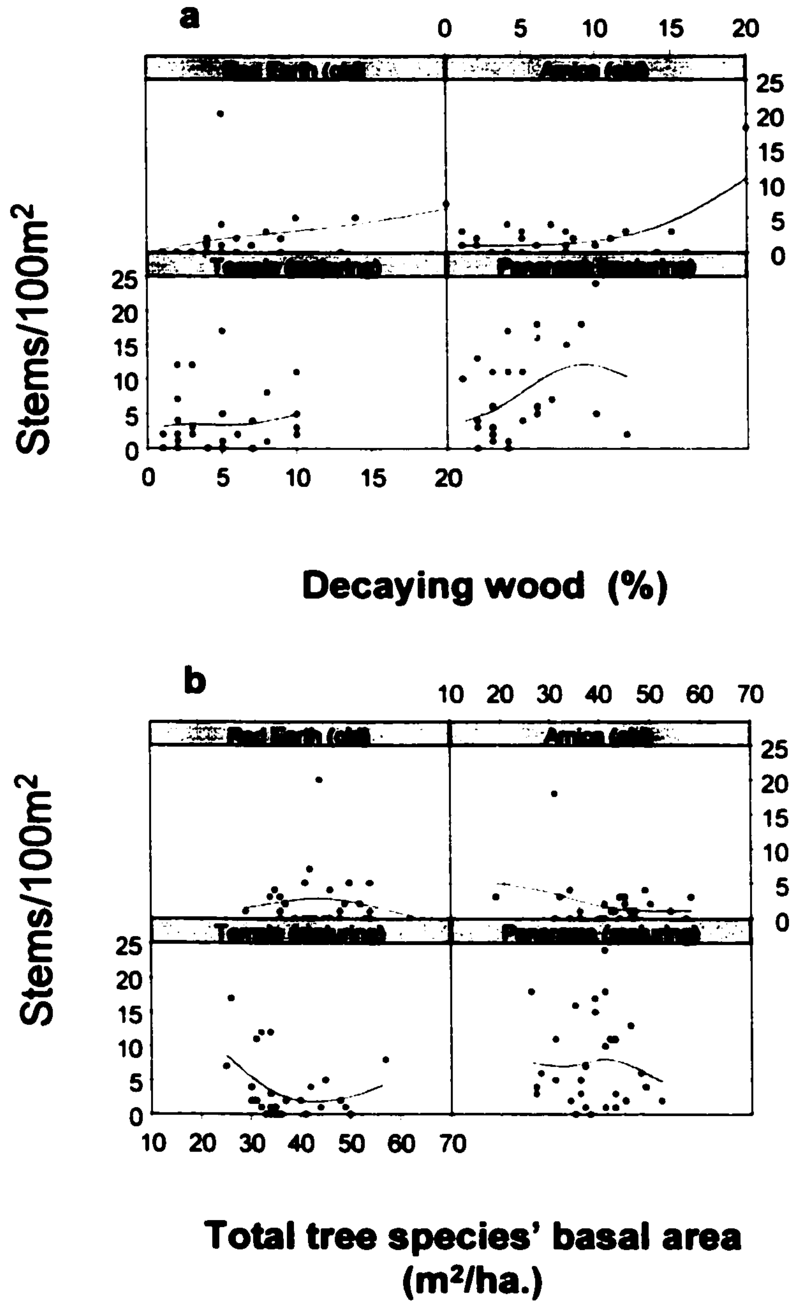


Figure 3.21: Response of Engelmann spruce seedlings to (a) the amount of decaying wood present on the forest floor, and (b) increases in combined species' basal area. Fitted lines are cubic smoothing splines to aid with visual interpretation, but are independent of the statistical model.

outlier at 55 m^2/ha. created a slight upward tendency at the end of this curve. Although the last term, canopy height, accounted for less of the variance in the model than basal area (Table 3.8), the positive association of canopy height with spruce seedling abundance was more apparent in all of the sites, and much more noticeably in the younger stands (Figure 3.22).

3.3.2.2.3 Subalpine fir

Only one term other than elevation comprised the subalpine fir seedling niche model (Table 3.9). Given the abundance of fir seedlings in all of the plots, simply log transforming these response data enabled the valid assumption of a normally distributed error distribution. The full model explained 54 % of the null model deviance, whereas, the forest structural model explained 47% of the partial model.

Table 3.9: Subalpine fir seedling niche model.

Model term	df	Deviance explained	Residual df	Residual Deviance	p-value (F)
Null model			119	287.29	
Transect elevation	2	39.65	117	247.64	0.00
Site location	3	109.67	114	137.97	0.00

Elevation was significant in explaining deviance in the subalpine fir seedling data where it was associated with greater densities of seedlings at the lower and middle transect elevations compared the upper transects (Figure 3.23). However, site location was a more important predictor of seedling abundance (Table 3.9), where there were up to four times the average number of stems per plot at the lower elevation in Panorama compared to the older stands (Figure 3.23).

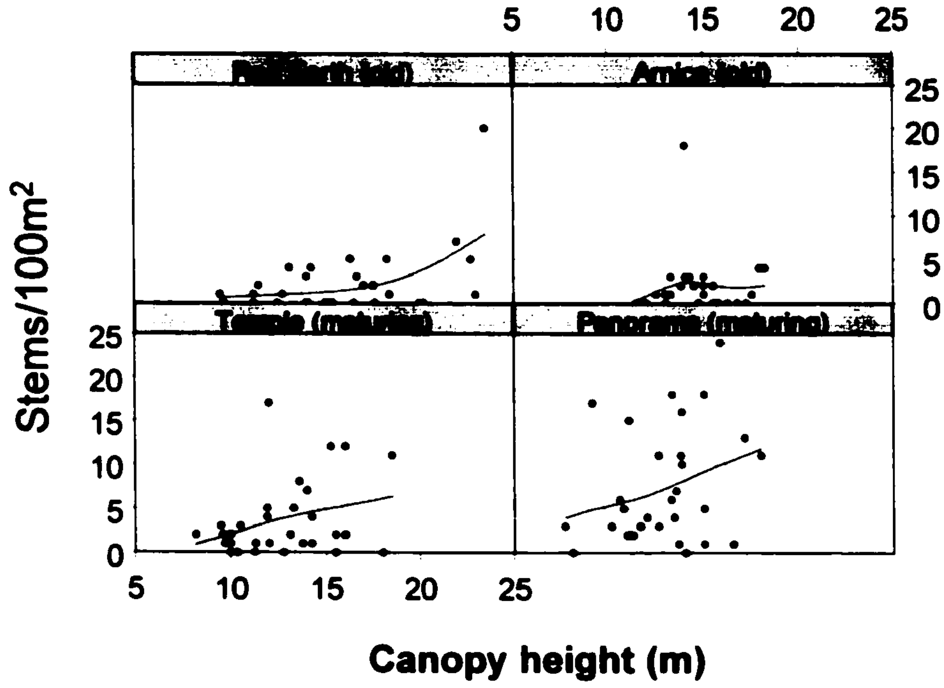


Figure 3.22: Response of Engelmann spruce seedlings to tree canopy height. Fitted lines are cubic smoothing splines to aid with visual interpretation, but are independent of the statistical model.

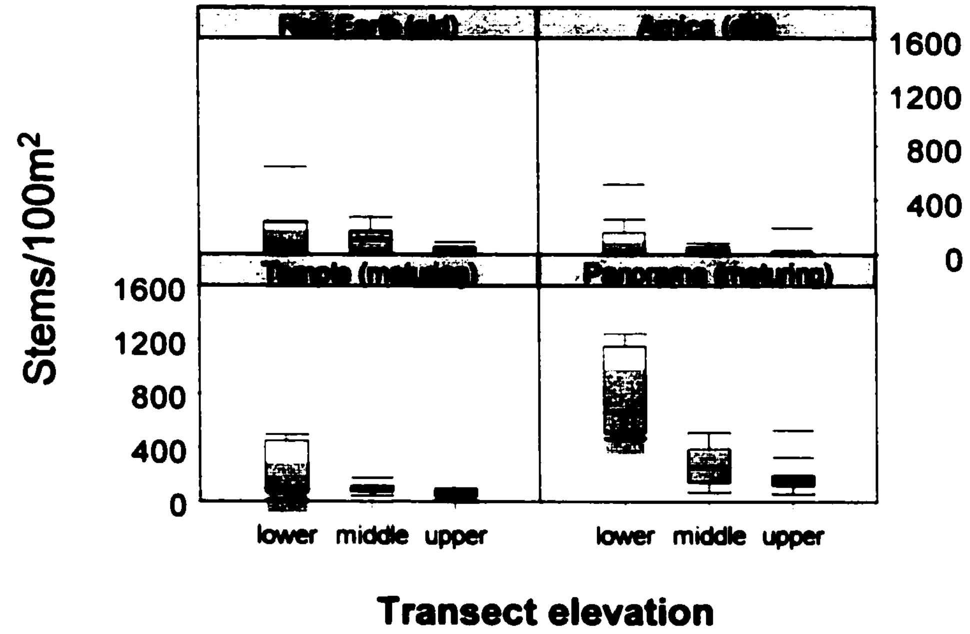


Figure 3.23: Response of subalpine fir seedlings to elevation and stage.

3.4 Discussion

3.4.1 Cohort response

In the maturing stands, the recruitment of the younger larch cohorts was diminished in comparison to the earlier post fire individuals that now were in the subcanopy or canopy (Figures 3.2 and 3.4). This suggests that these stands were entering what Oliver (1981) describes as a stand thinning stage, where the rapid growth and development of early successional species, like western larch (Schmidt and Shearer 1990), lodgepole pine (Lotan and Parry 1983) and, in some cases, Engelmann spruce (Johnston and Fryer 1989) create a competitive environment that causes greatly reduced seedling recruitment and increasing mortality of established stems. The mortality patterns for larch and the more shade tolerant fir and spruce also indicated that some stand thinning was occurring. However, the increases in the smaller spruce and especially fir cohorts, and the distinctly low mortality in the larch seedling cohort suggest that other factors may also be involved.

Alpine larch usually do not reach maturity until after 80 years, and do not produce substantial cone crops until they are several hundred years old (Arno 1970). This means that there may have been few years for the canopy sized larch that had reached maturity in either Temple or Panorama to produce seed *in situ* (Figure 3.2-3.4). This was apparent in these sites, as there were relatively few visible cones on even the largest larch trees. Both spruce and fir have been shown to produce cones within only several decades following germination (although, little seed is produced until the trees are taller; Alexander 1987). Therefore the dramatic increases in density of the two smaller and younger cohorts for subalpine fir and (to a lesser extent) Engelmann spruce, compared to that of larch at these sites may, in part, reflect a greater and longer availability of seed for these species.

Seed predation is another factor that may cause differences in the relative densities of the seedlings (Alexander 1987). Arno and Habeck (1972) noted that seed predation by an unknown dipteran larvae was common in several of the sites visited in their study. The data from a survey of alpine larch cones from 8 different timberline sites I conducted shows that pre-dispersal predation by dipteran larvae of larch seeds may vary by as much as 85% between some locations (Appendix III).

Taken together, this information points to a delayed, or slower stand development than is found in lower elevation forests. For example, Johnston and Fryer (1989) describe a rapid recruitment period (stand initiation; Oliver 1981) following fire in lower elevation lodgepole pine - Engelmann spruce forest for about the first decade. This is followed by considerable self-thinning of both species by the third decade, and then only sporadic recruitment for the next two centuries. In comparison, Agee (1993) suggests that the delayed development is common in several different high elevation forest types in North America; where a prolonged period of recruitment following coarse scale disturbance may change more directly into a phase of fine scale canopy disturbance, as the first senescing canopy trees start to fall (the understory reinitiation stage; Oliver 1981). The stem exclusion does appear delayed in Panorama and Temple. However, other evidence suggests that complete integration of stand initiation and understory retention may not be the normal pattern of events in subalpine forests in the Bow Valley either.

Although there were problems getting a suitably large, unbiased age sample of each of the tree species' cohorts, the substantial age differences noted between the canopy and smaller cohorts for both larch and spruce in several of the older stand sampling locations suggests that these species became locally rare or absent from the understory during a period of the stand development (Figures 3.13-14). Similar time lags between spruce cohorts have been found in age reconstructions in other old spruce – fir forests (Veblen et al. 1991, Roovers and Rebertus 1993, Parish et al. 1999). In these studies, the reoccurrence of the spruce was linked with some form of secondary disturbance. Parish et al. (1999) found that this disturbance was in the form of a larger scale attack of spruce beetle, whereas Veblen et al. (1991) and Roovers and Rebertus (1993) found the reinitiation of spruce was due to finer scale tree mortalities. One of the most obvious changes I found in the pattern of the cohort distributions between the older and maturing forest stands was the increased numbers of standing dead canopy individuals, especially fir, in the older stands (Figures 3.10-11). I also found numerous tree fall gaps in the older stands, which had been formed over the last 150 years (see Chapter 4), suggesting that reinitiation of the larch and the spruce was due to this more localized gap forming disturbance.

The regeneration of alpine larch in older subalpine forest is unusual, given that all of the species in the *Larix* genus are considered to be shade intolerant (Schmidt 1995), and alpine larch especially so (Richards 1981, Arno 1990, Arno et al. 1995). Almost all of the reported successional models of forests where *Larix* species occur find that these deciduous conifers are seral species that only regenerate following coarse scale disturbances, such as fire (Franklin and Dyrness 1979, Brunton 1984, Turner 1985, Fiedler and Lloyd 1995, Fowler et al. 1995, Barrett 1996), volcanic action (Toshihiko 1985), flooding, or extensive blowdown (Liu 1997, Taylor and Zisheng 1988). Only recently have there been reports from northern China that *L. gmelini*, a boreal larch species, uses finer scale tree fall gaps to re-initiate in older forest (Ban et al. 1998).

3.4.2 The regeneration niche

All of the terms following elevation except shrub cover in the alpine larch seedling niche model (Table 3.7) support the idea that gaps may also be important structures for alpine larch regeneration. The strong negative relationship of subalpine fir basal area and density of larch seedlings is most likely a reflection of the effect that the mature individuals of this most frequently occurring tree species had on the immediately surrounding area. A large proportion of the fir have considerable vegetative reproduction occupying the understory adjacent to their canopies. The interception of precipitation by this total leaf area in combination with the accumulated needle litter and limited transmitted light may have acted to exclude larch completely from beneath fir canopies. Only vegetatively produced fir shoots and spruce seedlings, on moist rotting wood, were found in these areas. This type of vegetative layering in subalpine fir has been noted by other workers, although generally only near timberline. (Shea and Grant 1985; see below)

Canopy cover in forests is not evenly distributed. Gaps in forest cover, due to the lack of complete crown closure in maturing forest, or created by the removal of individual trees in older forests, provide increases in the amount of light and precipitation that reach the forest floor (White 1979, Kimmins 1987). In high latitude forests the amount of light that reaches the ground beneath an overhead gap is largely a function of the size and shape of the gap, and the surrounding forest canopy height (Canham et al. 1990, Lieffers et al. 1999). As alpine larch is thought to be far more shade intolerant than Engelmann spruce or subalpine fir (Richards 1981, Arno et al. 1995), larch seedlings would be expected to be more abundant in larger gaps with shorter surrounding canopies.

Canopy height may also be an indicator for the extent of below ground competitive influence that a tree has on seedlings for soil moisture, and other nutrients. Coates (2000) has suggested that the competitive effect of mature canopy trees (ca. 30 m) on moisture and other nutrients may extend up to 10 m into artificially created gaps from the drip line in temperate conifer forests in northern British Columbia. Similarly, I have observed inhibition of western larch seedlings up to distances of 5m from the drip line of mature 30m tall forest on the well lit northern edge of artificially created gaps in mixed wood forests near Nakusp in southern BC (unpublished data). Casper and Jackson (1997) stress that it is important not to make assumptions regarding the relationship between aboveground biomass and root competition. However, the correlations presented here suggest the height of mature trees surrounding gaps may well indicate a limiting effect of within gap tree regeneration; where the radius of root competition could effectively close the gap below ground before this may be evident in the above ground canopy characteristics. More research is needed to explore this possibility.

As in many other studies, the spruce seedlings measured here were significantly associated with rotting wood (Table 3.7) (Smith 1954, Day 1964, Hofgaard 1993, Hiura et al. 1996, Anderson and Winterton 1996). This spatial dependence on substrate is most likely related to a provision of a buffered soil moisture supply for the first few weeks of growth (Knapp and Smith 1982). Hence, the establishment of spruce may be initially somewhat independent of the effects of a competitive overstory for soil moisture. The positive association of the canopy height and spruce seedlings found in this study (i.e., the reverse trend to that of larch) is probably related to an increased production of seeds as trees gain maturity in the younger sites (Figure 3.22), and by the greater volume of seeds produced by larger trees, generally (Shearer 1986). Although canopy cover was not a significant factor in the spruce seedling model, the negative association of spruce seedlings with total tree species basal area may be related to overstory light competition, but no longer correlated with canopy cover due the spruce seedlings' spatial dependence on decaying wood.

The abundant subalpine fir seedlings found in the sites I examined had no obvious association with the measured forest structural characteristics. This information supports previous suggestions that this species has little microsite preference (Day 1964, Alexander 1987). Another reason why there was little correspondence between fir seedlings and forest structure may be related to the abundant vegetative reproduction that was evident. Shoots that are still connected to the parent plant may be present in a wide range of environmental conditions that might otherwise be unfavourable to independent stems. Clonal reproduction is common in other temperate North American tree species, such as aspen (*Populus tremuloides* Michx.) (Shepperd 1987, Peterson and Peterson 1992), black spruce (*Picea mariana* var. brevifolia [Peck]; Uchytil 1991) and western red cedar (*Thuja plicata* Donn ex D. Don) (Tesky 1992).

3.4.3 Understory vegetation patterns

Shrub cover was identified as a significant dimension to the larch regeneration niche in both the conifer cohort ordination and the alpine larch seedling model. An informative way to look at this relationship is through the patterns of the understory community.

In his large scale analysis of the vegetation found with alpine larch over the Pacific Northwest, Arno (1970) concluded that there was a lack of 'distinct' associated understory communities types. This was because the presence of the larch overstory in the upper most reaches of the timberline appeared to facilitate the occurrence of some understory species generally found only in the subalpine forest. Arno (1970) also found the composition of this subalpine understory flora gradient to be quite different over the range of lithology and climate in the timberline areas that he sampled. Since that time there have been a number of land classification studies carried out at greater intensity that have found distinct patterns of understory association with alpine larch within both timberline and subalpine areas the Canadian Rockies (Baig 1972, Ogilvie 1976, Kuchar 1978, Corns and Achuff 1982, Achuff and Dudynsky 1984).

In the most comprehensive of these, the Ecological Land Classification (ELC) for Banff and Jasper National Parks, Corns and Achuff (1982) recognised several closed forest vegetation types that contained alpine larch. The main type in which larch frequently dominated the canopy, and where smaller cohorts were abundant in each of the forest strata, was the subalpine larch- subalpine fir/grouseberrry-everlasting vegetation type (C23). Alpine larch were also occasionally found in the different strata of the Engelmann spruce-subalpine fir/grouseberry vegetation type (C15). A range of larch cohorts were found less frequently in the Engelmann spruce-subalpine fir/tall bilberry/liverwort vegetation types (C21). Canopy individuals were found only rarely in the Engelmann spruce/false azalea (C14) type.

In the analysis of understory communities at my sites (Figure 3.16-3.17; Table 3.4), I found the shrub association - *Menziesia ferruginea, Rhododendron albiflorum, Vaccinium membranacem, Ledum groenlandicum* - that characterised lower elevation areas, where there were no seedling alpine larch, corresponded to the C21 and C14 vegetation types recognised by Corns and Achuff (1982). A similar shrub association was also found by Beil (1966). This shrub community gave way to greater abundances of the moist heath association - *Cassiope mertensiana, Pedicularis bracteosa, Hieracium gracile, and Arnica cordifolia* - higher in the subalpine forest where all of the size cohorts of larch were found. The communities in the upper transects of Panorama and Temple best corresponded to C23, a mature vegetation type (100 to 300 years old), with no strong shrub association. The higher locations of Arnica and Red Earth fit better with the older C21 (>350 years old), where the heath association was still likely to be found, but *Rhododendron* is also present.

All of the species in the heath association may be considered shade intolerant (Klinka et al. 1989, Kershaw et al. 1998). Most of these species also prefer more mesic conditions (Corns and Achuff 1982). Therefore, the preference of this plant association to the higher, more open sites, where there is more light and less canopy interception of precipitation, is understandable. The dominant *R. albiflorum* and *M. ferruginea,* are also generally found on more mesic sites; however, both species are shade tolerant. Therefore, the general organisation of these species' niches in this simple two dimensional habitat space suggest that, in absence of other constraining factors, the two most important species in the tall shrub association will (1) dominate the lower light environments; and (2) possibly succeed the heath association by virtue of their greater stature irrespective the overstory conditions. This is supported by the increase in the importance of Rhododendron between the C23 and the C21 vegetation types noted above. Why this has not happened over the entire habitat space already is most likely related to the individual physiological constrains that each of the shrub species experiences at higher elevations, and how the resulting reduced vigour affects their competitive ability. (Wardle 1974, Tranquillini 1979, Larcher 1983). Further research into which specific factors limit the niche space of these shrub species will help predict whether this association will move further upslope in the continued absence of disturbance, or under the influence of changing climatic conditions (McKenzie and Halpern 1999).

3.4.4 Elevation, forest structure, and alpine larch regeneration

The ordination of the tree species cohorts summarises the interaction of elevation with canopy and understory structure on the realised niche space for alpine larch (Figure 3.15). As I have shown, the larch canopy cohort initially maintains a broad distribution over elevation in maturing forests due to its establishment in more open environments following the stand replacing fires. Although some seedling recruitment in maturing forests still occurs at higher elevations, greater canopy and shrub cover associated with more rapid forest development at lower elevations act to prohibit seedling recruitment. In the lower older forest sites, in spite of tree fall gap disturbance, the greater canopy cover, shrub cover, and canopy height has continued to exclude larch recruitment. This prolonged absence in recruitment appears to lead to the loss of all larch cohorts in these lower sites. However, the reinititation of larch at the upper elevations indicates that the onset of fine scale gap disturbance may be an important mechanism for continued presence of the species in these subalpine areas.

Clearly, there remain some unresolved issues. Local estimates of basal area, canopy cover, and canopy height provide an average measure with which to predict the occurrence of seedling recruitment, but give no direct information about how the combination of these factors operate on the landscape to produce the effect. As canopy gaps appear to be the most important mechanism that regulate the local availability of light, moisture, and other nutrients in forests (Canham et al. 1990, Heinemann et al. 2000), information about how these units are distributed on the landscape (e.g., shape, area, frequency, turnover rate; White 1979, Spies and Franklin 1989, Runkle 1990) is also of great importance for understanding how alpine larch and the other conifers maintain their populations and realised niche space. Further research is needed to determine if the differences in the distribution of the fine scale disturbance that occurs between elevations in these older forests accounts for the difference in recruitment success of alpine larch.

3.5 Literature cited

Achuff, P. L. 1982. Vegetation: introduction and methods. Pages 71-73 *in:* Holland W. D. and G. M. Coen, editors. Ecological (biophysical) land classification of Banff and Jasper National Parks. **SS-82-44**. Alberta Institute of Pedology, University of Alberta. Edmonton, AB, Canada.

Achuff, P. L. and Dudynsky H A 1984. Vegetation. Pages 43-132 *in:* Achuff P. L., W. D. Holland, G. M. Coen, and K. Van Tighem, editors. Ecological land classification of Kootenay National Park, British Columbia. **M-84-10**. Alberta Institute of Pedology. Edmonton, AB, Canada.

Agee, J. K. 1990. The historical role of fire in Pacific Northwest forests. Pages 25-38 *in:* Walstad J. D., S. V. Radosevich, and D. V. Sandberg, editors. Natural and prescribed fires in Pacific Northwest forests. Oregon State University Press. Corvallis, Oregon, USA.

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press. Washington, DC, USA.

Alexander, R. R. 1987. Ecology, silviculture, and management of the Engelmann spruce-subalpine fir type in the Central and Southern Rocky Mountains. **Agricultural Handbook 659**. US Department of Agriculture, Forest Service. Washington DC, USA.

Anderson, L. J. and Winterton, A. J. 1996. Germination as a determinant of seedling distributions among natural substrates in *Picea engelmannii* (Pinaceae) and *Abies lasiocarpa* (Pinaceae). American Journal of Botany. **83:** 112-117.

Anonymous 1999. Canadian climate normals. Environment Canada URL: http://www.cmc.ec.gc.ca./climate/normals/ [2000]

Aplet, G. H., Laven, R. D., and Smith, F. W. 1988. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. Ecology. **69:** 312-319.

Arno, S. F. 1970. Ecology of alpine larch in the Pacific Northwest. PhD thesis University of Montana, Missoula, MT, USA.

Arno, S. F. 1990. Alpine Larch (*Larix lyallii* Parl). Pages 152-158 *in:* Burns R. M. and B. H. Honkola, editors. Silvics of North America. **Agricultural Handbook 654**. Forest Service, US Department of Agriculture. Washington, DC, USA.

Arno, S. F. and Habeck, J. R. 1972. Ecology of Alpine Larch (*Larix lyallii* Parl) in the Pacific Northwest. Ecological Monographs. **42:** 418-450.

Arno, S. F. and Hammerly, R. P. 1984. Timberline: Mountain and Arctic Forest Frontiers. The Mountaineers. Seattle, USA.

Arno, S. F. and Sneck, S. 1977. A method of determining fire history in coniferous forests of the Mountain West. **INT-42**. USDA Forest Service. Ogden, UT, USA.

Arno, S. F., Worrall, J., and Carlson, C. E. 1995. *Larix Lyallii:* colonist of tree-line and talus sites. Pages 72-78 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and Management of Larix Forests: A Look Ahead. **GTR-INT-319.** US Department of Agriculture, Forest Service. Ogden, UT, USA.

Austin, M. P. 1985 . Continuum concept, ordination methods and niche theory. Annual Review of Ecology and Systematics. **16:** 39-61.

Austin, M. P. and Smith, T. M. 1989. A new model for the continuum concept. Vegetatio. **83:** 35-47.

Baig, M. N. 1972. Ecology of timberline vegetation in the Rocky Mountains of Alberta. PhD thesis. University of Calgary. Calgary, Alberta, Canada.

Ban, Y., Xu, H., Bergeron, Y., and Kneeshaw, D. D. 1998. Gap regeneration of shade-intolerant *Larix gmelinii* in old-growth boreal forests of northeastern China. Journal of Vegetation Science. **9:** 529-536.

Barrett, S. W. 1996. The historic role of fire in Waterton Lakes National Park, Alberta. **KWL 30004**. Parks Canada contract report. Waterton, AB, Canada.

Beil, C. E. 1966. An ecological study of the primary producer level of the subalpine spruce - fir ecosystem of Banff and Jasper National Parks, Alberta. M.Sc. thesis, University of Alberta, Edmonton, AB, Canada.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. John Wiley and Sons. New York, NY, USA.

Brunton, D. F. 1984. The status of western larch, *Larix occidentalis*, in Alberta. Canadian field-naturalist. **98:** 167-170.

Canadian Heritage Parks Canada 1994. Guiding principles and operational policies. Minister of Supply and Services Canada. Ottawa, ON, Canada.

Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., and White, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research. **20:** 620-631.

Casper, B. B. and Jackson, R. B. 1997. Plant competition underground. Annual Review of Ecology and Systematics. **28:** 545-570.

Coates, K. D. 2000. Conifer seedling response to northern temperate forest gaps. Forest Ecology and Management. **127:** 249-269.

Connell, J. H. and Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist. **111:** 1119-1144.

Corns, I. G. W. and Achuff, P. L. 1982. Vegetation: vegetation type descriptions. Pages 75-141 *in:* Holland W. D. and G. M. Coen, editors. Ecological (biophysical) land classification of Banff and Jasper National Parks. **SS-82-44**. Alberta Institute of Pedology, University of Alberta. Edmonton, AB, Canada.

Crosbie, S. F. and Hinch, G. N. 1985. An intuitive explanation of generalised linear models. New Zealand Journal of Agricultural Research. **28:** 19-29.

Daubenmire, R. F. 1943. Vegetational zonation in the Rocky Mountains. The Botanical Review. **IX:** 325-393.

Daubenmire, R. F. 1974. Plants and the environment. Wiley. New York, NY, USA.

Day, R. J. 1964. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains. **Research Branch Publication 1037**. Canadian Department of Forestry. Ottawa, ON, Canada.

Day, R. J. 1972. Stand structure, succession and use of southern Alberta's Rocky Mountain forest. Ecology. **53:** 427-478.

Dubé, D. E. 1976. Early plant succession following a 1968 wildfire in the subalpine zone of the Vermilion Pass, Kootenay National Park. M.Sc. thesis, University of Alberta. Edmonton, AB, Canada.

Ecoregions Working Group Canada Committee on Ecological Land Classification 1989. Ecoclimatic regions of Canada: first approximation. **Ecological land classification series No 23**. Sustainable Development Branch, Canadian Wildlife Service, Conservation and Protection. Ottawa, ON, Canada.

Fiedler, C. E. and Lloyd, D. A. 1995. Autecology and synecology of western larch. Pages 118-121 *in:* W. C. Schmidt, and K. J. McDonald, Compilers. Ecology and Management of Larix Forests: A Look Ahead. **GTR-INT-319.** 72-78. U S Department of Agriculture, Forest Service. Ogden, UT, USA.

Fowler, D. P. 1995. *Larix laricina-* silvics and genetics. Pages 54-58 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and Management of Larix Forests: A Look Ahead. **GTR-INT-319**. US Department of Agriculture, Forest Service. Ogden, UT, USA.

Franklin, J. F. and Dyrness, C. T. 1979. Natural vegetation of Oregon and Washington. Oregon State University Press. Corvallis, OR, USA.

Goldsmith, F., Harrison, C., and Morton, A. 1986. Description and analysis of vegetation. Pages 437-524 *in:* Moore P. and S. Chapman, editors. Methods in plant ecology. Blackwell Scientific.

Grabherr, G., Gottfried, M., and Pauli, H. 1994. Climate effects on mountain plants. Nature. **369:** 448.

Graumlich, L. J. 1994. Long-term vegetation change in mountain environments. Pages 167-179 *in:* Beniston M., editor. Mountain environments in changing climates. Routledge. New York, NY, USA.

Hansen-Bristow, K. 1986. Influence of increasing elevation on growth characteristics at timberline. Canadian Journal of Botany. **64:** 2517-2523.

Harper, J. L. 1977. Population biology of plants. Academic Press. London, UK.

Heinemann, K., Kitzberger, T., and Veblen, T. T. 2000. Influences of gap microheterogeneity on the regeneration of *Nothofagus pumilio* in a xeric old-growth forest of northwestern Patagonia, Argentina. Canadian Journal of Forest Research. **30:** 25-31.

Hill, M. O. 1979. TWINSPAN: a fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics, Cornell University, Ithaca, NY, USA.

Hiura, T., Sano, J., and Konno, Y. 1996. Age structure and response to fine scale disturbances of *Abies sachalinensis, Picea jezoensis, Picea glehnii,* and *Betula ermanii* growing under the influence of a dwarf bamboo understory in northern Japan. Canadian Journal of Forest Research. **26:** 289-297.

Hofgaard, A. 1993. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. Journal of Vegetation Science. **4:** 601-608.

Horn, H. 1976. Succession. Pages 187-204 *in:* May R. M., editor. Theoretical ecology. WB Saudners Company. Philadelphia, Pa, USA.

Johnson, E. A. and Fryer, G. I. 1989. Population dynamics in lodgepole pine-Engelmann spruce forests. Ecology. **70:** 1335-1345.

Johnson, E. A. and Miyanishi, K. 1991. Fire and population dynamics of lodgepole pine and Engelmann spruce forests in the southern Canadian Rockies. Pages 77-91 *in:* Nakagoshi N. and F. B. Golley, editors. Coniferous forest ecology from an international perspective. Academic Publishing. The Netherlands.

Jongman, R. H. G., ter Braak, C. J. F., and Van Tongeren, O. F. R. 1995. Data analysis in community and landscape ecology. Cambridge University Press. Cambridge, UK.

Keane, R. E., Morgan, P., and Running, S. W. 1996. FIRE-BGC- A Mechanistic Ecological Process Model for Simulating Fire Succession on Coniferous Forest Landscapes of the Northern Rocky Mountains . **INT-RP-484**. US Department of Agriculture, Forest Service, Intermountain Research Station. Ogden, UT, USA.

Kershaw, L., MacKinnon, A., and Pojar, J. 1998. Plants of the Rocky Mountains. Lone Pine, Edmonton. AB, Canada.

Kimmins, J. 1987. Forest ecology. Macmillan. New York, NY, USA.

Klinka, K., Krajina, V. J., Ceska, A., and Scagel, A. M. 1989. Indicator plants of coastal British Columbia. University of British Columbia. Vancouver, BC, Canada.

Knapp, A. K. and Smith, W. K. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Canadian Journal of Botany. **60:** 2753-2761.

Kuchar, P. 1978. The vegetation of Yoho National Park. Report to Parks Canada. Calgary, Alberta.

Larcher, W. 1983. Physiological plant ecology. Springer-Verlag. Berlin.

Lieffers, V. J., Messier, C., Stadt, K. J., Gendron, F., and Comeau, P. G. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal Forest Research. **29:** 796-811.

Lindsey, J. K. 1995. Introductory statistics: a modelling approach. Oxford University Press. Oxford, UK.

Liu, Q. 1997. Structure and dynamics of the subalpine coniferous forest on Changbai mountain, China. Plant Ecology. **132:** 97-105.

Lotan, J. E. and Parry, D. A. 1983. Ecology and regeneration of lodgepole pine. **Agricultural Handbook 606**. US Department of Agriculture, Forest Service. Washington DC, USA.

McKenzie, D. and Halpern, C. B. 1999. Modelling the distributions of shrub species in Pacific Northwest forests. Forest Ecology and Management. **114:** 293-307.

Mathsoft 1999. S-Plus 2000 guide to statistics. **1:** Data Analysis Products Division, Mathsoft. Seattle, WA, USA.

Mathsoft 2000. S-Plus 2000 Professional Release 2. Data Analysis Products Division, Mathsoft, Seattle, WA, USA.

Ministry of Forests 2001. Forest practices code. Government of British Columbia. Available at: http://www.for.gov.bc.ca/tasb/legsregs/fpc/fpc.htm [2001]

Morrison, D. A., Le Brocque, A. F., and Clarke, P. J. 1995. An assessment of some improved techniques for estimating the abundance (frequency) of sedentary organisms. Vegetatio. **120:** 131-145.

Mueller-Dombois, D. and Ellenberg, H. 1974. Aims and methods of vegetation ecology. Wiley. New York, NY, USA.

Nicholls, A. 1989. How to make biological surveys go further with generalised linear models. Biological Conservation. **50:** 51-75.

Ogilvie, R. T. 1976. The alpine and subalpine in the Rocky Mountains of Alberta. Pages 34-46 *in:* Luttmerding H. A. and J. A. Shields, editors. Proceedings from a workshop on alpine and subalpine environments. BC Ministry of Environment. Victoria, BC, Canada.

Oliver, C. D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management. **3:** 153-163.

Parish, R., Antos, J. A., and Fortin, M. J. 1999. Stand development in an old-growth subalpine forest in southern interior British Columbia. Canadian Journal of Forest Research. **29:** 1347-1356.

Peterson, E. B. and Peterson, N. M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. **Special report 1**. Forestry Canada, Northwest Region. Edmonton, AB, Canada.

Richards, J. H. 1981. Ecophysiology of a deciduous timberline tree, *Larix lyallii* Parl. PhD thesis, Department of Botany, University of Alberta. Edmonton, Alberta.

Rogeau, M. P. 1996. Understanding the age-class distribution in the southern Canadian Rockies. M.Sc. Thesis, Department of Forest Science, University of Alberta. Edmonton, AB, Canada.

Rogeau, M. P. and Gilbride, D. 1994. Stand origin of Banff National Park. Parks Canada. Banff, AB, Canada.

Romme, W. H. and Knight, D. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology. **62:** 319-329.

Roovers, L. M. and Rebertus, A. J. 1993. Stand dynamics and conservation of an old-growth Engelmann spruce-subalpine fir forest in Colorado. Natural Areas Journal. **13:** 256-267.

Runkle, J. R. 1990. Gap dynamics in an Ohio *Acer-Fagus forest* and speculations on the geography of disturbance. Canadian Journal of Forest Science. **20:** 632-641.

Schmidt, W. C. 1995. Around the world with *Larix*: an introduction. Pages 6-18 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and Management of *Larix* Forests: A Look Ahead. **GTR-INT-319.** US Department of Agriculture, Forest Service. Ogden, UT, USA.

Schmidt, W. C. and Shearer, R. C. 1990. *Larix occidentalis* Nutt. Western Larch. Pages 160-172 *in:* Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC.

Shea, K. L. and Grant, M. C. 1985. Clonal growth in spire-shaped Engelmann spruce and subalpine fir trees. Canadian Journal of Botany. **64:** 255-261.

Shearer, R. C. 1986. Cone production on Douglas-fir and western larch in Montana. Pages: 63-67 *in:* Shearer R. C., Compiler. Proceedings- conifer tree seed in the inland mountain west symposium, Missoula, Montana, August 5-6, 1985. **General Technical Report INT-203**. United States Department of Agriculture, Forest Service. Ogden, UT, USA.

Shepperd, W. D. 1987. Silviculture research in Rocky Mountain aspen. Pages 25-29 *In* Troendle C. A., M. R. Kaufmann, R. Hamre, and R. P. Winokur, technical co-ordinators. Management of subalpine forests: building on 50 years of research. **RM-149**. USDA Forest Service. Fort Collins, Colo. USA.

Smith, J. H. G. 1955. Some factors affecting reproduction of Engelmann spruce and alpine fir. **Technical Publication 43**. BC Department of Lands and Forests, Forest Service. Victoria, BC, Canada.

Smith, T. M., Shugart, H. H., Bonan G. B., and Smith, J. B. 1992. Modelling the potential response of vegetation to global climate change. Advances in Ecological Research. **22:** 93-116.

Sokal, R. R. and Rohlf, J. F. 1995. Biometry. W. H. Freeman and Company. New York, NY, USA.

Spies, T. A. and Franklin, J. F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology. **70:** 543-545.

Sprugel, D. G. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. Journal of Ecology. **64:** 889-911.

Tande, G. F. 1979. Fire history and vegetation pattern of coniferous forest in Jasper National Park, Alberta. Canadian Journal of Botany. **57:** 1912-1931.

Taylor, A. H. and Zisheng, Q. 1988. Tree replacement patterns in subalpine *Abies-Betula* forests, Wolong natural reserve, China. Vegetatio. **78:** 141-149.

ter Braak, C. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology. **67:** 1167-1179.

ter Braak, C. J. 1988. CANOCO: a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis and redundancy analysis (version 31). Microcomputer Power, Ithaca, NY, USA.

ter Braak, C. J. and Prentice, I. C. 1988. A theory of gradient analysis. Advances in Ecological Research. **18:** 271-317.

Tesky, J. L. 1991. *Thuja plicata*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (2001, February). Fire Effects Information System, [Online]. Available: http://www.fs.fed.us/database/feis/ [2000]

Toshihiko, N. 1985. Forest succession the subalpine region of Mt. Fuji, Japan. Vegetation. **64:** 15-27.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European alps. Springer-Verlag. New York, NY, USA.

Turner, D. P. 1985. Successional relationships and comparison of biological characteristics among six northwestern conifers. Bulletin of the Torrey Botany Club. **112:** 421-428.

Uchytil, R. J. 1991. *Picea mariana*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (2001, February). Fire Effects Information System, [Online]. Available: http://www.fs.fed.us/database/feis/ [2001]

van der Valk, A. G. 1992. Establishment, colonization and persistence. Pages 60-102 *in:* Glenn-Lewin D. C., R. K. Peet, and T. T. Veblen, editors. Plant succession: theory and prediction. Chapman and Hall. London, UK.

Veblen, T. T. 1986. Treefalls and coexistence of conifers in subalpine forests of the central Rockies. Ecology. **67:** 644-649.

Veblen, T. T., Hadley, K. S., and Reid, M. 1991. Disturbance and stand development of a Colorado subalpine forest. Journal of Biogeography. **18:** 707-716.

Walker, B. D., Holland, W. D., and Coen, G. M. 1982. Soils. Pages 62-70 *in:* Holland W. D. and G. M. Coen, editors. Ecological (biophysical) land classification of Banff and Jasper National Parks. **SS-82-44**. Alberta Institute of Pedology, University of Alberta. Edmonton, AB, Canada.

Wardle, P. 1974. Alpine timberlines. Pages 371-402 *in:* Ives J. D. and R. Barry, editors. Arctic and alpine environments. Macmillan. New York, NY.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. The Botanical Review. **45:** 229-299.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon. **21:** 213-251.

Whittaker, R. H. 1978. Direct gradient analysis. Pages 9-50 *in:* Whittaker R. H., editor. Ordination of plant communities. Dr W Junk. The Hague, The Netherlands.

Wilson, B. C. 1998. Daer-Pitts prescribed burn research plan. **KKP05-98**. Cordilleran Ecological Research. Winlaw, BC, Canada.

Wilson, B. C. 1997. The ecology of alpine larch in the northern Rocky Mountains. Cordillera. **3:** 8-11.

Wilson, B. C. and Stuart-Smith, G. J. 2000. Whitebark pine conservation for the Canadian Rocky Mountain National Parks. **KNP03-00**. Cordilleran Ecological Research. Winlaw, BC, Canada.

CHAPTER 4: FINE-SCALE DISTURBANCE PROCESSES IN OLDER SUBALPINE FOREST AND THE RECRUITMENT OF ALPINE LARCH.

4.1 Introduction

Disturbance in subalpine forests creates openings that change the availability of plant resources that are necessary for the successful recruitment of new cohorts (Heinemann et al. 2000). Forest openings vary greatly in size and appearance, depending on the agent and intensity of disturbance (White 1979, White and Pickett 1985). However, in absence of coarse scale stand replacing fires, avalanches, or insect epidemics (Tande 1979, Schmid and Amman 1992, Veblen et al. 1994), older forests typically experience only fine scale disturbance resulting in the death of one to several canopy trees (Runkle 1981, Spies and Franklin 1989, Lertzman and Krebs 1991). In fine scale disturbance, tree deaths are most often caused by one agent, or a combination of wind throw, insect, or fungal damage (Blais 1983, Veblen 1986). The limited spatial extent of these disturbances maintains the greater average age of the resident tree populations at the larger stand level, but also limits the availability of the environmental gradients associated with the small newly disturbed areas.

Early successional species that disperse effectively and grow rapidly in large disturbed areas generally become excluded from older forests (Oliver and Larsen 1990). This is because their seedlings, which are usually poorly adapted to growth in the higher competition (low light) environments, are unable to survive and recruit to the mature canopy. Usually only late successional species, with seedlings that are able to exploit areas of relatively low light and greater competition for moisture and other nutrients, utilize the fine scale 'gap dynamic' disturbance regimes and form continuously recruiting populations (Whitmore 1988).

For more than one canopy species to persist in the same stand over the long term (i.e., more that one generation) some mechanism is required to adjust the relative success of each species' population. In forests under the influence of fine scale disturbance regimes, this is thought to take the form of regeneration niche partitioning (Grubb 1977). Although canopy gaps created by the fall of one or several mature trees are relatively small, at a stand level, this type of disturbance introduces considerable temporal and spatial heterogeneity (Denslow 1985). Coexisting plant species are thought to have evolved different life history strategies that reduce the overall amount of direct competition for a single resource at any one time (Whittaker 1972, Grime 1979). It has been suggested that in tropical forests, the size of tree fall gaps may represent a surrogate for changes in the physiological and resource gradients (e.g., temperature, light) over which regeneration of different tree species may be partitioned (Ricklefs 1977, Denslow 1980). Gaps have also been recognised as important structures for oldgrowth regeneration in more temperate climates (Runkle 1981, White et al. 1985, Heinemann et al. 2000), although, there is some debate as to whether different species are actually partitioned by gap size, especially in coniferous forests (Spies et al. 1990, Coates 2000).

There have been a number of studies looking at the maintenance of older Engelmann spruce and subalpine fir forests in the Rocky Mountains (Oosting and Reed 1952, Shea 1985, Veblen 1986, Aplet et al. 1988, Veblen et al. 1991, Rebertus et al. 1992). These studies indicate that a mixture of different scales, agents, and intensities of disturbance affect these forests, and may influence the relative composition of the spruce and fir differently depending on the local site conditions. However, no one study specifically documented the local distribution of gap size. In the subalpine forests of the southern Canadian Rocky Mountains, alpine larch coexists with Engelmann spruce and subalpine fir, well below the usual timberline habitat of the deciduous shade intolerant larch species. Although the alpine larch established at lower elevation by fire is rapidly out competed by lodgepole pine (Chapter 2), and then by the shrubby understory of maturing spruce – fir forests, all ages of the larch exist in areas of older forest (Chapter 3). In these older forests, tree fall gaps are common, and may well be important for providing opportunities for the maintenance of alpine larch in this situation.

4.1.1 Objectives

In this Chapter, I explore the relationships between fine scale forest gap structure and alpine larch regeneration in older Engelmann spruce – subalpine fir forest. My general study goal was to determine whether forest gaps were important for regeneration of alpine larch in older subalpine forest. There were several questions I wanted to answer:

1. Did the proportion of forest in a gap state, or the morphology of the gaps change over elevation?
2. Was there a direct association between forest gaps and alpine larch regeneration? And if so,
3. Was this regeneration likely to maintain the present proportion of larch in the canopy?
4. Were there measurable structural gap qualities that were associated with the regenerating larch that were different to those of spruce and fir?

4.2 Methods

4.2.1 Study area

The study was carried out in Arnica, one of the two older forest research stands I introduced in Chapter 3 (Figure 3.1). This site was located near 2000m on a broad, north facing ridge in the Bow Valley, Alberta. This area lies in the subalpine southern cordilleran ecoclimatic region (EWGCCELC 1989). The weather is characterised by cool summers and cold winters, but there are occasionally settled high pressure systems in this region of the Rockies that create prolonged hot, dry, forest fire conditions in the summers (Johnson and Miyanishi 1991). Data from the nearest weather station in Banff, Alberta (25 km to the east) show a mean maximum air temperature in July of 22.1° C, and a mean maximum temperature in January of –5° C. The average yearly precipitation is 468.0 mm, with the greatest precipitation occurring in the summer between May and August (Anonymous 1999).

4.2.2 Data collection and analysis

I stratified this stand over the elevation range in which any size of alpine larch was present. The lowest sampling area was located just below 2000 metres where only a few canopy and larger subcanopy individuals were found. The upper sampling area was located 200m higher at the last suitable sampling location within the forest stand. An intermediate sampling location was chosen close to the mean elevation of the upper and lower sampling locations.

4.2.2.1 Canopy cover types and gap areas

I categorised the 2-dimensional projection of the forest canopy stratum into "canopy gap", "expanded gap", or "closed canopy" classes (cf. Runkle 1982, Lertzman and Krebs 1991). Canopy gaps were defined as open areas bordered by the lateral extension of branches from surrounding mature trees that were greater than 10m in height. Thus, no direct overhead cover was present. Further, I defined these canopy gaps by some evidence that canopy disturbance had occurred (i.e., a recognisable fallen canopy tree in any state of decay). The boundary of the gap also had to be relatively continuous, where any break was less than one average canopy tree crown width. Expanded gaps were the gap area including the extra area covered by the lateral extension of branches between the edge of the canopy gap and the boles of the trees bordering the gap. Closed canopy was defined as areas covered by branches between gaps that were not directly adjacent to gaps. In practice, this included canopy openings not associated with tree mortality that were less than about $4m^2$.

To measure the proportion of the canopy stratum in each of these classes, I used 10 randomly located $100m^2$ plots at each sampling elevation. These were the same plots used to measure forest structure at this site (see Chapter 3). In each of these plots I systematically recorded the canopy stratum class directly overhead with the aid of a clinometer at 48 points in the plot (observations a pace apart, bisecting the plot four times). I used one-way analysis of variance (ANOVA) to determine whether each of the canopy cover types changed over elevation.

To choose gaps for further measurement I used a set of random distances and directions from a centrally located point at each sampling elevation. The closest gap to each of the generated coordinates was surveyed. At the upper sampling site, 16 gaps were selected. At the middle and lower locations, 15 and 11 gaps were surveyed, respectively. Logistical constraints prevented me from surveying more gaps at the lower locations to provide a balanced gap number over elevation.

Once a gap had been located by this procedure, I mapped both the gap and expanded gap area using a sequence of radii recording the lengths and bearings to obvious changes in gap perimeter from a centrally located point within the gap (cf. Lertzman 1992; see Appendix IV). To calculate the area covered by the two associated gap types, I wrote a "Visual Basic for Applications"© program in Microsoft Excel©. This program used the relationship between the radii lengths and the central angles between each radius to estimate triangular areas. These were summed to provide the total gap and expanded gap areas. Details can be found in Appendix IV. I compared the distributions of the gap and expanded gap areas between the elevations where I sampled using histograms and ANOVA.

4.2.2.2 Age-height relationships and forest turnover

To calculate the rotation time of the forest canopy, I followed the method described by Lertzman and Krebs (1991), where the average age of trees that have reached the canopy, the gap filling age, is divided by the proportion of the canopy that is presently in a gap state. I estimated the average age of each tree species at 10 m, the height at which I deemed any given gap to be filled (i.e., within the mature canopy class defined in Chapter 3). The average 10 m tree ages were estimated by fitting height measurements to individuals of known ages using linear regression. Obtaining the canopy gap proportion is described above.

4.2.2.3 Gap makers

Within each gap I attempted to identify the species of all fallen or dead standing trees rooted in the gap or in the expanded gap area that were greater than 10 m in height. I classified these individuals as "gap makers". I largely followed Lertzman and Kreb's (1991) criteria and assigned a qualitative age to each gap maker based on the degree of decay experienced. These categories were (1) new: where the small branches, and often needles, were still present; (2) medium: only large branches present and most of the bark had peeled; (3) old: branches and bark generally absent, clear evidence of decay in the heartwood, yet the majority of the bole uncovered by bryophytes, along with some cohesiveness to the decaying bole; (4) very old: most, if not all of the recognisable bole structure was cover by bryophytes and largely incorporated into the forest floor. In many cases, only the base of the tree, where the larger mass of wood associated with the start of the root system, remained. I also identified the mechanical mode of gap formation associated with tree mortality. For each gap maker I recorded whether the tree remained standing, snapped off above the ground, or tipped up on the edge of its root ball. Beatty and Stone (1986) distinguish two types of tip-up (hinge and rotational). However, these were too difficult to clearly separate in the older age classes. I therefore only recorded the general class.

Although assigning a range of ages to the decay categories was not possible because of considerable decay in the older classes, I was able to get a general qualitative marker by comparing the defined decay classes to fire killed-downed woody debris in the younger stands described in Chapter 3 with the well established fire history dates. These stands were 150 to 160 years old. As the decaying debris in those stands matched characteristics of both the medium and old categories defined above (i.e., approximated the class boundary), I used this as a rough guide to ageing gap makers.

4.2.2.4 Seedling microsites

I first wanted to assess the importance of differentiation in the seedling regeneration niches in relation to the different canopy stratum types defined above. Lieberman and Lieberman (1989) have pointed out that many gap dynamic studies fail to determine if tree fall gaps are important structures for regeneration, by not looking outside of the gap. Second, as pointed out in Chapter 3, forest floor rooting substrate varies at quite small scales, and I wanted better resolution of species' seedling preferences in the substrate type that may have been missed in the general forest structure assessment of Chapter 3. To assess seedling microsite preferences, I located 50 seedlings (< 30cm tall) of each tree species. This was done by generating random directions and distances and choosing the closest seedling to the resulting point. At each seedling I assessed the local overhead canopy stratum type as gap, expanded gap, or closed canopy. I also determined whether the seedling was rooted in a bryophyte mat, organic matter, or decaying wood (these were effectively the only types of substrate present; see Chapter 3). Because obvious sources of decaying wood were often concealed under a thin bryophyte layer that may have confounded the probability of finding the actual rooting substrate of a given species of seedling, I made the further distinction between these classes: where the bryoid rooting layer was less that 2 cm over top of decaying wood, I classified the substrate as decaying wood; where this layer was greater than 2 cm, the substrate was classified as bryophyte mat. This distinction was based on information from Knapp and Smith (1982), who showed that litter depth greater than this affected the abundance of spruce seedlings, due to poor initial root growth. This part of the study was only carried out at the upper sampling location.

I used contingency table analysis (G-tests; Sokal and Rohlf 1995) to determine if each seedling species was found more or less frequently under the different canopy categories. I used the proportion of these categories previously determined from the forest structure plot data to set the expected frequencies of each species in gap, expanded gap, or closed canopy. Similarly, I used the proportion of bryophyte mats, organic matter, and decaying wood determined from the forest structure plot data to provide the expected frequency distribution of each of the species' seedling counts in these different rooting substrate types.

4.2.2.5 Gap fillers and gap environment

To aid in determining future canopy composition, I identified the most likely tree(s) to fill a given gap. This choice of gap filler was based on a combination of criteria. All likely gap fillers had to be greater than breast height (1.3m). This was a useful cut-off because it limited the number of choices, and it was generally the height at which I observed all three tree species to show significant increases in leader growth, especially in areas with competing shrubs. Therefore, gap fillers were the individuals exhibiting healthy terminal leader extension, and were relatively free from physical damage, disease, or obvious competition. In many cases, more than one individual or species was chosen, and in only one gap was no gap filler identified. These gap filler criteria are analogous to those of Veblen's (1986) "potential successor" and Lertzman's (1992) "definitive gap filler".

I also determined the relative position of the gap fillers within a gap. Because many of the gaps were irregular and relatively small, I only identified two general aspect positions within each gap, north and south, as this would likely capture the orientation of the major environmental gradients. I used contingency tables to assess whether species of gap filler was independent of location.

Transition probability matrices are commonly used to predict the future canopy composition of forests undergoing gap-phase disturbance regimes (Barden 1980, Lertzman 1992, Wilson 1992). Although it is possible to base the expected frequencies, or replacement probabilities of these matrices on several different estimates of species proportions, estimates derived from gap fillers appear to provide the most realistic assessment of future canopy compositions (White et al.1985, Dahir and Lorimer 1986). Therefore, I used contingency tables to determine if the proportional representation of gap filler species differed significantly from what was expected based on the identity of gap maker species.

However, this information only provides an estimate of canopy composition following a single transition step (i.e., the rotation time of the forest canopy described above). To gain insight into possible longer term changes in the proportion of canopy tree species, I used the expected proportion of canopy species from the gap filler data as an initial starting point for a simple transition model. This model estimates the new proportion of the canopy that each species will fill as a function of both the species' surviving canopy proportion and the expected recruitment canopy proportion (Table 4.0).

Table 4.0: Canopy composition transition model. The three elements in bold are the required data. The example data shown are for the lower transect in Arnica.

	Species		
Model elements	fir	spruce	larch
starting proportion of canopy	0.833	0.111	0.056
proportion of forest in gap phase	0.580	0.580	0.580
gap maker proportion	0.733	0.200	0.067
gap filler proportion	0.833	0.111	0.056
survived:(startCanopy-(startCanopy x gapMakers)	0.222	0.089	0.052
recruited (gapFiller x proportionGap)	0.483	0.064	0.032
sum of survived and recruited	0.706	0.153	0.084
new proportion of trees (sumSurvRecrt /total sumSurvRecrt)	0.748	0.163	0.089

To calculate the proportion of canopy held by each species in the next time step, the output for the new proportion of trees (the bottom line in Table 4.0) is substituted as the starting proportion of canopy (the top line in Table 4.0). The model assumes that the proportion of forest in a gap phase, the proportion of each species' gap makers, and the proportion of the gap fillers remain constant over time.

In Chapter 3, I showed that variation in basal area, canopy cover (as a surrogate for attenuated light; see Appendix II), and local canopy height were significantly related to early establishment of larch or spruce seedlings. Therefore, in addition to the gap area measurements, I collected these environmental variables as potential predictors of the occurrence of the gap fillers. I recorded the average canopy cover using a convex densiometer at a minimum of four locations around the perimeter of each gap. I measured average height of the canopy at opposite sides of the gaps using a clinometer and a measuring tape. I also recorded the average basal area of the tree species surrounding each of the gaps using a Bitterlich gauge with an eye to sight distance of 25cm (Mueller-Dombois and Ellenberg 1974).

Other workers have found that gap aperture is a useful descriptor of photosynthetically active radiation (PAR), and gap size (Lawton and Putz 1988). Gap aperture is the average angle of sky visible between gap horizons viewed from the centre of the gap. Although Lertzman (1992) found no significant correlation between gap aperture and gap fillers in Pacific subalpine forest, this measure may be a useful predictor in systems where there is a greater discrepancy in shade tolerance between species. I measured this average angle standing at the centre of each plot using a clinometer.

I used multiple regression to model the occurrence of each gap filler species as a function of the measured gap environmental characteristics. As the gap filler data were counts, and not normally distributed , I used a generalised linear modelling (GLM) approach (Crosbie and Hinch 1985, Nichols 1989, Lindsey 1995, Mathsoft 1999). I used a forward selection and residual examination procedure similar to that described by Nichols (1989) to select the most parsimonious set of predictor variables for each gap filler species, with one exception. Because the individual gaps acted as the plots, or "quadrats" (Meuller-Dombios and Ellenberg 1974) in which the response was measured, I chose to standardise the influence of the different sized gap areas by first fitting the logarithm of the gap area as a covariable. The logarithm of this variable was used because gap area varied over several orders of magnitude. I chose alpha = 0.05 as a criteria to reject terms for model inclusion. As with the previous Chapters, I visually explored the data prior to these analyses to detect any non-linear relationships between the response and predictor variables that may have been better described by polynomial or logarithmic transformations of the predictors. I used boxplots and smoothing functions to aid these interpretations. All analyses, except that of the contingency tables, were carried out using Splus statistical software (Mathsoft 2000).

4.3 Results

4.3.1 Canopy cover types and gap areas

There was a significant change in the proportion of forest area in gap between elevations (Figure 4.1). The average for the lower transect was 42.9% compared to 60% and 57.9% for the middle and upper elevations. However, the proportion of forest in expanded gap did not vary significantly over elevation (upper 38.8%, middle 30.0%, and lower 34.0%). The proportion of forest in closed canopy showed the opposite trend to that of the gap. There was significantly more at the lower elevation compared to the higher elevations (upper 18.4%, middle 10.0%, lower 8.1%).

Although the average gap and expanded area appeared smaller in the lower sampling location compared to the middle and upper locations (Table 4.1), ANOVA of both the raw and the log transformed data failed to reject the null hypothesis that these values were the same. However, examination of the distribution of the data shows that at each elevation there is at least one outlying larger gap area from the main cluster of gap areas (Figure 4.2). This is most pronounced in the lower sampling location where the three larger gaps double the size of the mean compared to the median area value (Table 4.1). Omitting these outliers produces a significant difference between the lower sampling location and the higher locations for both the gap and expanded gap area measurements (gap area $p < 0.01$, df 2; expanded gap area: $p < 0.01$, df 2).

Table 4.1: Summary statistics for canopy gaps And expanded gaps.

Sampling location	summary statistics	gap area (m^2)	expanded gap area (m^2)
lower	Mean:	46.0	68.8
n = 11	Median:	26.9	52.2
	Sum:	506.5	757.0
middle	Mean:	64.4	96.9
n = 15	Median:	67.5	94.8
	Sum:	966.1	1454.1
upper	Mean:	73.5	108.2
n = 16	Median:	67.3	102.8
	Sum:	1175.4	1730.9

n = number of gaps.

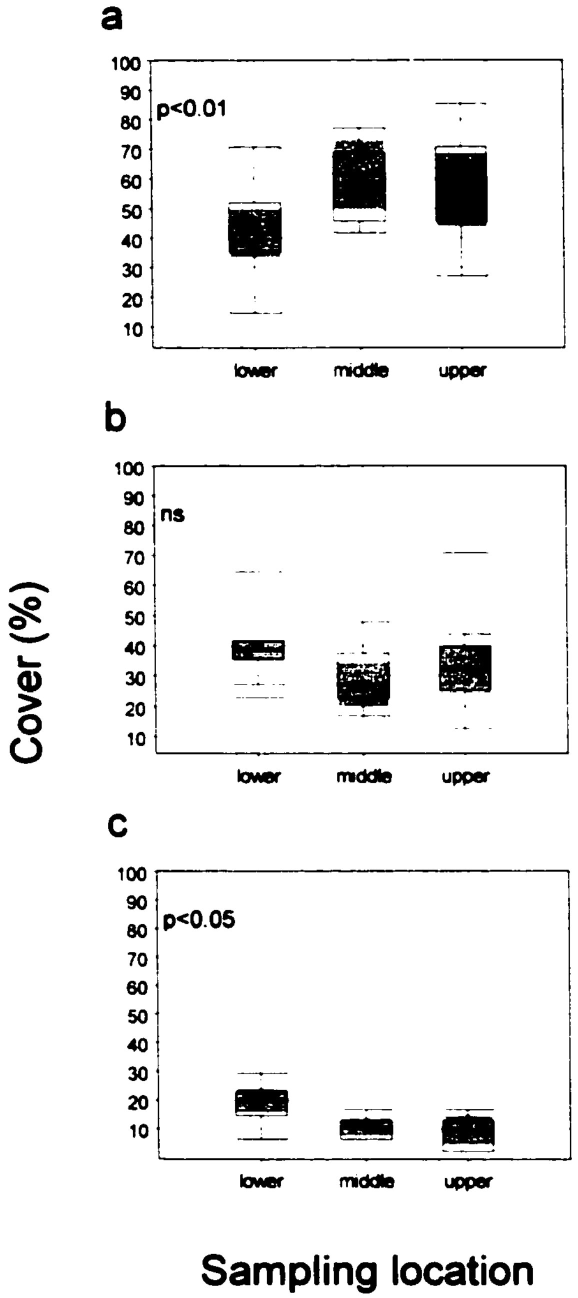


Figure 4.1: Box plots of percent (a) canopy gap, (b) expanded gap , and (c) closed canopy for each elevation sampling location. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box. Single horizontal lines indicate one observation. P-values indicate the outcome of one-way analysis of variance between transect elevations. ns: not significant.

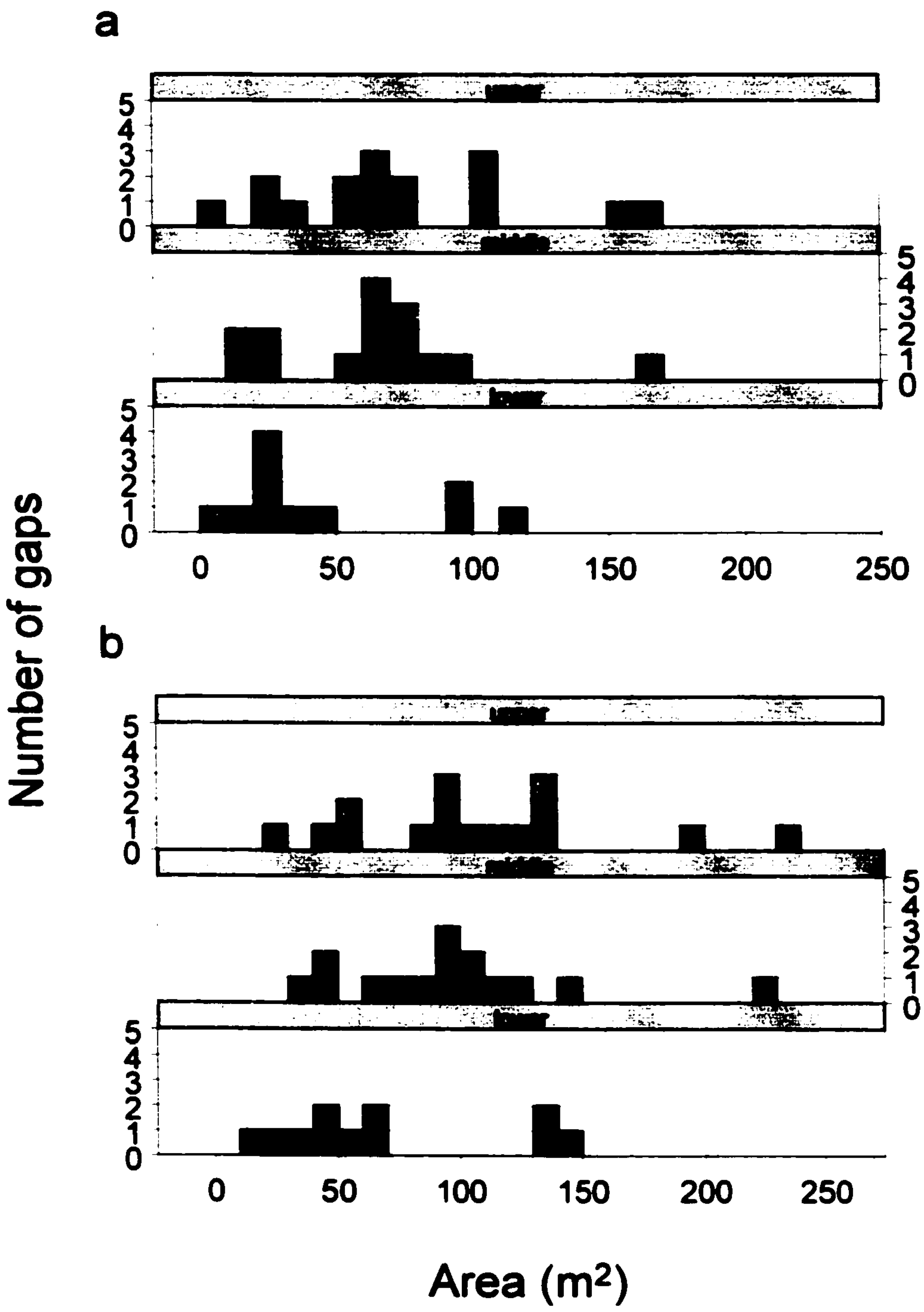


Figure 4.2: Distributions of (a) gap area and (b) expanded gap area at Arnica. Note the outlying larger gaps at each elevation.

However, these large gaps were still meaningful observations, as they accounted for large proportions of the total area disturbed at each elevation. The distinction is that the median, rather than the mean, was perhaps the more informative comparative measure of gap size.

4.3.2 Age-height relationships and forest canopy turnover

For each of the species the height data significantly predicted the age. The exception was for alpine larch in the lower transect, where there were only six age observations (Figure 4.3, table 4.2). Most of these regression models explained greater than 60% of the variance in the age data. The most common relationships were age as a power function of height, although the log of height was also used. Both of these data transformations describe slow initial growth for each tree species until about 2-2.5m, followed by more rapid periods of growth as the tree gains height (Figure 4.3).

The estimated canopy turnover time of each species at each elevation in the study area indicated forest turnover was long (Table 4.2). Averaging the species rates gave the lower stand elevation the longest turnover period of 556 years. The middle and upper areas had average turnover periods of 365 years, and 315 years respectively. Weighting the average turnover period by each species' gap filler proportion reduces the lower and middle values to 470 years and 356 years, respectively.

Table 4.2: Height - age models and the estimated turnover period for each tree species at sampling locations in Arnica.

Sampling elevation	species	curve fit equation	p-value	R^2	estimated age at 10m	estimated turnover period (years)
low	alpine larch	$y = 4.09X + 233.4$	0.12	0.49	274	637
low	subalpine fir	$y = 87.19 X + 104$	0.00	0.8	191	444
low	Engelmann spruce	$y = 132.6 \log X + 119.2$	0.00	0.91	252	586
mid	alpine larch	$y = 67.39 X^{0.4758}$	0.00	0.92	202	337
mid	subalpine fir	$y = 43.06 X^{0.6512}$	0.00	0.91	193	322
mid	Engelmann spruce	$y = 68.6 X^{0.5813}$	0.00	0.87	262	437
high	alpine larch	$y = 63.3 X^{0.5063}$	0.00	0.67	203	350
high	subalpine fir	$y = 84.0 \log X + 98.28$	0.00	0.73	182	314
high	Engelmann spruce	$y = 80.87 \log X + 83.24$	0.00	0.54	163	281

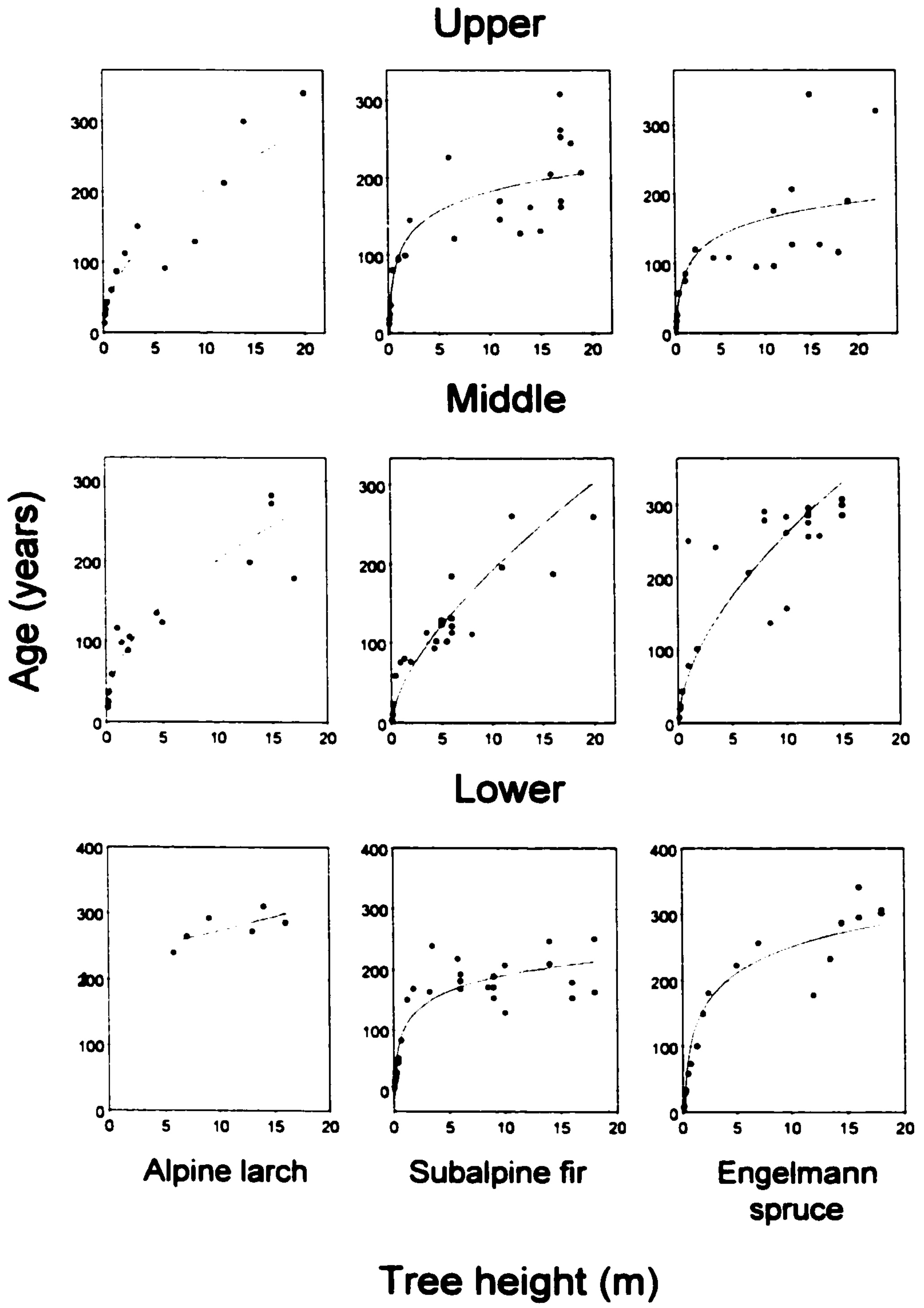


Figure 4.3: Age height curves for the main tree species at each sampling elevation. See Table 4.8 for curve equations.

4.3.3 Seedling microsites

The G-tests of tree species' seedling canopy cover type associations showed that both alpine larch and Engelmann spruce seedling numbers differed significantly from expected (Figure 4.4a). Aside from 3 individuals, alpine larch seedlings were only found in canopy gaps. Engelmann spruce seedlings also showed a strong association with canopy gaps, but a small number were found under both closed canopy and expanded gap. On the other hand, subalpine fir showed no significant association for canopy type. In the rooting substrate association tests, alpine larch showed no significant association with substrate type. Engelmann spruce were significantly more frequent in the decaying wood category, and fir were more commonly in the organic matter (Figure 4.4b).

4.3.4 Gap makers

I recorded a total of 134 gap makers in the 42 gaps that I surveyed (Table 4.3). The greatest percentage of these were subalpine fir (45%), followed closely by the group of gap makers that were too decayed to identify (40%). Only 5 identifiable alpine larch gap makers were encountered in the study, roughly 4% of the total (Table 4.3). The most frequently encountered gap maker cause was tip-up, and the majority of these were associated with unknown species. Subalpine fir was most closely associated with the next two most common gap maker types; snapped boles and dead standing. The rest of the gap maker species, including alpine larch, were too few to choose a common gap maker type confidently.

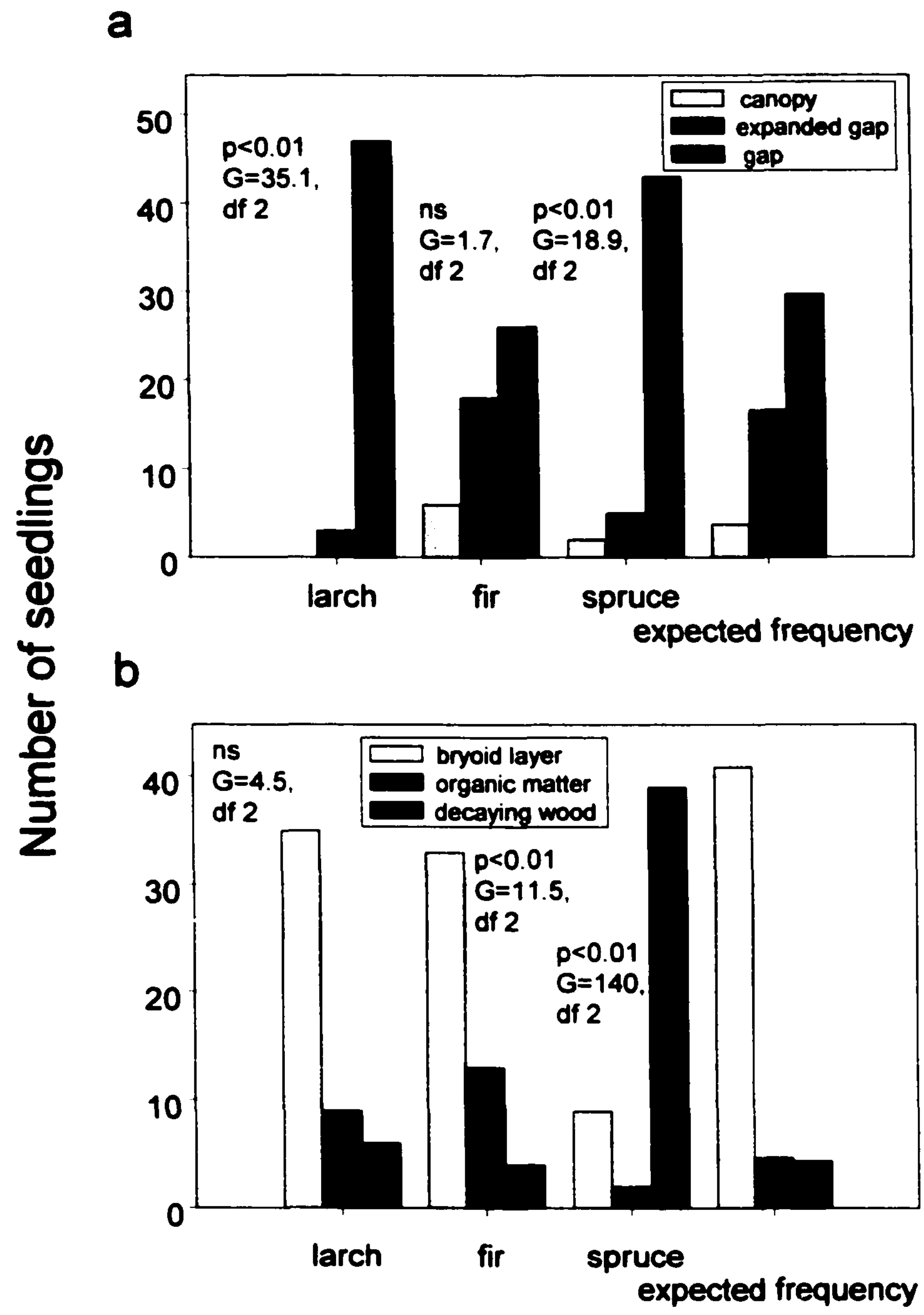


Figure 4.4: Seedling microsite associations. Bars represent the distribution of conifer seedlings found (a) under closed canopy, expanded gap, or gap cover environments, and (b) rooted primarily in either the bryoid mats, organic material, or decaying woody debris. Departure from expected distributions (derived from forest structure plots) were assessed using G-tests. P-values are indicated. ns: not significantly different.

Table 4.3: Type of gap maker mortality arranged by species and elevation.

Gap maker	Type				
species	snapped	standing	tip-up	unknown	total
Subalpine fir	31	16	13	0	60
Alpine larch	3	1	1	0	5
Lodgepole pine	0	1	0	0	1
Engelmann spruce	6	4	4	0	14
Unknown	9	0	36	9	54
Total	49	22	54	9	134
Elevation	snapped	standing	tip-up	unknown	total
lower	10	6	14	1	31
middle	21	8	17	1	47
upper	18	8	23	7	56
Total	49	22	54	9	134

The gap maker age data contained several interesting trends. In general, the numbers of gap makers declined with age, from new to old, followed by a jump in numbers of the very old to almost that of the new gap makers (Table 4.4). The greatest proportion of the largest gap maker type, tip-up, was associated with the old and the very old. Whereas, the greatest proportion of the next two largest gap maker types, snapped and standing, were associated with the younger gap maker ages (Table 4.4). This last pattern likely reflected the susceptibility of the stands' trees to windthrow as they matured and became decadent. The large numbers of very old tip-up gap makers are likely the remnants of the previous coarse scale disturbance.

Table 4.4: Distribution of gap makers arranged by type of mortality and elevation. Qualitative age categories: new (most bark and small branches still present), medium (most bark peeled, large branches still present), old (bark and branches gone, evidence of decay in heartwood), very old (most of bole covered with bryophytes and largely incorporated into the forest floor).

Gap maker	Age				
type	new	medium	old	very old	total
Snapped	17	19	8	5	49
Standing	17	5	0	0	22
Tip-up	7	7	14	26	54
Unknown	0	0	1	8	9
Total	41	31	23	39	134
elevation	new	medium	old	very old	total
Lower	5	7	7	12	31
Middle	14	15	10	8	47
Upper	22	9	6	19	56
Total	41	31	23	39	134

4.3.5 Gap fillers and gap environment

I identified a total of 97 gap fillers over the three sampling elevations in the study area (Table 4.5), 28% fewer identified gap fillers than the total number of gap makers. Over 64% of the gaps had more that one gap filler, with 8 as the greatest number in any one gap. Using the proportions of the main identified gap makers (i.e., fir spruce, and larch; Table 4.5) to produce expected frequencies of gap fillers, I determined that there were significantly greater numbers of alpine larch likely to fill canopy gaps than expected. This appeared to be at the expense of the more abundant subalpine fir (Figure 4.6). There were also slightly more spruce gap fillers.

Table 4.5: Breakdown of gap filler and maker species by elevation.

Species	Sampling location			
Gap filler	lower	middle	upper	total
Subalpine fir	15	27	23	65
Engelmann spruce	2	13	4	19
Alpine larch	1	7	5	13
Total	18	47	32	97
Gap maker				
Subalpine fir	11	21	28	60
Engelmann spruce	3	10	1	14
Alpine larch	1	2	2	5
Total	15	33	31	79

The future canopy composition trajectories produced from the transition model (Figure 4.6) shows that in the middle and upper areas of the stand, larch increased to capture roughly a third of the canopy – largely at the expense of fir. However at the lower site, larch captured only a fifth of the canopy, and given that no seedlings or samplings were found at that elevation it would be more likely that larch would be lost from the forest by the end of the second transition.

There was also a general trend in the position of the species recruitment in gaps. Table 4.6 shows that both spruce and larch were somewhat more frequent on the northern side of gaps; the larch significantly so (G = 3.98, df 2). However, the low numbers of these less common gap filler species make it difficult to have confidence in these trends.

Table 4.6: Position of gap fillers in gaps.

Gap filler	location in gap		
species	south	north	total
Subalpine fir	33	32	65
Engelmann spruce	8	11	19
Alpine larch	3	10	13
Total	45	52	97

4.3.5.1 Gap environmental models

There were very few gaps with more than one larch or spruce gap filler, but there were many gaps where one or the other species was absent. Therefore, I converted these multiple gap filler occurrences to a single presence, and specified a binomial error distribution for these response data, and then fit them using logistic regression. Multiple subalpine fir gap fillers were found in 17 gaps, with only four gap with no fir gap fillers. Because these data more strongly followed a Poisson distribution, I the fit the data using a log-linear model (Mathsoft 1999).

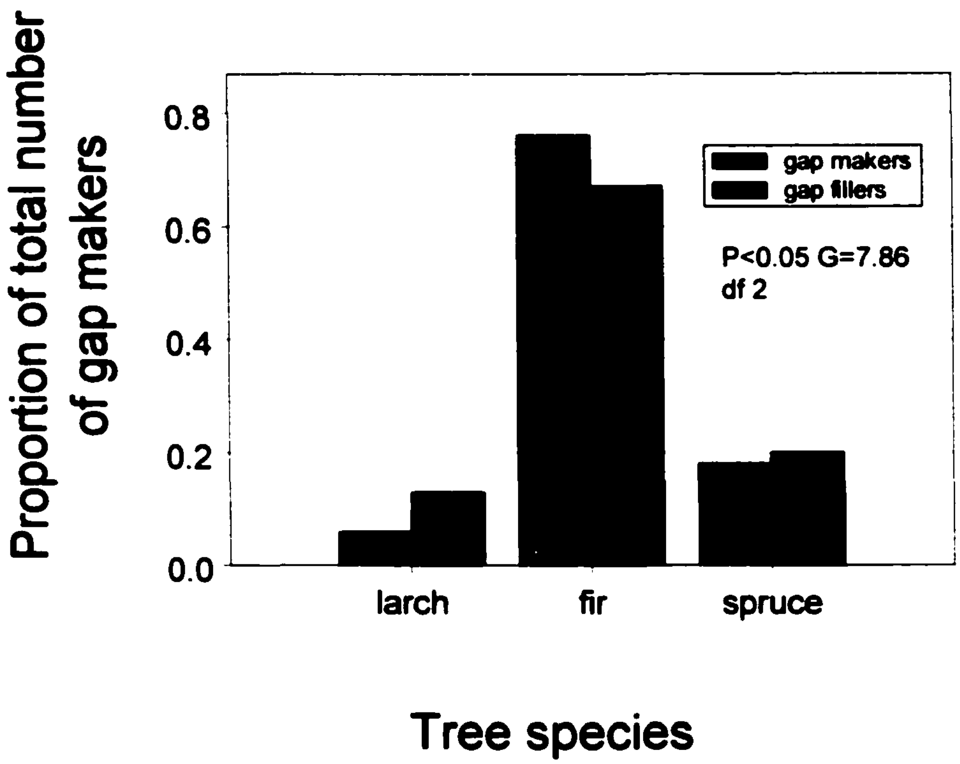


Figure 4.5: A comparison of the proportion of gap makers species to gap filler species. Greater numbers of alpine larch gap fillers, and fewer subalpine fir gap fillers were found, given that expected from the proportion of the total number of gap makers species surveyed. Note that G was calculated on observed and expected counts, whereas only proportions are shown here.

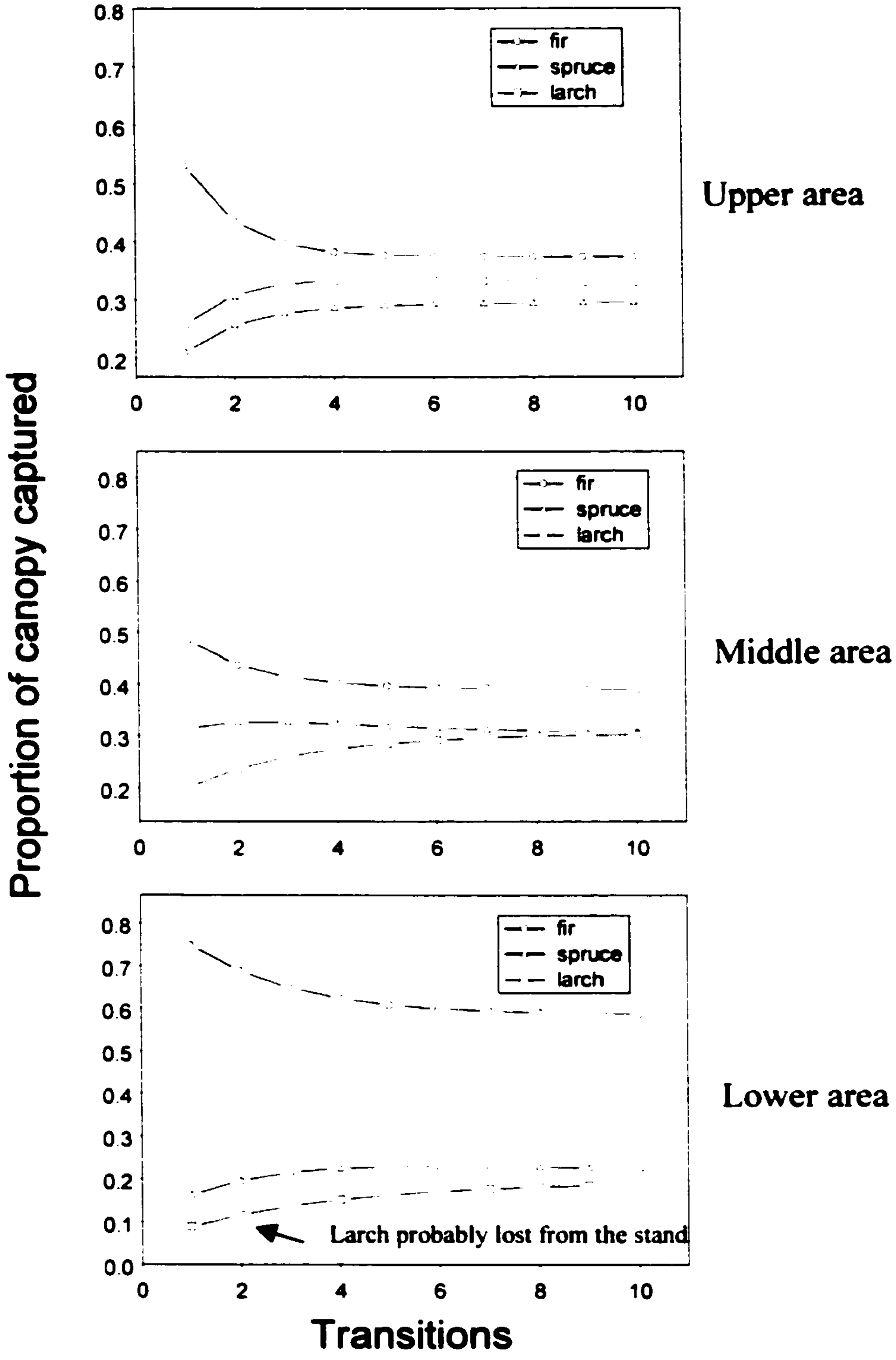


Figure 4.6: Canopy proportion trajectories for larch, spruce and fir based on 10 transitions of the model described in Table 4.0. Note that the presence of larch in the canopy at the lower elevation site is unlikely following the second transition as no seedlings or saplings were present in the understory.

There were two significant terms in the best fit alpine larch model after fitting the log of gap area (the partial model). These were a negative relationship with canopy cover and canopy height. These two terms explained 24% of the partial model deviance (Table 4.7). Only the log of gap area was important in explaining the deviance in either the Engelmann spruce or the subalpine fir data. This term explained 10 % and 21% of the null model deviance in each of the tree species' data, respectively (Table 4.7).

Table 4.7: Best fit gap filler models.

Gap filler species	Term	df	Deviance explained	Residual df	Residual deviance	p-value
Alpine larch	Null model			41	30.07	
	log (Gap area)	1	7.47	40	22.59	0.00
	Canopy cover	1	2.98	39	19.61	0.02
	Canopy height	1	2.52	38	17.09	0.03
Engelmann spruce	Null model			41	30.89	
	log (Gap area)	1	3.01	40	27.88	0.05
Subalpine fir	Null model			41	30.07	
	log (Gap area)	1	6.46	40	23.61	0.00

Although greater numbers of gap fillers with increasing gap area might be expected merely as a result of the greater area surveyed, examining the patterns of gap filler occurrence over the range of this covariable provides important information. Figure 4.7a shows how each of the species of gap filler responded to increasing gap size. The proportion of Engelmann spruce gap fillers initially peaked about at about 70m^2, and then started to oscillate with increasing area. The alpine larch gap fillers appeared more abruptly, but also initially peaked at 70m^2. However, the greatest response of this species was not reached until at about 115m^2; a local minimum for the spruce. Subalpine fir gap fillers were present over the range of gap areas sampled, but increased dramatically in the large gap sizes after the alpine larch response peak (Figure 4.7a).

The response to canopy cover shows that larch occupied only the higher light environments, where the smoothed response of both spruce and fir were lower (Figure 4.7b). The larch response declined steadily with increasing cover, and disappeared from gaps where canopy cover exceeded about 55%. Subalpine fir gap fillers were present over the range of light environments; however, the fir's response was reduced in the higher light environments, peaking at about 50-55% canopy cover, before gradually declining

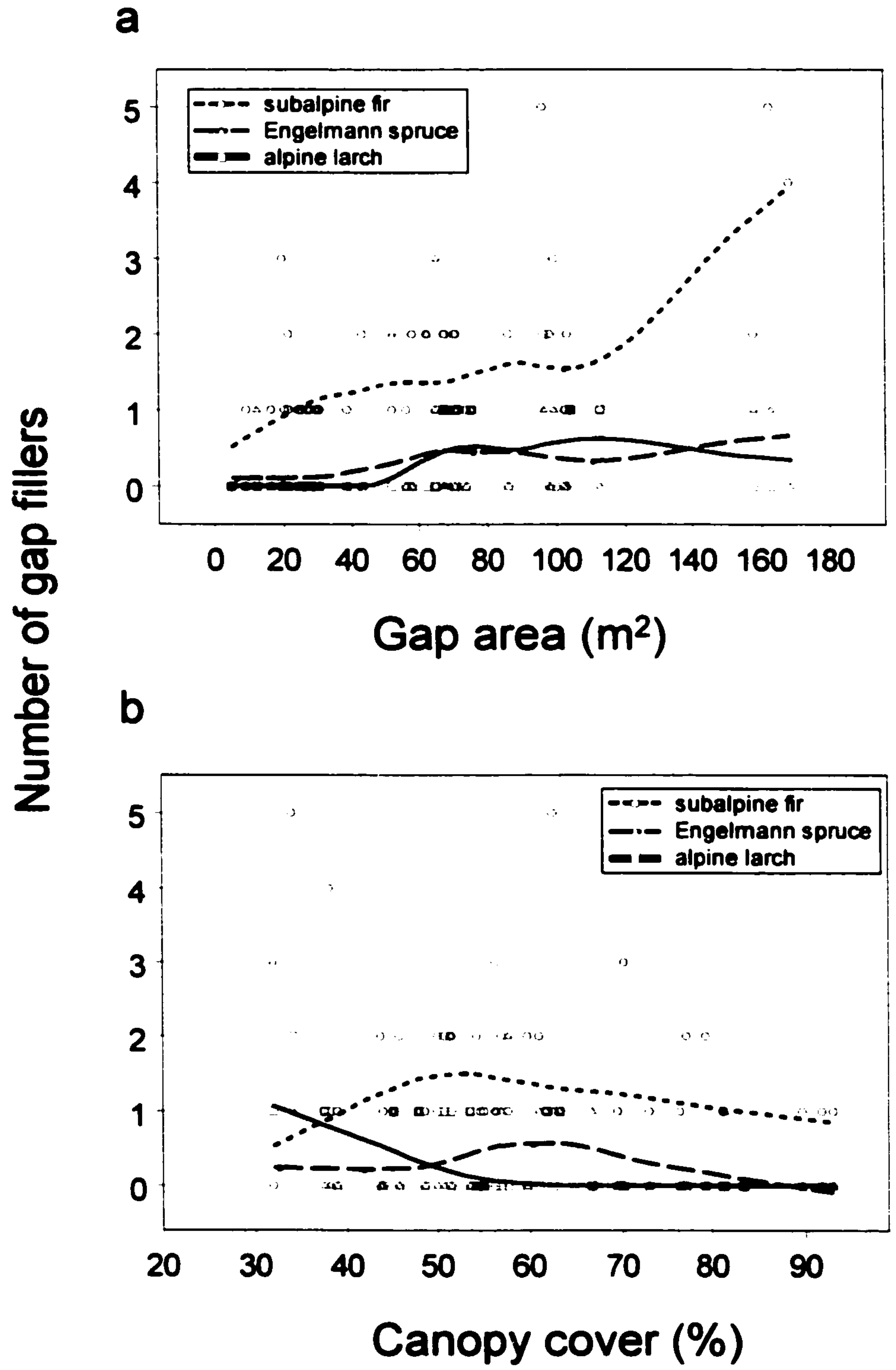


Figure 4.7: The relationship between gap filler species and (a) gap area, and (b) canopy cover. The lines are locally weighted regression smoothers to aid with visual interpretation, but are independent of the statistical model.

again with increasing cover. Although the Engelmann spruce gap fillers were still present in the higher light environments, the peak response of this species was at 60% cover, in slightly lower light environments than the peak response of subalpine fir. Engelmann spruce was absent from gaps where cover exceeded 80%.

Examining the relationship between gap area and canopy cover helps clarify these somewhat different patterns of gap filler species response in the range of gap sizes and light environments (Figure 4.8a). Regions of higher canopy cover and smaller gap size are strongly correlated. This relationship starts to weaken at a gap size of about 70m^2, roughly corresponding to the initial peaks of larch and spruce in Figure 4.7a. The matching canopy cover value of 55% from Figure 4.8a also corresponds to the region of peak fir abundance with canopy cover, and the rise of the larch gap fillers (Figure 4.7.b). This weakening of the relationship likely represents the increasingly irregular shapes of the larger canopy gaps, indicating that the gap light environment was no longer related to increasing area. This is further indicated by the point of inflection at 115m^2 in Figure 4.8a, where canopy cover started to increase again. Here, the corresponding larch response in Figure 4.7a reached its maximum – and then started to decline, and the response of subalpine fir increased dramatically with gap area.

The significant gradual decline of the presence of larch gap fillers with height is shown in Figure 4.8b. Both spruce and fir gap fillers are present in gaps with surrounding canopy of all heights. Alpine larch gap fillers declined with increasing canopy height and were absent from gaps where the canopy exceeded 17m. For comparative purposes I also ran the forward selection procedure without the covariable to see if any of the variables correlated with gap area, such as gap aperture and canopy cover, were better predictors of the gap fillers. The only model for any gap filler species was the significant relationship between canopy cover and alpine larch. This explained 29% of the null model deviance. It is interesting to note that surrounding canopy height was only selected in the alpine larch gap filler model after the effect of gap area had been partialled out by the inclusion of the covariable. This suggests that the biomass of the surrounding trees has a separate negative effect on the success of larch gap fillers, beyond that of canopy cover.

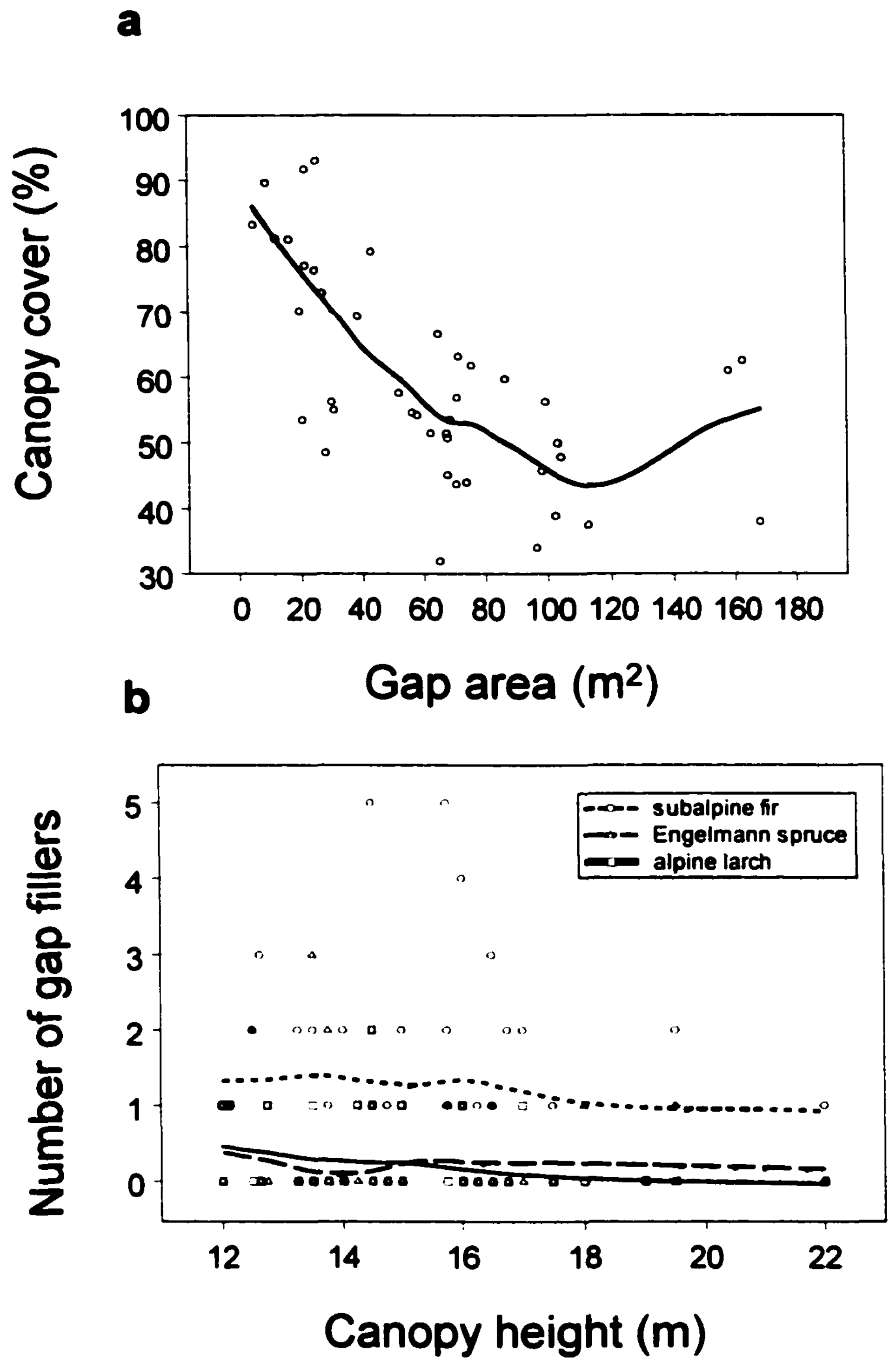


Figure 4.8: (a) the relationship between canopy cover and gap area. (b)The response of gap filling species to gaps with different canopy height. Presence of larch gap fillers declines with surrounding canopy height, whereas, the spruce and fir show no consistent trend. The lines are locally weighted regression smoothers to aid with visual interpretation, but are independent of the statistical model.

4.4 Discussion

4.4.1 Canopy cover types and gap areas

The average proportions of forest gap at each of the sampling elevations were considerably higher than reported for many of the other temperate gap-phase systems. (Runkle 1982, Veblen 1988, Spies et al. 1990, Lertzman 1992, Lertzman et al. 1996, Tanaka and Nakashizuka 1997, Battles et al. 1995). One similar value reported (56%) to the higher two sampling areas was from a higher elevation giant fir-mixed pine stand in the Sierra Nevada mountains (Van Pelt and Franklin 2000). Also, Kneeshaw and Bergeron (1998) describe older fir dominated boreal forest which have gap percentages (40.4%) that approached the lower sampling location values. Although there are not enough reported data to thoroughly compare differences in gap proportions between montane and subalpine forests, the general trend to larger total land area covered by gap as timberline is approached is relatively well documented (Wardle 1974, Tranquillini 1979).

Higher elevation areas typically have lower air and soil temperatures (Daubenmire 1974), and snow cover that persists longer than at lower elevations. These factors reduce the length of the growing season. Persistent snow cover, in particular, retards seedling growth well past normal bud break in the taller trees free from the snow pack (Arno and Hammerly 1984, Worrall 1995). This means that larger gaps, which are more likely to be in filled by gap filler recruitment than lateral extension of surrounding canopy trees (Connell and Slayter 1977), may be further delayed as seedlings slowly pass through this height barrier.

A graphic example of this mechanism is the documentation of a wide spread even-aged cohort of timberline trees whose ages correlate with the consistently shallower snow packs experienced in the "dust bowl" years of the 1930s to the mid 1940s across North America (Franklin et al. 1971, Arno and Hammerly 1984). On north aspects in the Bow Valley, snow remains on the ground at high elevations until late June. In contrast, southern aspects and lower elevations may be clear of snow up 3 weeks earlier (personal observation). Thus, part of the elevation difference in the total forest area in gap reported in this study is likely related to climatic factors. The increased median gap sizes at the higher two sites support the view of larger gaps being primarily responsible for the greater forest gap proportions. Yet, the slow canopy turnover at the lower sampling location (Table 4.2) suggests that the cause of the larger gaps may be also related to a greater rate of canopy disturbance

4.4.2 Gap makers: patterns of distribution

A difference in disturbance rate between elevations is supported by comparing the ratio of the sum of new and mid, to old and very old gap makers (Table 4.4). At the lower sampling location the ratio is less that 1, indicating that the gaps there were dominated by older canopy disturbances. In the higher two locations the ratios were greater than one, indicating that gaps were dominated by more recent disturbances. This type of differential disturbance rate could arise from the position on the ridge, as increasing wind velocities with elevation increase the probability of windthrow at the higher two sampling areas (Alexander 1987, Battles et al. 1995).

Veblen (1986), in his study of spruce-fir forests further south in the Rocky Mountains, attributed the majority of treefalls to wind-snap. However, he also indicated that he believed the majority of these were dead before they fell. In the present study, snapped and dead standing stems were equally prevalent (about 41% each) as the main mortality mode for new gap makers (Table 4.4). In the medium age category, snapped stems increased to about 61% of the total mortality mode, more than compensating for the decrease in the amount of standing dead. Although I did find several of the new snapped individuals that were obviously still alive before their boles broke, the above accounting exercise suggests that most of the recent mortality was due to factors that left the affected tree standing.

Two common sources of smaller scale canopy disturbance that leave affected trees standing in Engelmann spruce – subalpine fir forest are spruce beetle (Alexander 1987) and trunk rot (generally *Phellinus* sp.; Hind 1977). Evidence of each of these pathogens was observed at low levels throughout the site. A more novel source of stress may also have added to premature tree mortality at the higher sites. High density of arboreal lichen in the upper parts of the stand commonly covered large areas of the available photosynthetic tissue of the spruce and fir trees. The most prolific lichens were species in the *Bryoria, Alectoria,* and *Usnea* genera. The added light interception created by the lichen may have aided in accelerating death in old trees already experiencing low carbon budgets and other health issues whose management demand an output of extra energy. An interesting feature here was that the larch were not nearly as badly affected. Although some lichen would be draped over the main branches of the larger trees, the architecture of the needles and branches did not appear to effectively hold the same mass of filaments. Also, any accumulated tufts caught in the needles would be lost annually in the fall, unlike the evergreen conifers. Clearly more research is required to determine the extent and magnitude of these observations.

4.4.2.1 The influence of past large scale disturbance

The large number of very old gap makers, compared to the steady decrease in gap maker numbers over decay class, indicates that a pulse of mortality occurred at a time consistent with the time of death of the very old gap makers (Table 4.4). These dead trees are most likely the remnants of the original stand-replacing fire (ca.1620; Rogue and Gilbride 1994), given the decay class age verification for the difference between medium and old gap maker classes described above (Methods). Further support for this view is the far greater numbers of tip-ups in the very old class (Table 4.4). This mode of tree fall is particularly common in fire killed trees of this area of the Rockies (Dubé 1976; personal observations). The predominance of tip-ups appears to be the result of much more rapid root decay within the soil, compared to the above ground structural wood of the fire killed tree. On a number of occasions, I witnessed winds of less that 60 km/h push over 30 year old snags in the Vermillion Pass burn (see Chapter 2) in a tip-up fashion. These events expose a greatly reduced root system and disturb far less soil than tip-ups resulting from the wind throw of live trees in surrounding forest.

4.4.3 Seedling microsites

The substantial input of wood from past coarse scale disturbances may be especially important for spruce regeneration in older forests. The results of the seedling substrate analysis showed that 72% of spruce seedlings were found rooting in decaying wood that covered only 8.8% of the forest floor (Figure 4.4b). Based on the distribution of the very old tip-up gap makers, up to 50% of the observed decaying wood may be the result of a single past stand replacing disturbance (Table 4.4).

The strong association of spruce seedlings with decaying wood is a common feature in a number studies examining regeneration in older forests (Smith 1955, Day 1964, Hofgaard 1993, Hiura et al. 1996, Anderson and Winterton 1996). Knapp and Smith (1982) found that early root growth of Engelmann spruce was substantially less than subalpine fir. They suggest that the success of Engelmann spruce regeneration on decaying wood over the other kinds of substrate in older forest is due to more consistent moisture availability in decaying wood, compared to the deeper layers of other substrates that dry out rapidly. This dependence on decaying wood means that spruce regeneration is not only limited by available substrate, but also spatially dependent on where the substrate occurs. This situation appears to relax a little in canopy gaps, where Engelmann spruce was found more frequently than expected (Figure 4.4a). All of the seedlings sampled that were either in organic matter, or the bryoid layer, were found in gaps. This correlates with the greater surface soil moisture expected in gaps because of lower levels of canopy interception and soil moisture depletion by roots of overstory trees. Where spruce occurred under closed canopy and expanded gap, it was exclusively found on decaying wood.

Subalpine fir seedlings were found more commonly than expected in the organic matter within the stand. The main source of organic matter was the needle litter and dried twigs found directly adjacent to the canopy of individual trees. This was a somewhat surprising result, given the arid nature of these microsites. However, this pattern was likely due to inadvertently sampling clonal reproduction of adjacent mature subalpine fir individuals. I attempted to not select vegetative reproduction by rejecting the obvious examples that were presented by the random selection procedure. However, the basal branches of subalpine fir, in particular, tended to create suckers that would run out, in some cases, up to 2m, making this assessment sometimes difficult. This tendency for vegetative layering of subalpine fir has been noted in other high elevation stands (Shea and Grant 1986). Subalpine fir were not significantly more frequent in any of the canopy stratum types. This corresponds well with this species' documented shade tolerance (Knapp and Smith 1982; Alexander 1987; Alexander et al. 1990), but may also reflect the clonal reproduction.

The lack of a significant substrate association in the alpine larch seedlings is most likely related to the fact that this species was almost exclusively found in canopy gaps (Figure 4.4a). Richards (1981) determined that seedlings of alpine larch were highly susceptible to both soil drought and low light conditions. In particular, he found the diffusive conductance of the needles was greatly reduced by low soil water potentials, and that conductance would remain low for prolonged periods even after drought was released. This means that seeds germinating under canopy where soil moisture is highly variable would also be internally subject to periods of low photosynthetic activity. The combination of these suboptimal conditions of fluctuating moisture and low light would likely prohibit any seedling establishment. In areas where adequate soil moisture was available, Richards (1981) found that alpine larch seedlings put considerable effort into creating large tap root systems in the first few years of seedling development. Thus, in gap areas where there was adequate light, alpine larch seedlings may be able to allocate more resources to developing tap roots to regions of the soil profile where moisture is consistent, making seedlings less dependent on rooting substrate type.

4.4.4 Gap fillers and gap environment

The greater numbers of alpine larch gap fillers than expected (Figure 4.5) and the results from the transition model (Figure 4.6) suggests that, rather than declining in absence of large scale disturbance as a long lived seral species, like the closely related western larch (Schmidt and Shearer 1990), alpine larch is able to exploit smaller scale canopy disturbances to recruit new individuals in older forest. Although this is unexpected behaviour for alpine larch, given its reputation as a very shade intolerant timberline species (Arno 1990, Arno et al. 1995), there are many examples of shade intolerant tree species maintaining viable populations in older forests dominated by shade tolerant species (Barden 1981, Runkle 1982, White et al. 1985, Dahir and Lorimer 1986, Taylor and Zisheng 1988). In these cases, one of the main findings was that gap filler species were partitioned into gap sizes according to their relative shade tolerance. In this study, gap area was a useful predictor of the minimum size of gap in which each species could be found, but provided little extra information about the relative species' competitiveness after these thresholds had been reached. The significance of this covariable in each model appeared mostly due to increasing numbers of gap fillers with larger areas sampled (Table 4.7; Figure 4.7a), and was poorly correlated with an increasing light environment as gap size increased due most likely to the oddly shaped larger gaps. Lertzman and Krebs (1991) also found this kind of increasing complexity of gap shape with size.

Canopy cover was the best discriminating factor between the gap filler species studied here (Figure 4.7b). Although this environmental gradient was only selected in the alpine larch model, the smoothed responses for both the spruce and fir also appear to indicate local competitive optima for these species. Several workers have discussed the occurrence of skewed species response curves as expressions of realised niche optima for a given environmental gradient (Mueller-Dombois and Ellenberg 1974, Austin and Smith 1989, Dale 1999). These occur where a species' fundamental response to a gradient is displaced by competition away from what would be a physiological optimum. The general shape of the gap filler response curves for spruce and fir relative to the position of peaks indicate that stronger competition by the larch for higher light levels has pushed these species' response peaks to areas of greater canopy cover (Figure 4.7b). Support for this is indicated by the trends in the species response to low canopy cover and the correlation of the residuals from the gap filler – gap maker transition analysis (Figure 4.5). In that analysis, the residuals indicate that fewer subalpine fir return than expected, compared to the almost equal increase in larch. The slightly positive increase in spruce is also indicated.

The importance of the surrounding canopy height in the larch gap filler model may be an indication of more competition for light, competition for soil resources, or a combination of the two (Figure 4.8.b). With increases in the height of the surrounding canopy, the length of time that gap areas receive direct solar radiation is decreased. This effect would be exacerbated on steeper north facing slopes where direct radiation may not even touch the forest floor in a number of gaps, given the low summer midday angle of the sun (Lieffers et al. 1999). These factors would favour species that are able to maintain growth on greater percentages of diffuse light. Species with higher light compensation and saturation points, such as alpine larch, would perform better in environments with greater amounts of direct radiation. The greater abundance of larch gap fillers in the northern halves of the gaps (Table 4.6) suggests this kind of relationship between increasing canopy height and the decreasing numbers of larch gap fillers. However, the effects of root competition for soil moisture cannot be ruled out. Coates (2000) discusses the impact of mature canopy trees (30m average height) on planted seedlings in gap edge environments. He notes that competition for moisture and nitrogen may negatively influence regeneration for up to 10m into an artificially created gap. I have also observed this kind of influence in the southern parts of the BC, where western larch regeneration is inhibited at the northern well lit edge of harvested areas next to tall forest, where I would have otherwise expected the shade intolerant species to grow well (unpublished data).

Further support for regulation of larch recruitment by gap environmental characteristics is shown by the rough correspondence in the proportion of the canopy that larch is likely to capture over many generations (Figure 4.6) to the proportion of gaps that might have suitable environmental characteristics for larch gap filler recruitment. For example, only about 40% of the gaps surveyed in both the upper and middle stand elevations were suitable to support larch gap fillers based on size alone. This indicates that, in absence of a change to the distribution of gap characteristics, the future abundance of mature larch is limited by to the proportion of suitable gaps.

At present, this study is the only report of the species' regeneration in older subalpine forest. The ability of alpine larch to maintain recruitment under a closed canopy in the Bow Valley appears to be critically related to the creation of forest gap sizes of greater than 70m^2 where average canopy cover is less than 55%, and the height of the surrounding mature forest is less than 17 metres. How important the local climatic influences are to the occurrence of this presently expanding population and these structural model parameters reported is not known. Further work will be required to determine how robust this gap filler model is in other locations. To provide greater confidence in the relationship between the forest structural features and the light and moisture presumed to be of importance here, there also is a need to examine the competitive interactions between spruce, fir, and larch along environmental gradients in controlled environments.

4.5 Literature cited

Alexander, R. R. 1987. Ecology, silviculture, and management of the Engelmann spruce-subalpine fir type in the Central and Southern Rocky Mountains. **Agricultural Handbook 659**. US Department of Agriculture, Forest Service. Washington DC, USA.

Alexander, R. R., Shearer, R. C., and Shepperd, W. D. 1990. *Abies lasiocarpa* (Hook) Nutt. Pages 60-70 *in:* Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC.

Anderson, L. J. and Winterton, A. J. 1996. Germination as a determinant of seedling distributions among natural substrates in *Picea engelmannii* (Pinaceae) and *Abies lasiocarpa* (Pinaceae). American Journal of Botany. **83:** 112-117.

Anonymous 1999. Canadian climate normals. Environment Canada URL: http://www.cmc.ec.gc.ca./climate/normals/ [2000]

Aplet, G. H., Laven, R. D., and Smith, F. W. 1988. Patterns of community dynamics in Colorado Engelmann spruce-subalpine fir forests. Ecology. **69:** 312-319.

Arno, S. F. 1990. Alpine Larch (*Larix lyallii* Parl). Pages 152-158 *in:* Burns R. M. and B. H. Honkola, editors. Silvics of North America. **Agricultural Handbook 654**. Forest Service, US Department of Agriculture. Washington, DC, USA.

Arno, S. F. and Hammerly, R. P. 1984. Timberline: Mountain and Arctic Forest Frontiers. The Mountaineers. Seattle, USA.

Arno, S. F., Worrall, J., and Carlson, C. E. 1995. *Larix Lyallii:* colonist of tree-line and talus sites. Pages 72-78 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and Management of Larix Forests: A Look Ahead. **GTR-INT-319.** US Department of Agriculture, Forest Service. Ogden, UT, USA.

Austin, M. P. and Smith, T. M. 1989. A new model for the continuum concept. Vegetatio. **83:** 35-47.

Barden, L. S. 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. Oikos. **35:** 16-19.

Barden, L. S. 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. Oikos. **37:** 205-209.

Battles, J. J., Fahey, T. J., and Harney, E. M. 1995. Spatial patterning in the canopy gap regime of a subalpine *Abies-Picea* forest in the northeastern United States. Journal of Vegetation Science. **6:** 807-814.

Beatty, S. and Stone, E. L. 1986. The variety of soil microsites created by tree falls. Canadian Journal of Forest Research. **16:** 539-548.

Blais, J. R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Canadian Journal of Forest Research. **13:** 539-547.

Coates, K. D. 2000. Conifer seedling response to northern temperate forest gaps. Forest Ecology and Management. **127:** 249-269.

Connell, J. H. and Slatyer, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist. **111:** 1119-1144.

Crosbie, S. F. and Hinch, G. N. 1985. An intuitive explanation of generalised linear models. New Zealand Journal of Agricultural Research. **28:** 19-29.

Dahir, S. E. and Lorimer, C. G. 1996. Variation in canopy gap formation among developmental stages of northern hardwood forest. Canadian Journal of Forest Research. **26:** 1875-1892.

Dale, M. R. T. 1999. Spatial pattern analysis in plant ecology. University Press. Cambridge, UK.

Daubenmire, R. F. 1974. Plants and the environment. Wiley. New York, NY, USA.

Day, R. J. 1964. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains. **Research Branch Publication 1037**. Canadian Department of Forestry. Ottawa, ON, Canada.

Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. Biotropica. **12 (supp.):** 47-55.

Denslow, J. S. 1985. Disturbance-mediated coexistence of species. Pages 307-323 *in:* Pickett S. T. A. and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press. Orlando.

Dubé, D. E. 1976. Early plant succession following a 1968 wildfire in the subalpine zone of the Vermilion Pass, Kootenay National Park. M.Sc. thesis, University of Alberta. Edmonton, AB, Canada.

Ecoregions Working Group Canada Committee on Ecological Land Classification 1989. Ecoclimatic regions of Canada: first approximation. **Ecological land classification series No 23**. Sustainable Development Branch, Canadian Wildlife Service, Conservation and Protection. Ottawa, ON, Canada.

Franklin, J. F., Moir, W. H., Douglas, G. W., and Wiberg, C. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. Arctic and Alpine Research. **3:** 215-224.

Grime, J. 1979. Plant strategies and vegetation processes. John Wiley & Sons. Chichester, UK.

Grubb, P. 1977. The maintenance of species-richness in the plant communities: the importance of the regeneration niche. Biological Review. **52:** 107-145.

Heinemann, K., Kitzberger, T., and Veblen, T. T. 2000. Influences of gap microheterogeneity on the regeneration of *Nothofagus pumilio* in a xeric old-growth forest of northwestern Patagonia, Argentina. Canadian Journal of Forest Research. **30** : 25-31.

Hind, T. E. 1977. Heart rots of Engelmann spruceand subalpine fir in the central Rocky Mountains. **Forest insect and disease leaflet**. US Department of Agriculture, Forest Service. Washington, D.C.

Hiura, T., Sano, J., and Konno, Y. 1996. Age structure and response to fine scale disturbances of *Abies sachalinensis, Picea jezoensis, Picea glehnii,* and *Betula ermanii* growing under the influence of a dwarf bamboo understory in northern Japan. Canadian Journal of Forest Research. **26:** 289-297.

Hofgaard, A. 1993. Structure and regeneration patterns in a virgin *Picea abies* forest in northern Sweden. Journal of vegetation Science. **4:** 601-608.

Johnson, E. A. and Miyanishi, K. 1991. Fire and population dynamics of lodgepole pine and Engelmann spruce forests in the southern Canadian Rockies. Pages 77-91 *in:* Nakagoshi N. and F. B. Golley, editors. Coniferous forest ecology from an international perspective. Academic Publishing. The Netherlands.

Knapp, A. K. and Smith, W. K. 1982. Factors influencing understory seedling establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) in southeast Wyoming. Canadian Journal of Botany. **60:** 2753-2761.

Kneeshaw, D. D. and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology. **79:** 783-794.

Lawton, R. O. and Putz, F. E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical forest. Ecology. **69:** 764-777.

Lertzman, K. P. 1992. Patterns of gap-phase replacement in a subalpine, old growth forest. Ecology. 657-669.

Lertzman, K. P. and Krebs, C. J. 1991. Gap-phase structure of a subalpine old-growth forest. Canadian Journal of Forest Research. **21:** 1730-1741.

Lertzman, K. P., Sutherland, G. D., Inselberg, A., and Saunders, S. C. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology. **77:** 1254-1270.

Lieberman, M. and Lieberman, D. 1989. Forests are not just swiss cheese: canopy stereogeometry of non-gaps in tropical forests. Ecology. **70:** 550-552.

Lindsey, J. K. 1995. Introductory statistics: a modelling approach. Oxford University Press. Oxford, UK.

Mathsoft 1999. S-Plus 2000 guide to statistics. **1:** Data Analysis Products Division, Mathsoft. Seattle, WA, USA.

Mathsoft 2000. S-Plus 2000 Professional Release 2. Data Analysis Products Division, Mathsoft, Seattle, WA, USA.

Mueller-Dombois, D. and Ellenberg, H. 1974. Aims and methods of vegetation ecology. Wiley. New York, NY. USA.

Nicholls, A. 1989. How to make biological surveys go further with generalised linear models. Biological Conservation. **50:** 51-75.

Oliver, C. D. and Larson, B. C. 1990. Forest stand dynamics. McGraw-Hill, Inc. New York, NY, USA.

Oosting, H. J. and Reed, J. F. 1952. Virgin spruce-fir of the Medicine Bow Mountains, Wyoming. Ecological Monographs. **22:** 69-91.

Rebertus, A. J., Veblen, T. T., Roovers, L. M., and Nystrom-Mast, J. 1992. Structure and dynamics of old-growth Engelmann spruce-subalpine fir in Colorado. Pages 139-153 *in:* Kaufmann M. R., W. H. Moir, and R. L. Bassett, technical coordinators. Old-growth forests in the southwest and Rocky Mountain regions. **GTR RM-213** 139-153. USDA Forest Service. Fort Collins, CO, USA.

Richards, J. H. 1981. Ecophysiology of a deciduous timberline tree, *Larix lyallii* Parl. PhD thesis, Department of Botany, University of Alberta. Edmonton, Alberta.

Ricklefs, J. R. 1977. Environmental heterogeneity and plant species diversity: A hypothesis. American Naturalist. **111:** 376-381.

Rogeau, M. P. and Gilbride, D. 1994. Stand origin of Banff National Park. Parks Canada. Banff, AB, Canada.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology. **62:** 1041-1051.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology. **63:** 1533-1546.

Schmidt, J. M. and Amman, G. D. 1992. *Dendroctonus* beetles and old-growth forests in the Rockies. Pages 51-59 *in:* Kaufmann M. R., W. H. Moir, and R. L. Bassett, technical coordinators. Old-growth forests in the southwest and Rocky Mountain regions. **GTR RM-213.** US Department of Agriculture, Forest Service. Fort Collins, CO, USA.

Schmidt, W. C. and Shearer, R. C. 1990. *Larix occidentalis* Nutt Western Larch. Pages160-172 *in*: Burns R. M. and B. H. Honkala, Technical co-ordinators. Silvics of North America. **Agricultural Handbook 654**. US Department of Agriculture, Forest Service. Washington, DC, USA.

Shea, K. L. 1985. Demographic aspects of coexistence in Engelmann spruce and subalpine fir. American Journal of Botany. **72:** 1823-1833.

Shea, K. L. and Grant, M. C. 1985. Clonal growth in spire-shaped Engelmann spruce and subalpine fir trees. Canadian Journal of Botany. **64:** 255-261.

Smith, J. H. G. 1955. Some factors affecting reproduction of Engelmann spruce and alpine fir. **Technical Publication 43**. BC Department of Lands and Forests, Forest Service. Victoria, BC, Canada.

Sokal, R. R. and Rohlf, J. F. 1995. Biometry. W. H. Freeman and Company. New York, NY, USA.

Spies, T. A. and Franklin, J. F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology. **70:** 543-545.

Spies, T. A., Franklin, J. F., and Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research. **20:** 649-658.

Tanaka, H. and Nakashizuka, T. 1997. Fifteen years of canopy dynamics analyzed by aerial photographs in a temperate deciduous forest, Japan. Ecology. **78:** 612-620.

Tande, G. F. 1979. Fire history and vegetation pattern of coniferous forest in Jasper National Park, Alberta. Canadian Journal of Botany. **57:** 1912-1931.

Taylor, A. H. and Zisheng, Q. 1988. Tree replacement patterns in subalpine *Abies-Betula* forests, Wolong natural reserve, China. Vegetatio. **78:** 141-149.

Tranquillini, W. 1979. Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European alps. Springer-Verlag. New York, NY, USA.

Van Pelt, R. and Franklin, J. F. 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. Canadian Journal of Forest Research. **30:** 1231-1245.

Veblen, T. T. 1986. Treefalls and coexistence of conifers in subalpine forests of the central Rockies. Ecology. **67:** 644-649.

Veblen, T. T. 1988. *Nothofagus* regeneration in treefall gaps in northern Patagonia. Canadian Journal of Forest Research. **19:** 365-371.

Veblen, T. T., Hadley, K. S., Nel, E. M., Kitzberger, T., Reid, M., and Villalba, R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology. **82:** 125-135.

Veblen, T. T., Hadley, K. S., and Reid, M. 1991. Disturbance and stand development of a Colorado subalpine forest . Journal of Biogeography. **18:** 707-716.

Wardle, P. 1974. Alpine timberlines. Pages 371-402 *in:* Ives J. D. and R. Barry, editors. Arctic and alpine environments. Macmillan. New York, NY.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. The Botanical Review. **45:** 229-299.

White, P. S., MacKenzie, M. D., and Busing, R. T. 1985. A critique on overstory/understory comparisons based on transition probability analysis of an old growth spruce - fir stand in the Appalachians. Vegetatio. **64:** 37-45.

White, P. S. and Pickett, S. T. A. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3-13 *in:* Pickett S. T. A. and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press. London, UK.

Whitmore, T. C. 1988. The influence of tree population dynamics on forest species composition. Pages 271-292 *in:* Davy A. J., M. J. Hutchings, and A. R. Watkinson, editors. Plant population ecology. Blackwell Scientific Publications. London, UK.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon. **21:** 213-251.

Wilson, B. C. 1992. The effects of selective logging on the floristic composition of snow gum-mountain gum forest on the Barrington Tops plateau, New South Wales. B.Sc. honours thesis. University of Technology, Sydney. Sydney, NSW, Australia.

Worrall, J. 1995. Intermittent long and short shoot growth in subalpine larch leaders. Pages 282-284 *in:* Schmidt W. C. and K. J. McDonald, Compilers. Ecology and Management of Larix Forests: A Look Ahead. **GTR-INT-319.** US Department of Agriculture, Forest Service. Ogden, UT, USA.

CHAPTER 5: SUMMARY AND CONCLUSIONS

5.1 A model of succession

The pioneering work of Arno (1970) and Richards (1981) provides important background information about the general ecology and ecophysiology of alpine larch. However, the presence of this "timberline" species in a range of age classes of subalpine forest presented a number of questions that could not be answered by this previous work. Given that land managers are now actively involved in manipulating disturbance regimes in high elevation forests in both federally and provincially administered lands, the pertinent questions surrounding the subalpine distribution of alpine larch seemed related to the regeneration dynamics of the species. Because the recruitment of alpine larch had not been directly looked at before, I designed the study to address the question of recruitment over the range of forest age and associated stand structure. The findings from each of the Chapters progressively help to build a general model of forest succession, and show how the changing forest structure affects the temporal and spatial population dynamics of alpine larch.

The objectives of Chapter 2 were to describe the regeneration niche of alpine larch following coarse scale stand replacing fire that occurred over a broad elevation range. Fire is an important source of disturbance in the southern Canadian Rockies (Tande 1979, Johnson and Miyanishi 1992, Rogeau 1996). There is evidence that in many cases fires have started low in the valleys from lightening strikes and burned upslope following the continuous fuels to timberline (Rogeau and Gilbride 1994, personal observation). These openings appear to provide initial avenues for the subalpine recruitment of alpine larch. The results showed that considerable regeneration of the species occurred over the entire elevation range of disturbed Engelmann spruce – subalpine fir forest (Figure 5.1), although mostly on north aspects. The lower boundary of the successful recruitment appeared to be the taller, rapidly growing lodgepole pine forest community. Alpine larch regeneration was typically found within 100m of the surrounding mature forest trees that

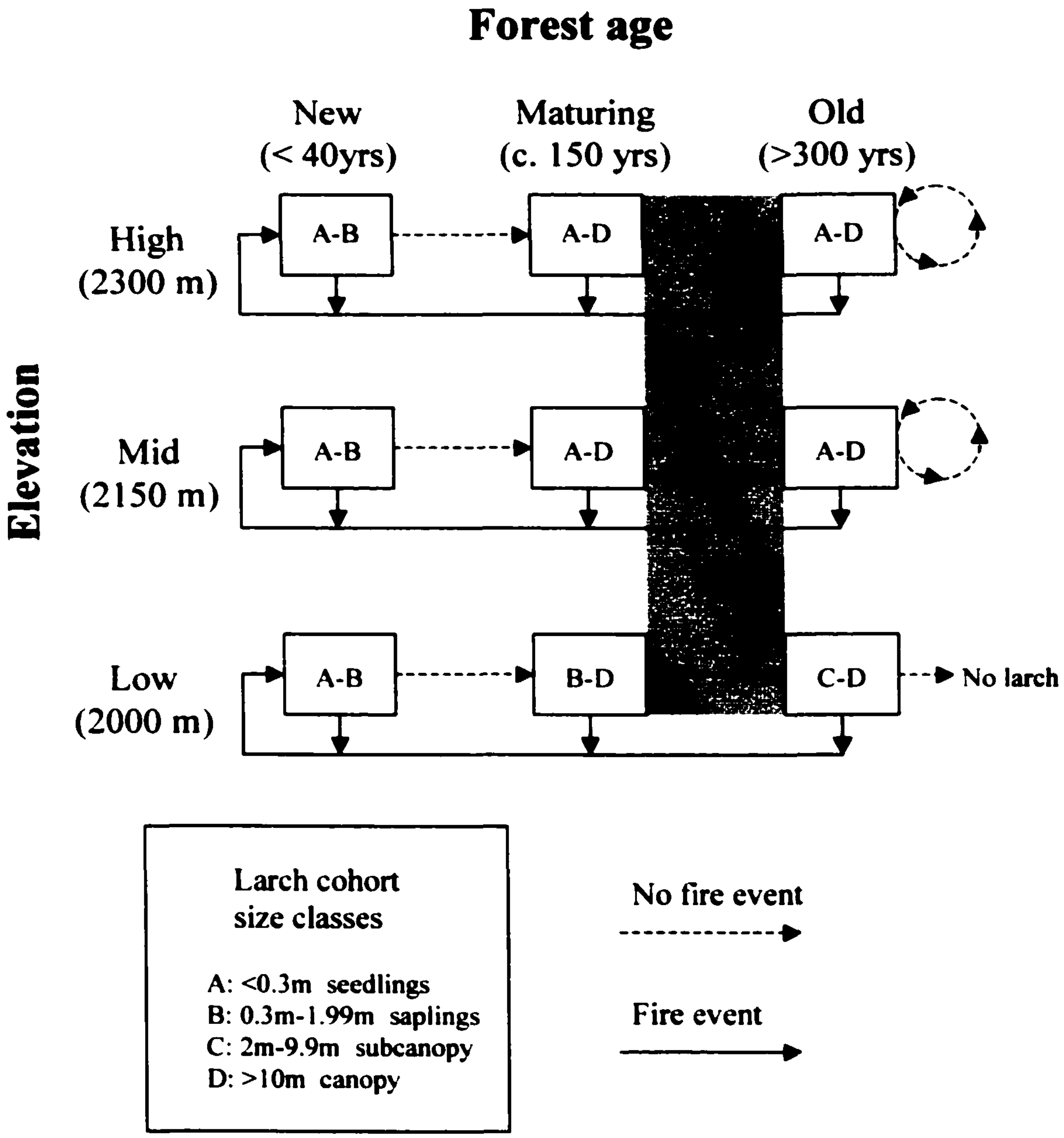


Figure 5.1: Diagrammatic model of the fate of larch cohorts in north-facing Engelmann spruce – subalpine fir forests over time. All cohorts of larch are predicted in absence of fire in old forest at mid and high subalpine forest elevations, whereas, the absence of smaller cohorts in lower older forest indicates that larch will eventually excluded from those areas.

could provide a wind dispersed seed source. However, in some cases seedlings or saplings were found greater than 500m from a seed source.

The predominance of recruitment on the northern exposures is likely related to the more moderated moisture environment. The greater numbers of larch seedlings found in association with intermediate levels of shrub cover on these northern aspects supports this conclusion, as does the interaction between taller shrub cover and aspect. Seedlings found on the southern exposures were associated with greater than 10% overhead tall shrub cover. Arno (1970) and Richards (1981) both recognised that high ambient light levels and moist environment were important for timberline establishment of alpine larch. The apparent facilitative role that intermediate vegetative cover has on seedling establishment in burn areas (see below) suggests that moisture may be the more critical factor, especially in subalpine environments.

In Chapter 3, I surveyed the elevation range of closed canopy Engelmann spruce – subalpine fir forest on northern aspects. My objectives in that Chapter were to describe the realised niche of alpine larch in maturing and older forests. The forest structure in the mature stands that I sampled (150 years and 160 years old) created understory conditions that were no longer suitable for the recruitment of larch seedlings at the lower edge of the spruce – fir dominated forest, although taller larch size classes remained (Figure 5.1). In those transitional areas, greater competition for light and perhaps soil moisture, due to the combination of increased shrub and canopy cover, and greater biomass generally, acted to inhibit the recruitment of larch seedlings. This intermediate period of forest development may also mark a low point for the total average input of larch seed, as supply from adjacent older stands no longer benefits from an unobstructed flight path due to the height of the maturing stand. The maturing larch trees also had relatively little time to produce cones, given this species' late sexual development (Arno and Habeck 1972). The few cones at this stage of forest development may also have been related to the competitive nature of the subalpine environment where vertical growth may be favoured over seed development (Harper 1977). In the older forests (>300 years), larch recruitment remained inhibited at lower elevations where canopy height, canopy cover, and shrub cover remain high, even though fine scale tree fall gap disturbance had started. However, in higher elevations, where there was a reduction in these structural competitive influences, larch regeneration reinitiated (Figure 5.1). This appeared largely in response to the onset of the fine scale gap formation.

The importance of gap disturbance in recruitment of alpine larch was confirmed by the data presented in Chapter 4. In that investigation I wanted to determine if larch recruitment was dependent on the formation of gaps in the older forest, and if so, whether there were measurable structural features of the gaps that distinguished whether larch, spruce, or fir would most likely dominate the opening. I also wanted to find out if there were differences in gap structure that changed over elevation, and could account for the differences that were found in the structural observations in Chapter 3. My findings indicated that initial larch recruitment was strongly dependent on gaps, because seedlings were found, almost without exception, in treefall gaps where they had an unobscured sky overhead. It also appeared that gap structure was important as the smaller, darker, gaps surrounded by taller forest trees found at lower elevation contributed to the exclusion of larch recruitment. Alpine larch gap fillers were competitive in gaps where there was more light (i.e., where there was less than about 50% canopy cover) and likely more available water.

Distinct understory vegetation patterns accompanied the success of larch recruitment within the different developmental forest stages. Initial establishment of seedlings shortly after fire coincided with species that appeared to offer an ameliorated environment. On northern aspects where regeneration was greatest, the presence of resprouting shrub species like *Rhododendron albiflorum* and *Menziesia ferruginea* that quickly would have provided "safe" microsites were important. However, in the older forest the combination of the greater density of these same shrub species with the overstory canopy acted to exclude larch recruitment in the lower elevations. Larch seedlings in higher sites were commonly found in a moist heath association dominated by *Cassiope mertensiana, Pedicularis bracteosa, Hieracium gracile,* and *Arnica cordifolia.*

5.2 Confirmation of the model

Support for this succession model is provided by querying the new Ecological Land Classification (ELC) database for Banff, Kootenay, and Yoho National Parks (Wilson and Stuart-Smith 1999). This database accesses over 4500 vegetation plots within the Rocky Mountain National Parks and contains detailed information on vegetation structure and the associated environmental conditions (see Holland and Coen 1982 for details on the collection of this data). Figure 5.2a shows the elevation distribution of the main subalpine conifers; as expected, the main transition between the lower elevation lodgepole pine and Engelmann spruce - subalpine fir forest occurs around 1800m. Alpine larch becomes prominent at about 2100m. However, note that lower elevation range of the larch is about 1900m, the same elevation at which the larger larch size cohorts were displaced by the taller, more competitive spruce – fir forest in the present study.

The breakdown of the distribution ranges for the different size cohorts of the ELC alpine larch data shows further support for the pattern of recruitment migrating upslope following the changing forest structural conditions. Figure 5.2b shows that the lowest elevation alpine larch are the larger canopy individuals, with each smaller cohort distribution found starting at successively higher elevations. As there have been relative few subalpine stand replacing fire events in the last century, the lack of larch seedlings in the lower subalpine from the ELC data is understandable. The average stand age for the area under consideration is 193 years old (Rogeau and Gilbride 1994).

Further confirmation of both overstory and understory successional patterns could usefully be obtained from the ELC and other data. One approach would be to use the parameter estimates from the statistical structure models that I built, to predict the occurrence of larch regeneration given structural data from the ELC. This kind of approach will enable the further spatial modelling of the data at the landscape level by linking the analyses with existing digital information in Parks Canada's Geographical Information System (GIS).

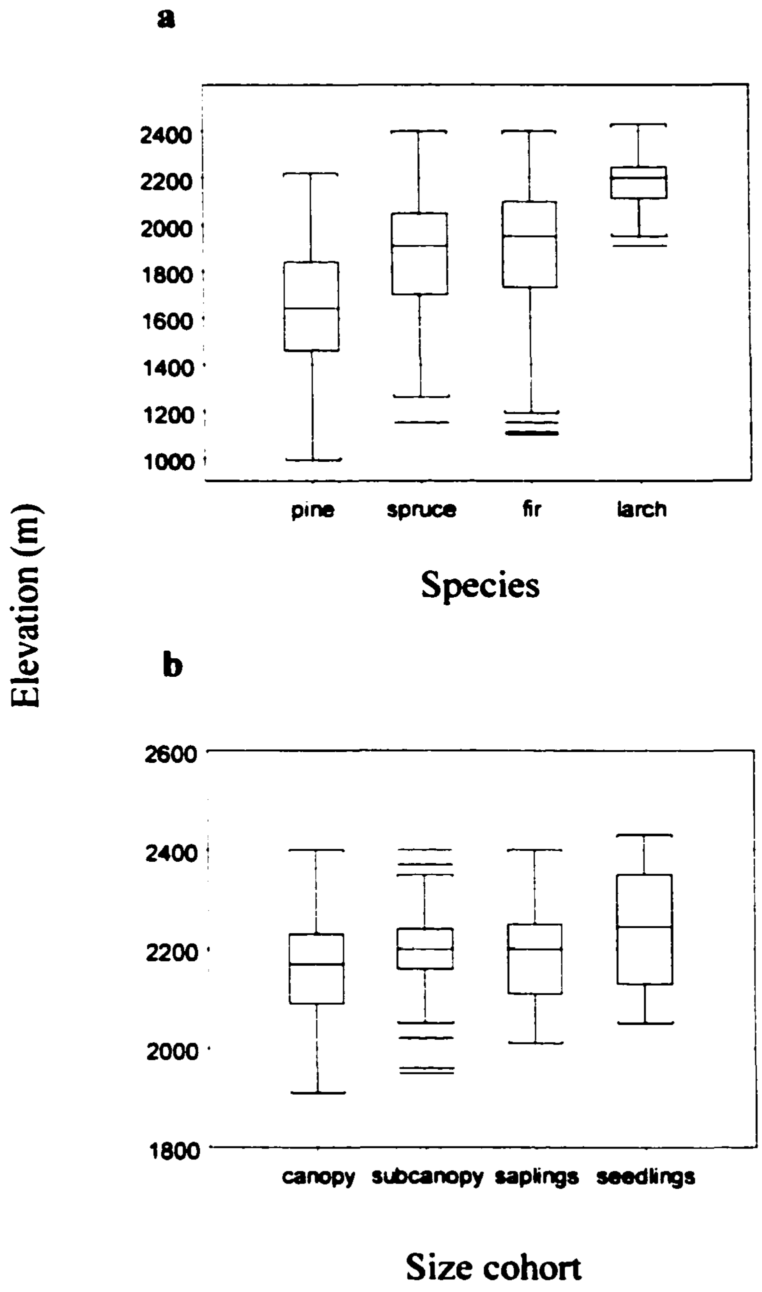


Figure 5.2: (a) The elevation distribution of the four major subalpine tree species on north aspects in Banff, Kootenay and Yoho National Parks. (b) The elevation distribution of alpine larch size cohorts. Note the consistent rise of the lower distribution boundary with a reduction in cohort size. The median value is indicated by the dark line within the 25-75% quartile box. Data from Wilson and Stuart-Smith (1999).

5.3 The subalpine distribution of alpine larch: hypotheses

Why is there a conspicuous subalpine distribution of alpine larch in the Canadian Rockies? There likely are a number plausible answers to this question, however, I will discuss two general non-mutually exclusive hypotheses here.

(1) The unique topography of the southern Canadian Rockies in combination with previous climatic change has selected for more competitive physiological traits in alpine larch than in regions further south.

The timberline ecotone in this region of the Rocky Mountains occurs over a short elevation range. In many areas subalpine forest abruptly ends in steep rocky terrain (Figure 5.3). The areas of alpine meadow that would have provided higher elevation refugia that could be rapidly colonized during previous periods of warmer regional weather are only extensive in a few locations. Therefore, the higher timberline elevations that occurred in the past in the southern Canadian Rockies (Beaudoin 1986, Luckman and Kearney 1986, Reasoner and Hickman 1989) may have been limited to a small number of areas. In other places bounded by talus and cliffs, shifts in species composition and changes in forest cover may have occurred with little actual upslope movement in the tree limit. These structural changes may have exerted selective pressure on larch populations unable to migrate upslope, favouring individuals that showed greater tolerance toward competition.

a

b

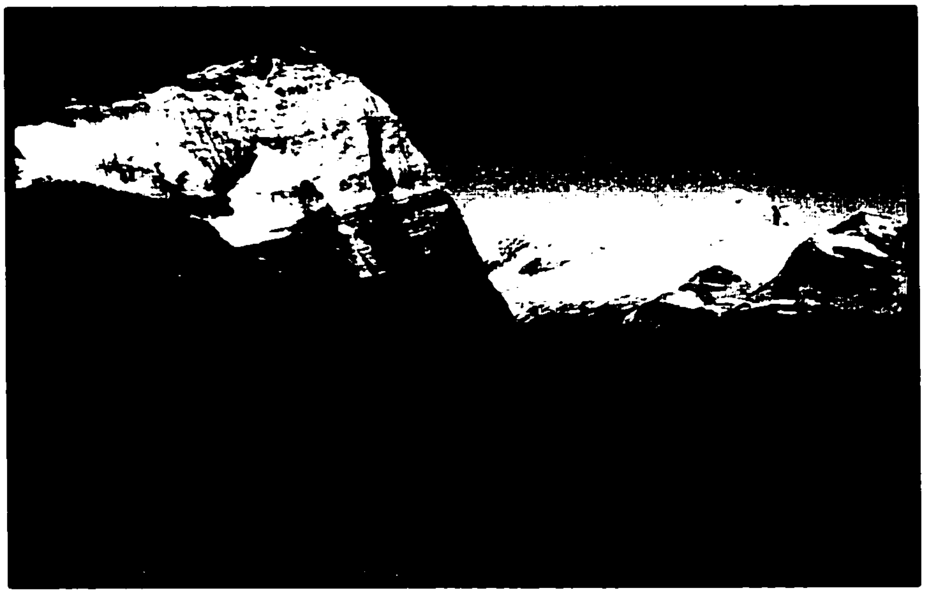


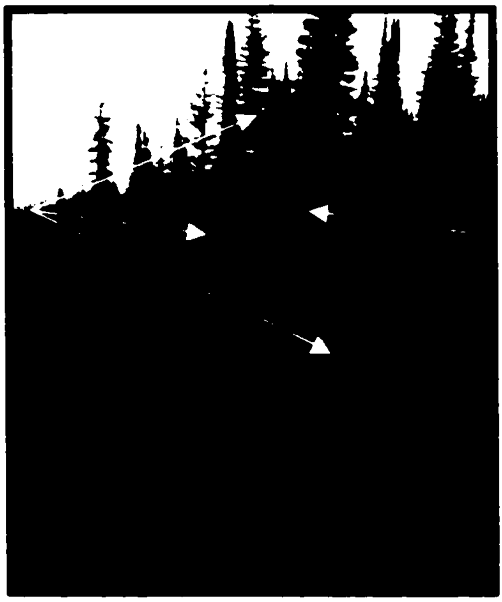
Figure 5.3: (a) Edaphic timberline on the east side of the upper Cascade River Valley, Banff National Park, Alberta. Larch are present here but difficult to distinguish from the spruce and fir. (b) A larch dominated timberline in the Cataract Creek drainage in Yoho National Park, British Columbia. The transition from larch to spruce – fir dominated forest occurs over a short distance here as the height and cover of the canopy rapidly increase.

(2) That a unique precipitation and/or temperature regime found at this northern edge of the distribution of alpine larch enables the species to exploit subalpine habitats that would only exist outside of the species' physiological or fundamental niche in regions further south.

Arno (1970) compared the climatological data for the different regions of the larch's distribution and one notable difference that he found in the data recorded near the present subalpine study was that this area had the coldest extreme early spring and fall temperatures compared to the rest of the species' continental distribution. It is possible that extreme temperature fluctuations during these periods adversely affect Engelmann spruce and subalpine fir compared to alpine larch, and therefore confer some sort of competitive advantage to the larch. However, bud break and early season growth appears to be roughly synchronized in all three species (personal observation), eliminating the stress avoidance advantage that the deciduous larch is noted for (Arno and Habeck 1972, Richards 1981).

Perhaps more likely is the possibility that winter desiccation damage to the other conifers during temperature inversions provide alpine larch with an advantage even at subalpine elevations. Inversions and Chinooks are often experienced in this region of the Rockies (Gadd 1995). These warm air events can raise the ambient air temperature from well below zero to above zero in the space of a few hours. A good example of this kind of differential damage occurred in the lower subalpine Vermilion Pass region during the winter of 1999/2000 (Figure 5.4). During this temperature inversion event a distinct layer of warmer air settled in the region, causing wide spread damage to evergreen vegetation that was exposed above the snow pack.

In Arno and Hammerly's (1984) book on timberlines, they suggest that absence of summer drought may be the reason for more luxurious growth of alpine larch north of the USA - Canadian border. This, and other more subtle differences in the patterns of precipitation that occur over the distribution may also account for the greater presence of



Both recent and older evidence of desiccation damage to spruce and fir

Unaffected healthy growth of alpine larch.

Figure 5.4: An alpine larch sapling showing characteristic benefits of winter stress avoidance at 1800m in the Vermilion Pass burn, Banff National Park, Alberta.

alpine larch in subalpine forests of the north. Further examination of more detailed climatic data may uncover relationships between factors such as individual storm cycle precipitation, canopy throughfall, temperature, and resulting soil moisture (Daubenmire 1974). Differences in valley bottom and timberline climatic patterns will also be useful to examine, as latitudinal trends in winter warm air events may be present, but are not possible to detect from only valley based weather recording stations.

Selective grazing of herbivores has been shown to regulate species composition in other subalpine plant communities (Burdon and Chilvers 1974, Wimbush and Costin 1979). However, there does not appear to be any evidence herbivory plays a role in the regulation of the conifer populations in this study. Although there was obvious ungulate and rodent damage to seedlings and saplings of each tree species present in the surveyed areas, these instances were infrequent and warranted little consideration.

Support for the above mentioned hypotheses might be found by designing a controlled experiment that compared germination and establishment of several provenances of larch (e.g., from the different geographical edges of the distribution) to different levels of moisture, temperature, and light. However, only long term monitoring of populations in the wild would provide information on the effects of damaging agents such as winter temperature inversions, herbivory, and pests.

A useful consideration in a controlled experimental design or a long term monitoring project will be noting the presence of wintergreen needles. One of the important findings from Richards' (1981) work was the presence of wintergreen needles on young alpine larch and their role in limiting summer desiccation in seedlings and saplings before these individuals' root systems had time to develop fully. Richards (1981) also found evidence of compensation in the allocation of these needles between shady sites compared to open sites. Wintergreen needles have a higher light compensation point compared to deciduous needles, and were more common in sunny areas. Therefore, examining the proportion and persistence of wintergreen needles during the early growth period of alpine larch under the influence of different environmental conditions may provide insight to the mechanisms that control the creation and allocation of these specialized organs, and help explain some of the establishment patterns that are present in the field.

5.4 Disturbance and management implications

Although alpine larch appears to be able to maintain a presence in older upper subalpine forest by recruiting in larger treefall gaps, the coarse scale disturbance of fire clearly plays an important role in maintaining a presence of the species in lower Engelmann spruce – subalpine fir forests. The significance of this may be related to the conservation of the genetic diversity of the species. As discussed above, the higher elevation topography of the Canadian Rockies is highly dissected. There are many forested side valleys and cirques that end abruptly in steep rock walls or unvegetated talus slopes. However, these connect to relatively few large river valleys that support continuous tracts of lower subalpine vegetation (Holland and Coen 1982). This means that isolated timberline or upper subalpine forest populations may use adjacent fires as a means to maintain genetic connection. Furthermore, successive fires over the long term may have provided the means of migration for the species in the face of changing regional climatic conditions. This movement is also likely aided by the seed harvesting and caching behaviour of the Clark's nutcracker (Lanner 1996). For example, I have found several multi-stemmed clumps of juvenile larch trees (the multiple stems suggesting individual trees arising from a seed cache), slightly further north of Arno's (1970) stated distribution limit in the Bow Valley.

Current management in Canadian Rocky Mountain National Parks uses a system of primarily wildfire suppression, or containment and then the prescription of fire as a means of delivering a controlled disturbance regime to the vegetated land base. The general management goal is to "maintain and where feasible, restore native vegetation communities to reflect the long-term ecosystem states and processes" (Canadian Heritage 1997). The difficulty comes deciding what previous time period to base the present management regime on, as clearly the regional temperature and precipitation patterns, and associated fire frequency have oscillated considerably since the retreat of the Cordilleran ice sheet and the establishment of vegetation in these areas around 10 000 years ago (Pielou 1991, Hallett and Walker 2000). Furthermore, our present global climate trajectory is now confounded by the increase in anthropogenic greenhouse gases, which makes attempting to predict what the future "natural" climatic conditions, and hence, vegetation communities and disturbance regimes might be like.

The regional populations of alpine larch observed in the course my study do not, at present, appear critically endangered through lack of regeneration resulting from the previous management culture of total fire suppression. Therefore, the need for *immediate* management intervention to provide a greater disturbed area for larch recruitment on the northern aspects of Engelmann spruce – subalpine forests at this stage is unnecessary. This is not to say that a greater emphasis on suppression is desirable either. Rather, I believe that a comprehensive research, monitoring, and management approach is necessary, whether that management advocates imposing "natural" disturbance for conservation purposes in protected areas, or harvesting timber for economic reasons in other areas.

An important starting point is to recognize the key life history characteristics of the different species that were, or are likely to be affected by a management action. In the case of alpine larch, consideration must be focused firstly on the length of time the species requires to become sexually mature. Because the first cones do not appear until the tree is between 80 and150 years of age, any consideration of a coarse scale stand replacing management disturbance regime (such as fire or clear cuts) must recognise that a canopy turnover rate needs to be substantially greater than this, or the species may eventually become excluded due to diminishing seed availability.

5.4.1 Long term monitoring and adaptive management

By examining the patterns of disturbance history that are left on the landscape, we may find useful initial parameters to help with the implementation of an adaptive management approach to maintaining the regional distribution of alpine larch and other species that depend on disturbance. However, to uncover the important subtleties of how a species responds to varied environmental conditions within a given management scenario, or to changing regional climatic conditions, long term monitoring will be required. In this study I have made the first attempt at describing how the alpine larch population responds to the different stand structural conditions found within a range of stand ages of subalpine forest. It is important to note that the chronosequence approach that I have used has limitations. In particular, substituting spatially separate areas with a range of ages for time may include other differences that confound the desired temporal comparison. Now what is needed is long term permanent plot vegetation monitoring program to assess changes in plant communities from the lower subalpine to the alpine in representative vegetation/structural stage types over both north and south aspects to provide a better system description. These should be linked with previous (Corns and Achuff 1982) and current (Wilson 1998, Wilson and Stuart-Smith 2000) vegetation description and prescribed burn monitoring programs.

To complement the vegetation program, we should be developing not only a comprehensive understanding of previous environmental conditions that affected the landscape, but also a sophisticated monitoring program to aid future local and regional environmental prediction. We are entering into an era of climate change that appears to be far more rapid than previous changes (Beniston 1994). Not only can we expect global temperatures to rise 1.5-4.5° C (Melillo et al. 1990), but there will also be considerable changes to other climatic patterns, such as precipitation, that will vary over considerably smaller scales in mountainous environments and may be of greater consequence to species such as alpine larch (Barry 1992, Krannitz and Kesting 1997).

This information would be an important part of a monitoring, management action, modelling feedback loop that could provide greater direction to species conservation in both federal and provincial lands. Furthermore, we need to develop a consistent approach to setting management goals for species such as alpine larch that take into account the entire current and future predicted ranges. This will require considerable collaboration between provincial, state, national, and international jurisdictions, and continued support from both applied and academic research.

5.5 Literature cited

Arno, S. F. 1970. Ecology of alpine larch in the Pacific Northwest. PhD thesis University of Montana, Missoula, MT, USA.

Arno, S. F. and Habeck, J. R. 1972. Ecology of Alpine Larch (*Larix lyallii* Parl) in the Pacific Northwest. Ecological Monographs. **42:** 418-450.

Arno, S. F. and Hammerly, R. P. 1984. Timberline: Mountain and Arctic Forest Frontiers. The Mountaineers. Seattle, USA.

Beaudoin, A. B. 1986. Using *Picea/Pinus* ratios from the Wilcox Pass core, Jasper National Park, Alberta, to investigate Holocene timberline fluctuations. Geographie Physique et Quaternaire. **XL:** 145-152.

Beniston, M. 1994. Introduction. Pages xxv-xxxi *in:* Beniston M., Editor. Mountain environments in changing climates. Routledge. New York, NY, USA.

Barry, R. G. 1992. Mountain weather and climate. Routledge. New York, NY, USA.

Burdon, J. J. and Chilvers, G. A. 1974. Leaf parasites on altitudinal populations of *Eucalyptus pauciflora* Sieb ex Spreng. Australian Journal of Botany. **22:** 265-269.

Canadian Heritage 1997. Banff National Park management plan. Minister of Public Works and Government Services. Ottawa, ON, Canada.

Corns, I. G. W. and Achuff, P. L. 1982. Vegetation: vegetation type descriptions. Pages 75-141 *in:* Holland W. D. and G. M. Coen, editors. Ecological (biophysical) land classification of Banff and Jasper National Parks. **SS-82-44**. Alberta Institute of Pedology, University of Alberta. Edmonton, AB, Canada.

Daubenmire, R. F. 1974. Plants and the environment. Wiley. New York, NY, USA.

Gadd, B. 1995. Handbook of the Canadian Rockies. Corax Press. Jasper, AB, Canada.

Hallett, D. and Walker, R. C. 2000. Palececology and its application to fire and vegetation management in the Kootenay National Park, British Columbia. Journal of Paleolimnology. **24:** 401-414.

Harper, J. L. 1977. Population biology of plants. Academic Press. London, UK.

Holland, W. D. and Coen, G. M. 1982. Ecological (biophysical) land classification of Banff and Jasper National Parks. **SS-82-44**. Alberta Institute of Pedology, University of Alberta. Edmonton, AB, Canada.

Johnson, E. A. and Miyanishi, K. 1991. Fire and population dynamics of lodgepole pine and Engelmann spruce forests in the southern Canadian Rockies. Pages 77-91 *in:* Nakagoshi N. and F. B. Golley, editors. Coniferous forest ecology from an international perspective. Academic Publishing. The Netherlands.

Krannitz, P. G. and Kesting, S. 1997. Impacts of climate change on the plant communities of alpine ecosystems. Pages 10-1 - 10-13 *in:* Taylor E. and B. Taylor, Editors. Responding to global climate change in British Columbia and Yukon. Aquatic and Atmospheric Sciences Division, Environment Canada. Vancover, BC, Canada.

Lanner, R. M. 1996. Made for each other. A symbiosis of birds and pines. Oxford University Press. New York, NY, USA.

Luckman, B. H. and Kearney, M. S. 1986. Reconstruction of Holocene changes in alpine vegetation and climate in the Maligne Range, Jasper National Park, Alberta. Quaternary Research. **26:** 244-261.

Melillo, J. M., Callaghan, T. V., Woodward, F. I., Salati, E., and Sinha, S. K. 1990. Effects on ecosystems. Pages 287-306 *in:* Houghton J. T., G. J. Jenkins, and J. J. Ephraums, Editors. Climate Change: the IPCC Scientific assessment. Cambridge University Press. Cambridge, UK.

Pielou, E. C. 1991. After the ice age. University of Chicago Press. Chicago, USA.

Reasoner, M. A. and Hickman, M. 1988. Late quaternary environmental change in the Lake O'Hara region, Yoho National Park, British Columbia. Palaeogeography, Palaeoclimatology, Palaeoecology. **72:** 291-319.

Richards, J. H. 1981. Ecophysiology of a deciduous timberline tree, *Larix lyallii* Parl. PhD thesis, Department of Botany, University of Alberta. Edmonton, Alberta.

Rogeau, M. P. 1996. Understanding the age-class distribution in the southern Canadian Rockies. M.Sc. Thesis, Department of Forest Science, University of Alberta. Edmonton, AB, Canada.

Rogeau, M. P. and Gilbride, D. 1994. Stand origin of Banff National Park. Parks Canada. Banff, AB, Canada.

Tande, G. F. 1979. Fire history and vegetation pattern of coniferous forest in Jasper National Park, Alberta. Canadian Journal of Botany. **57:** 1912-1931.

Wilson, B. C. 1998. Daer-Pitts prescribed burn research plan. **KKP05-98**. Cordilleran Ecological Research. Winlaw, BC, Canada.

Wilson, B. C. and Stuart-Smith, G. J. 2000. Whitebark pine conservation for the Canadian Rocky Mountain National Parks. **KNP03-00**. Cordilleran Ecological Research. Winlaw, BC, Canada.

Wilson, B. C. and Stuart-Smith, G. J. 1999. Conversion of the Mountain National Parks Ecological Land Classification database. **JNP01-99**. Cordilleran Ecological Research. Winlaw, BC, Canada.

Wimbush, D. J. and Costin, A. B. 1979. Trends in vegetation at Kosciusko. I Grazing trials in the subalpine zone, 1957-1971. Australian Journal of Botany. **27:** 741-787.

Appendix I: densiometer calibration

Radiation in the form of visible light is one of the most important resources that plants need to generate usable energy for their survival and growth. In forests, competition for this resource is great, and in many cases low light is the limiting factor for recruitment and growth of understory plants, including tree seedlings (Daubenmire 1974, Kimmins 1987). The spectral range that plants use for photosynthesis lies between 380 and 710 nm (Larcher 1983). Lieffers et al. (1999) discuss the variety of methods available to quantify this photosynthetically active radiation (PAR) beneath forest canopies. These fall into two general categories: (1) direct measurement using apparatuses that are light sensitive, and (2) indirectly estimating the intensity of light transmitted through the canopy by measuring the amount of canopy cover.

The benefits of directly measuring light intensity are obvious. The observer has more control over the measuring process, and there is likely to be better accuracy in defining the light environment in most situations. The drawbacks include cost and durability of equipment, and more importantly, limitations on getting instantaneous above canopy light comparisons in continuous forest cover. This is especially an issue in mountainous terrain were weather and topography rapidly change, also changing the quality of the ambient light. Because of this, it is not practical to rely only on periodic calibrations in full light were sporadic clearings might allow this.

I chose to measure canopy cover as a surrogate for transmitted light in my study because of these impracticalities. Although spherical densiometers have been shown to over estimate the amount of directly overhead cover (Bunnell and Vales 1990, Cook et al. 1995), their use to estimate the light attenuation may be much better (Lieffers et al. 1999). Lemmon (1956, 1957) originally introduced the spherical densiometer as an instrument to measure canopy cover. His design used either a convex or a concave mirror with a grid pattern that contained 24 cells etched on the surface. The user was to imagine four equally spaced dots within each of these cells and record whether these were covered by overhead vegetation. Thus, a score out of 96 was converted to canopy cover by multiplying the tally by 1.04. In practice, I found that the amount error associated with different users incorrectly tallying covered squares, and the extra time necessary for correcting forgotten tallies was too great – so I made a modified version.

I constructed a densiometer using a 7.5 cm diameter convex mirror. I scribed a 7 by 7 regular line grid onto the mirror surface, providing 49 line intersections (Figure I.1a). To estimate proportion of canopy cover, I counted the number of intersections that were covered by overhead vegetation and divided by the total 49. This reduction in subjective cover estimation within cells appeared to greatly improve user confidence, and improved memory retention of the total tally. The view angle of the grid captured 50° - from the zenith above the observer, forward to the adjacent trees (Figure I.1b). To obtain an average value for the vegetation plots in this study the densiometer was read standing at the edge of the plot facing toward the plot centre at four cardinal points. The meter was held level at 1 m above the ground.

To link the cover estimates with actual light attenuation I preformed a calibration trial of the instrument in a coniferous forest surrounding a large cleared field near my study areas. I used two General Electric ^{tm} type 217 light meters to simultaneously record light intensity in the open field and at the centre of 27 trial plots located randomly within the surrounding forest. I recorded the average canopy cover surrounding the plots using the densiometer as described above. Each of the plot locations were randomly selected, but were at least 50 meters from the edge of the clearing to minimise edge effects. I fit a linear regression line to these data to determine how well my cover estimates predicted light attenuation (Figure I.2).

The densiometer cover estimates explained over 90% of the variation in the transmitted light data (Figure I.2). The slope of the fitted line was –0.84, indicating an almost directly proportional reduction in transmitted light with increasing canopy cover. The y-intercept of 91.6% transmitted light may reflect a bias in the sampling. Most of the data were clumped around high canopy cover values, as the forest was approximately 120 years old, with only a few areas of reduced cover. Greater sampling intensity in lower cover areas would be useful to provide more confidence in the relationship between transmitted light and canopy cover in more open stands.

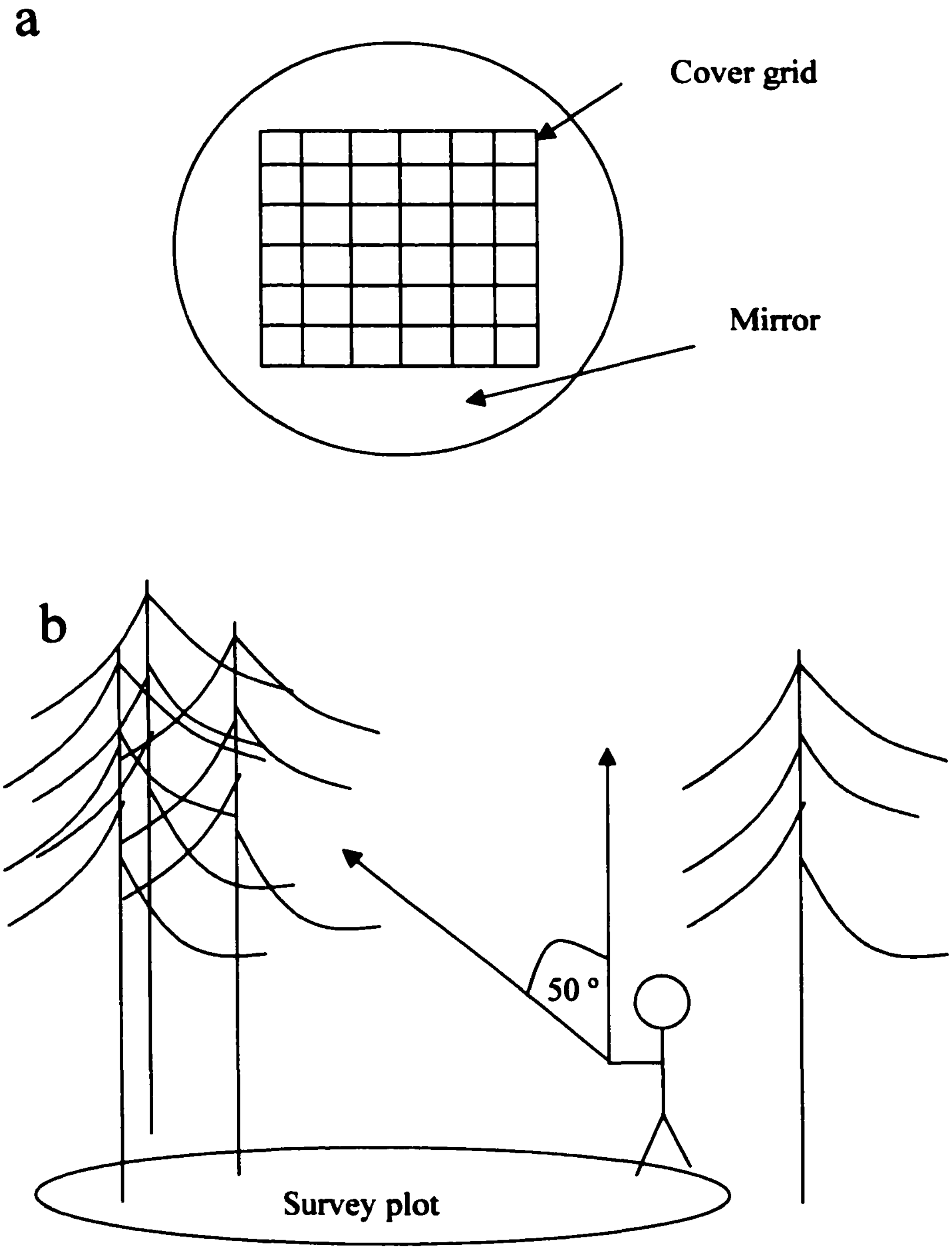


Figure I.1: (a) The overhead view of the intersection grid on the mirror surface. (b) A diagram of the densiometer in use at a survey plot.

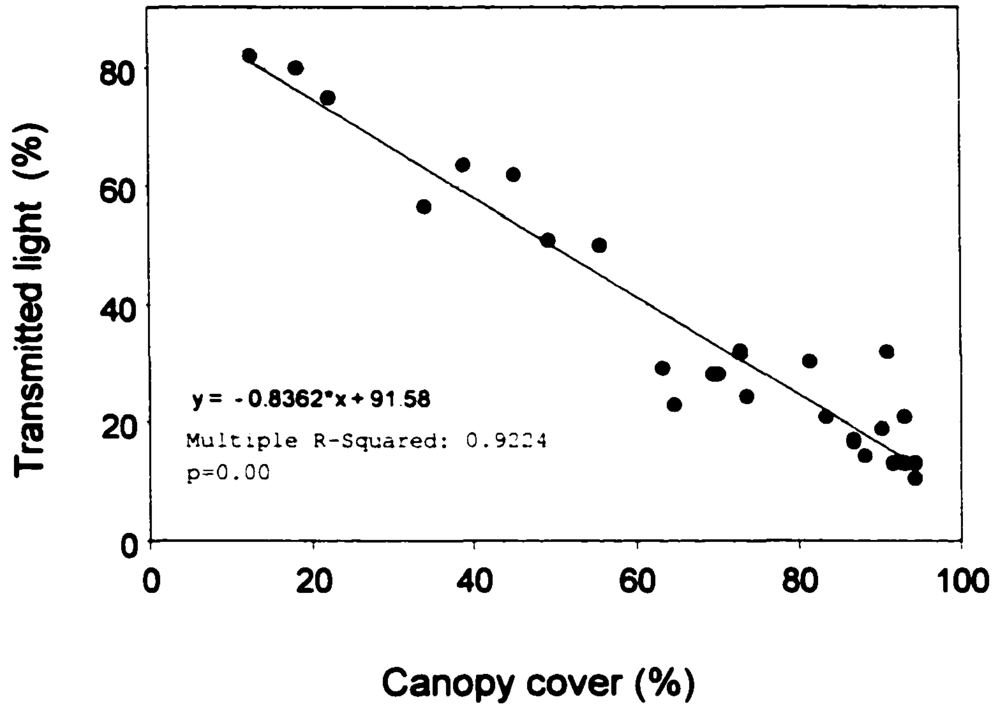


Figure I.2: Linear relationship between canopy cover measured with my hand held densiometer and the percentage of light transmitted through the canopy. Line is a least-squares regression

Literature cited

Bunnell, F. L. and Vales, D. J. 1990. Comparison of methods for estimating forest overstory cover: differences among techniques. Canadian Journal of Forest Research. **20:** 101-107.

Cook, J. G., Stutzman, T. W., Bowers, C. W., Brenner, K. A., and Irwin, L. L. 1995. Spherical densiometers produce biased estimates of forest cover. Wildlife Society Bulletin. **23:** 711-717.

Daubenmire, R. F. 1974. Plants and the environment. Wiley. New York, NY, USA.

Kimmins, J. 1987. Forest ecology. Macmillan. New York, NY, USA.

Larcher, W. 1983. Physiological plant ecology. Springer-Verlag. Berlin.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science. **2:** 314-320.

Lemmon, P. E. 1957. A new instrument for measuring forest overstory density. Journal of Forestry. **55:** 667-668.

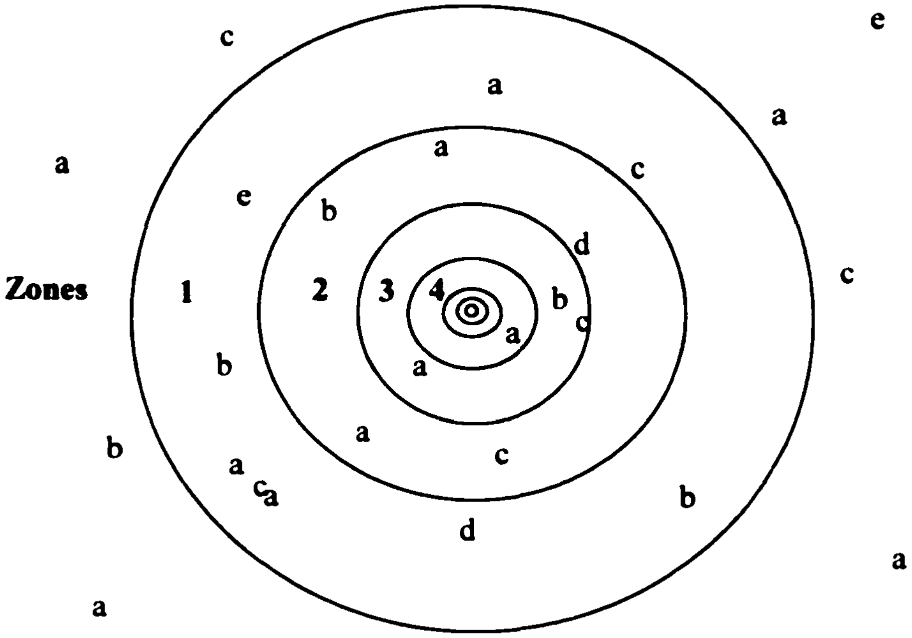
Lieffers, V. J., Messier, C., Stadt, K. J., Gendron, F., and Comeau, P. G. 1999. Predicting and managing light in the understory of boreal forests. Canadian Journal Forest Research. **29:** 796-811.

Appendix II: sampling plot layout.

Importance scores (Outhred 1984, Morrison et al. 1995, Wilson and Stuart-Smith 2000) were used in this study to survey plant communities because the method has several favourable characteristics. These include:

1. Collecting importance scores as nearly as fast as only collecting frequency data;
2. The importance estimates have a strong log-linear relationship with density over several orders of magnitude;
3. Estimates are less affected by spatial dispersion than those of frequency; and
4. The dependence on quadrat size for reliable abundance estimates is greatly reduced.

The method was originally carried out using square nested sub-quadrats, defined by a series of strings attached to corner poles (Outhred 1984, Morrison et al. 1995). My experiences using this set-up indicated that the strings often became tangled over the course of moving the quadrat to different sampling locations, and often required lengthy untangling. I decided to simplify the apparatus by using nested circular plots; where each plot's radius was defined by a mark on a single cord attached to a central pole (Figure II.1). The user holds the cord for reference as they search from the smallest zone around the centre of the plot outwards. The occurrence of a species is only recorded once, the first time it is encountered. An importance score is assigned to the species depending on the size of zone it is first found in (Figure II.1). Hence, the greater area searched, the less importance assigned.



	Species:				
	a	b	c	d	e
Importance score:	4	3	3	2	1

Figure II.1: Diagram of the nested circular plot placed in an artificial community of four species, a, b, c, d, and e. The table shows each species' score relative to the zone in which they were first encountered. Note that only 7 sub-plots are shown here for display.

Although there is no limit to the number of zones that can be used, the largest useful quadrat size will be related to the trade-off between the scale of variation in the environment the investigator is interested in, and the associated abundance of the organism(s). The smallest practical sub-quadrat size will be related to the size and relative density of the organisms to be sampled. I used 10 zones with the largest total area of 100m^2 (zone 1). For my study, I felt that the relationship between the precision of my description of the vegetation structure, and the relative abundance of larch seedlings (which was often low) would be maximised at about 100m^2. My choice of 10 sub-zones was related to the often very high densities of species like *Vaccinium spp.* and subalpine fir seedlings. The following table (Table II.1) shows the plot cord radii lengths that describe the zones of geometrically increasing size corresponding to decreasing importance value.

Table II.1: Relationship between the sub-plot area searched, plot cord radius, and importance score.

Area (m^2)	plot cord radius (m)	importance score (I.S.)
100.00	5.64	1
50.00	3.99	2
25.00	2.82	3
12.50	1.99	4
6.25	1.41	5
3.13	1.00	6
1.56	0.71	7
0.78	0.50	8
0.39	0.35	9
0.20	0.25	10

Literature cited

Morrison, D. A., Le Brocque, A. F., and Clarke, P. J. 1995. An assessment of some improved techniques for estimating the abundance (frequency) of sedentary organisms. Vegetatio. **120:** 131-145.

Outhred, R. K. 1984. Semi-quantitative sampling in vegetation survey. Pages 87-100 *in:* Myers K., C. R. Margules, and I. Musto, Editors. Survey methods for nature conservation. CSIRO. Canberra, ACT, Australia.

Wilson, B. C. and Stuart-Smith, G. J. 2000. Whitebark pine conservation for the Canadian Rocky Mountain National Parks. KNP03-00. Cordilleran Ecological Research. Winlaw, BC, Canada.

Appendix III: seed predation

There was a large alpine larch cone crop in 1995 that appeared to be synchronous over much of the species' distribution in Banff National Park and Kananaskis Country in Alberta. Arno and Habeck (1972) have previously noted heavy seed predation during a bumper cone crop At Libby Lake in the Washington Cascades. They found that by mid August, much of the seed had been eaten by larvae of an unidentified dipteran species. As part of my study reconnaissance, I decided to collect cones from timberline locations above each of the maturing and older forest sites described in Chapter 3 to see if there was evidence of seed predation. I also collected seeds from timberline areas around Fortress and Sunshine ski areas, and from Quartz hill on the Sunshine meadows.

I selected 5 five trees at the 8 different sites and removed 5 cones from each tree. Sampling took place during the second and third week of August, before the seeds were completely ripe and ready to fall. I removed all of the seeds from each cone and determined the percentage that had been predated. For the large majority of seeds it was easy to tell if there had been any insect damage by visually examining the integrity of the seed coat. I also found many cones still filled with live diperan larvae feeding on seeds. The larvae were small (Figure III.1), approximately 6 to 8 mm long. David Langor from the Canadian Forest Service (Northern Forestry Centre in Edmonton) kindly identified several of my preserved larval specimens to the genus of *Strobilomyia*, in the family Anthomyidae. Unfortunately, I was not able to successfully pupate the adults in captivity to provide identification to species. However, Michelesen (1988) has revised this genus and there are only 3 species, *S. laricis*, *S. carbonaria*, and *S. macalpinei*, that appear in North America. Of these, only *S. macalpinei* had been recorded from alpine larch (collecting in 1962 from Highwood Pass, Alberta).

Figure III.2 shows that the percentage of seed mortality was quite variable both within and between the different sites. The very high level of predation at Temple, and to a lesser extent at Arnica, indicate that these insects may be a significant cause of pre-dispersal predation for the species, and likely contribute to periods of low seedling recruitment.

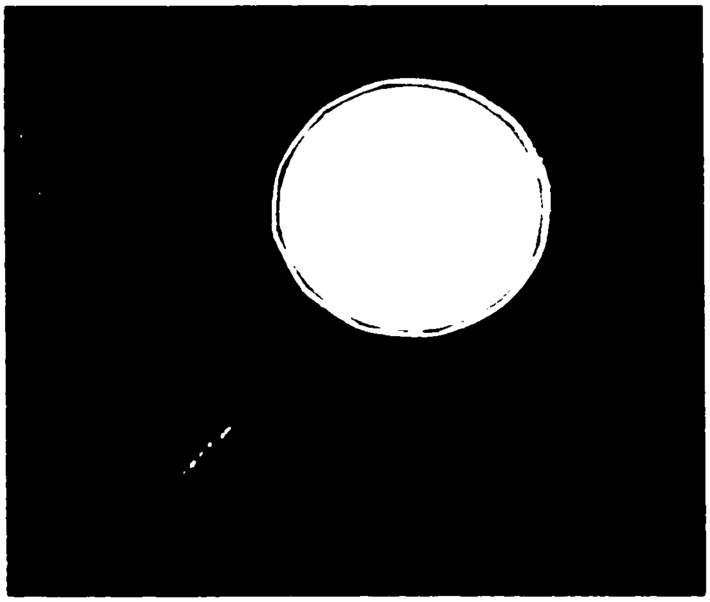


Figure III.1: *Strobilomyia* sp. larvae, a species of root maggot fly found frequently in cones of alpine larch in, and around Banff National Park, Alberta. The coin is a penny for scale.

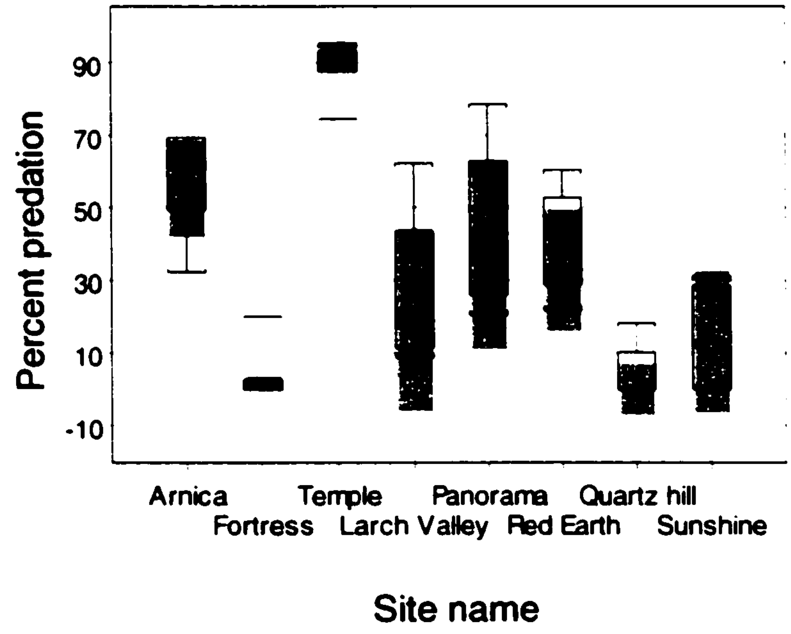


Figure III.2: Seed predation levels at 8 different sites during a high cone production year near the northern alpine larch distribution boundary. The gray shaded area surrounding individual boxes indicates 95 % confidence intervals. The median value is indicated by the dark line within the 25-75% quartile box.

Literature cited

Arno, S. F. and Habeck, J. R. 1972. Ecology of Alpine Larch (*Larix lyallii* Parl) in the Pacific Northwest. Ecological Monographs. **42:** 418-450.

Michelesen, V. 1988. A world revision of *Strobilomyia* gen.n.: the anthomyiid seed pests of conifers (Diptera: Anthomyiidae). Systematic Entomology. **13:** 271-314.

Appendix IV: gap area calculator

There have been two general methods suggested for measuring the gap area created in forests by the fall or removal of one or more canopy trees. The first of these involves measuring the length of a limited number of gap axes and then fitting an ellipse equation to the data (e.g. Runkle 1992, Wilson 1992, Gray and Spies 1996, Spies et al. 1990). This approach appears to work well for gaps that have relatively regular shapes. The second method involves a more detailed mapping approach; usually by measuring a number of radii from the centre of a gap to obvious changes in the perimeter shape defined by the surrounding mature trees. The area is then estimated by either drawing a scale diagram, or by summing the area of the individual triangles described by the radii (e.g., Spies et al. 1990, Lerztman and Kerbs 1991). This method is better at estimating the area for irregularly shaped gaps. In my study of gap disturbance detailed in Chapter 4, my initial observations indicated that many of the gaps in the older Engelmann spruce – subalpine fir forest were oddly shaped and therefore likely to better described by more detailed mapping. The following is a description of the mapping procedure and copy of the computer program that I used to calculate the areas of both canopy gaps and expanded canopy gaps (see Chapter 4 methods for "gap" definitions).

Once I located a gap to survey, I chose a roughly central point from which to start the mapping procedure. I laid measuring tape along a known bearing towards the bole of a surrounding canopy tree. I first measured the distance between the centre point and the edge of the tree's canopy to give the first radius of the canopy gap (Figure IV.1a). Then I proceeded to measure the rest of the distance to the bole of the tree. This complete measurement gave the first radius of the expanded gap. I would then move to the next tree that marked the change in the gap perimeter shape and record the same information. The procedure was continued until the entire gap had been surveyed (Figure IV.1b). This provided enough information to calculate the area of the both the gap and expanded gap (Figure IV.1a). To visualise these area calculations, first consider the shaded gap triangle formed by the two radii and the perimeter trees in Figure IV.1a.

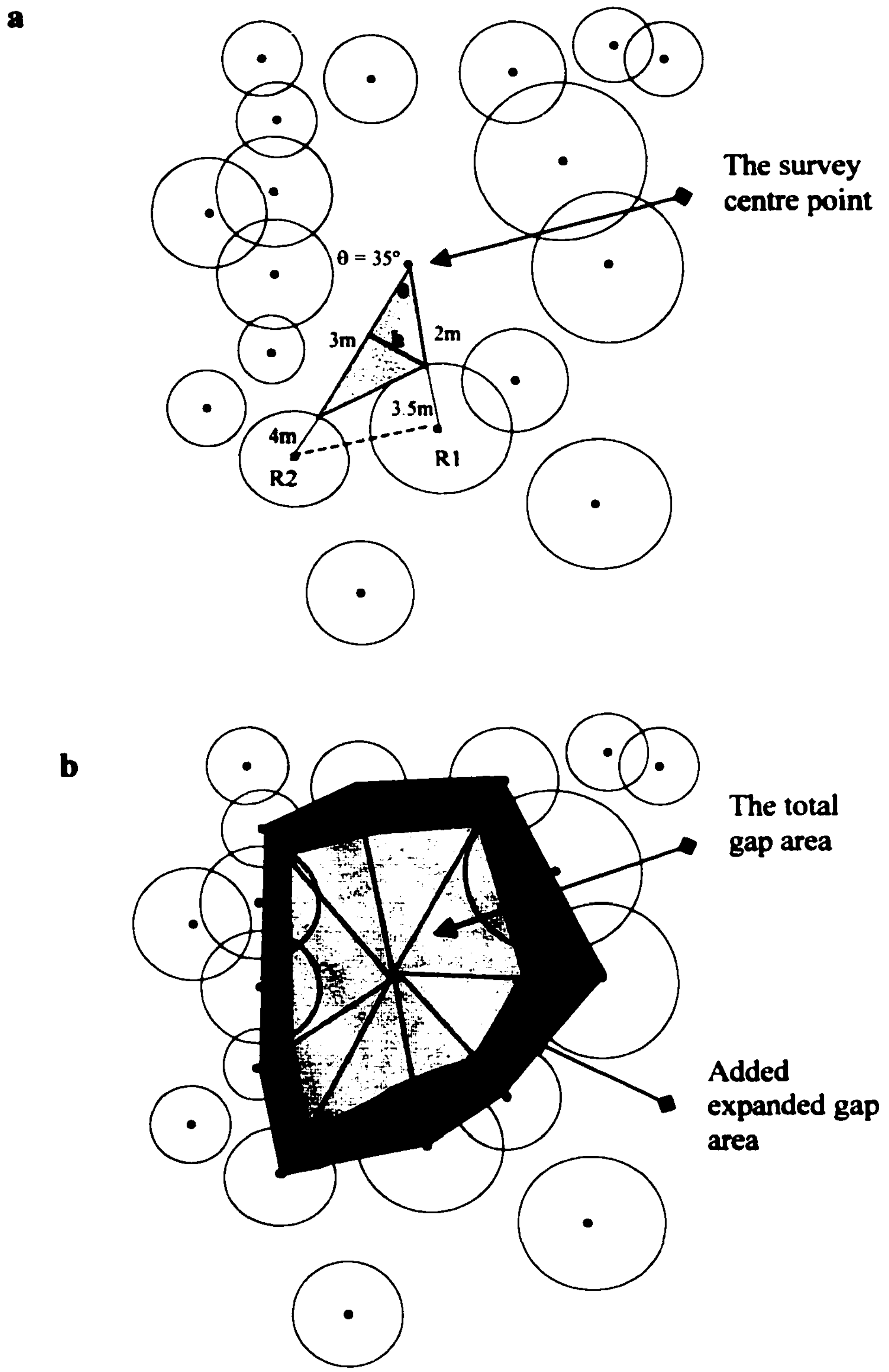


Figure IV.1: an overhead diagrammatic view of a typical forest gap (not to scale). Tree canopies are shown as circles, the trunk locations are shown as the dark centres. (a) The triangular area to be estimated by the survey measurements for the gap area. The expanded gap area is left unshaded. (b) The completed survey radii and the total gap areas. See text for details.

The area of a triangle is given by the formula:

Area = 0.5 base x height (1)

To calculate the height of the triangle, h, I took the sine of the angle θ between the two measured radii (R1 and R2) multiplied by the shortest radius (the hypotenuse of the smaller height triangle of R2 in Figure IV.1a). Thus,

$$h = \sin \theta \times R2. \qquad (2)$$

The longer of the two radii, R1, is used as the triangle base in equation 1. Therefore, the portion of gap area defined by these two radii in Figure IV.1a is: $h = \sin 35 \times 2 = 1.147$, so Area = $0.5 \times 1.147 \times 3 = 1.72$ m^2.

These two steps can be combined in a more general formula:

$$\text{Area} = 0.5 \times R1 \times R2 \times \sin \theta. \qquad (3)$$

I used equation 3 as the basis for a computer algorithm to calculate both the area for canopy gaps and expanded canopy gaps by summing the individual triangular areas of each gap. The program runs as a macro in Microsoft Excel© (Visual Basic for applications©). The data need to be organised in the following fashion (Table IV.1).

Table IV.1: Organised data from Figure IV.1b for the gap area calculator macro.

GapName	GapEdgePoint	ExpandedGapEdgePoint	Bearing
Gap1	2	3.5	175
Gap1	3	4	210
Gap1	2.25	3	240
Gap1	3.3	4	315
Gap1	3	4.2	350
Gap1	3	4.5	30
Gap1	2.5	1.75	93
Gap1	2	1.25	135
Gap2	...	...	...

Where the first column contains the gap name or number, the next two columns contain the distances to the gap and expanded gap edges, and the fourth and last column contains the bearing of each radius. Note that the radii data for each gap need to be in sequence. The cursor needs to be on the first name cell below the header to run (R2, C1). The area calculation is appended to the right hand side of the data (Table IV.2).

Table IV.2: The gap area calculator output (in bold).

Bearing	PolyAngle	GapPolyArea	ExGapPolyArea					
175	**35**	**1.720729**	**4.015034**					
210	**30**	**1.6875**	**2.999999**					
240	**75**	**3.585999**	**5.795555**					
315	**35**	**2.839203**	**4.818041**					
350	**40**	**2.892544**	**6.074342**					
30	**63**	**3.341274**	**3.508338**					
93	**42**	**1.672826**	**0.731861**					
135	**40**	**1.285575**	**1.406098**	**Gap1**	**GapArea**	**19.02565**	**ExGapArea**	**29.34927**
...	...	...	...					

The area for each triangle is shown, and the sum of the areas for each individual gap is presented at the end of those data (Table IV.2). The macro will run through multiple gaps until there is a space found at the bottom of the data. Below is the macro code with comments explaining the different parts.

```
Sub GapAreaCalculator()
‘By Brendan Wilson 2000/9/1
‘This macro calculates the gap and expanded area
‘defined by a gap survey.
Dim GapNumber As String
Dim GapEdgePoint As Double
Dim ExGapEdgePoint As Double
Dim Bearing As Integer
Dim PolyAngle As Long
Dim GapArea As Double
Dim ExGapArea As Double
Dim ExGapPolyArea As Double
Dim GapPolyArea As Double
Dim counterA As Double
Dim summgap As Double
```

```
'write column headings
activecell.Offset(-1, 4) = "PolyAngle"
activecell.Offset(-1, 5) = "GapPolyArea"
activecell.Offset(-1, 6) = "ExGapPolyArea"

'loop through the data
Do While activecell <> ""

'check to see if area calculation of gap polygons is finished,
'conduct the total gap and expanded gap area calculation.
If activecell.Offset(1, 0) <> activecell Then
   summgap = 0
   For CounterB = 0 To counterA
      summgap = activecell.Offset(-(CounterB), 5).Value + summgap
   Next
   activecell.Offset(0, 7) = activecell
   activecell.Offset(0, 8) = "GapArea"
   activecell.Offset(0, 9) = summgap
    summgap = 0
   For CounterB = 0 To counterA
      summgap = activecell.Offset(-(CounterB), 6).Value + summgap
   Next
   activecell.Offset(0, 10) = "ExGapArea"
   activecell.Offset(0, 11) = summgap
activecell.Offset(1, 0).Select
End If

'calculate the angle of the polygon
PolyAngle = theta(activecell.Offset(0, 3), activecell.Offset(1, 3))
activecell.Offset(0, 4) = PolyAngle
'calculate the gap and expanded gap area based on the radii distances
'and measured angle.
GapPolyArea = GapPolyAreaCal(activecell.Offset(0, 1), activecell.Offset(1, 1),
PolyAngle)
ExGapPolyArea = ExGapPolyAreaCal(activecell.Offset(0, 2), activecell.Offset(1, 2),
PolyAngle)
activecell.Offset(0, 5) = GapPolyArea
activecell.Offset(0, 6) = ExGapPolyArea
'count back and calculate the final gap polygon segment using the first and last values.
    If activecell.Offset(2, 0) <> activecell Then
         counterA = 0
         Do While activecell.Offset(-(counterA), 0) = activecell
         counterA = counterA + 1
         Loop
      PolyAngle = theta(activecell.Offset(1, 3), activecell.Offset(-(counterA - 1), 3))
      activecell.Offset(1, 4) = PolyAngle
```

```
    GapPolyArea = GapPolyAreaCal(activecell.Offset(1, 1), activecell.Offset(-
(counterA - 1), 1), PolyAngle)
    ExGapPolyArea = ExGapPolyAreaCal(activecell.Offset(1, 2), activecell.Offset(-
(counterA - 1), 2), PolyAngle)
    activecell.Offset(1, 5) = GapPolyArea
    activecell.Offset(1, 6) = ExGapPolyArea
  End If
activecell.Offset(1, 0).Select
Loop

End Sub
Function theta(A As Double, B As Double)

theta = B - A

  If B - A < 0 Then
    theta = A - B
    End If
  If theta > 180 Then
    NewTheta = 360 - theta
    theta = NewTheta
  End If
End Function

Function GapPolyAreaCal(SideA As Double, SideB As Double, PolyAngle As Long)
 GapPolyAreaCal = SideA * SideB * (Sin(PolyAngle * 3.141592 / 180) / 2)

End Function

Function ExGapPolyAreaCal(SideA As Double, SideB As Double, PolyAngle)
ExGapPolyAreaCal = SideA * SideB * Sin(PolyAngle * 3.141592 / 180) / 2

End Function
```

Literature cited

Gray, A. N. and Spies, T. A. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. Journal of Ecology. **84:** 635-645.

Lertzman, K. P. and Krebs, C. J. 1991. Gap-phase structure of a subalpine old-growth forest. Canadian Journal of Forest Research. **21:** 1730-1741.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology. **63:** 1533-1546.

Spies, T. A., Franklin, J. F., and Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research. **20:** 649-658.

Wilson, B. C. 1992. The effects of selective logging on the floristic composition of snow gum-mountain gum forest on the Barrington Tops plateau, New South Wales. BSc honours thesis. University of Technology, Sydney. Sydney, NSW, Australia.

Appendix V: Environmental variable correlation matrixes

Table V.1: Correlation matrix for continuous variables used in chapter 2.

	elevation	aspect	slope	Dist.to.seed	shrub_ht
elevation	1.00	-0.22	0.18	-0.41	-0.60
aspect	-0.22	1.00	-0.11	-0.05	-0.10
slope	0.18	-0.11	1.00	-0.18	-0.19
duff%	-0.39	0.36	-0.05	0.16	0.26
shrub_ht	-0.60	-0.10	-0.19	0.43	1.00
herb_ht	-0.10	-0.15	-0.01	0.30	0.14
tall_shrub%	-0.52	-0.17	-0.14	0.37	0.66
low_shrub%	-0.54	0.37	-0.04	-0.09	0.16
herb%	0.32	-0.05	-0.11	-0.18	-0.20
bryoid%	-0.10	0.70	-0.13	-0.09	-0.08
organic%	0.04	-0.57	-0.04	0.13	0.16
rocks%	-0.06	-0.26	0.28	-0.09	-0.03
mineral_soil%	0.31	-0.41	0.28	0.06	-0.09
decayed.wood%	-0.07	0.09	-0.27	0.04	0.01
dist.to.seed	-0.41	-0.05	-0.18	1.00	0.43

	decayed.wood%	duff%	organic%	rocks%	mineral_soil%
elevation	-0.07	-0.39	0.04	-0.06	0.31
aspect	0.09	0.36	-0.57	-0.26	-0.41
slope	-0.27	-0.05	-0.04	0.28	0.28
duff%	0.05	1.00	-0.21	-0.24	-0.28
shrub_ht	0.01	0.26	0.16	-0.03	-0.09
herb_ht	0.04	0.04	0.10	-0.06	0.01
tall_shrub%	-0.06	0.17	0.35	0.02	-0.05
low_shrub%	-0.03	0.34	-0.23	-0.14	-0.34
herb%	-0.07	0.03	0.12	-0.47	-0.29
bryoid%	0.03	0.37	-0.75	-0.52	-0.46
organic%	-0.23	-0.21	1.00	-0.05	0.03
rocks%	0.00	-0.24	-0.05	1.00	0.26
mineral_soil%	-0.07	-0.28	0.03	0.26	1.00
decayed.wood%	1.00	0.05	-0.23	0.00	-0.07
dist.to.seed	0.04	0.16	0.13	-0.09	0.06

Table V.1 Continued: Correlation matrix for continuous variables used in chapter 2.

	tall_shrub%	low_shrub%	herb%	bryoid%	herb_ht
elevation	-0.52	-0.54	0.32	-0.10	-0.10
aspect	-0.17	0.37	-0.05	0.70	-0.15
slope	-0.14	-0.04	-0.11	-0.13	-0.01
duff%	0.17	0.34	0.03	0.37	0.04
shrub_ht	0.66	0.16	-0.20	-0.08	0.14
herb_ht	0.16	-0.11	-0.03	-0.05	1.00
tall_shrub%	1.00	0.00	-0.17	-0.27	0.16
low_shrub%	0.00	1.00	-0.13	0.37	-0.11
herb%	-0.17	-0.13	1.00	0.24	-0.03
bryoid%	-0.27	0.37	0.24	1.00	-0.05
organic%	0.35	-0.23	0.12	-0.75	0.10
rocks%	0.02	-0.14	-0.47	-0.52	-0.06
mineral_soil%	-0.05	-0.34	-0.29	-0.46	0.01
decayed.wood%	-0.06	-0.03	-0.07	0.03	0.04
dist.to.seed	0.37	-0.09	-0.18	-0.09	0.30

Table V.2: Correlation matrix for continuous variables used in chapter 3.

	La.basal.area	Bl.basal.area	Se.basal.area	decayed.wood	mineral.soil%	rock%
La.basal.area	1.00	-0.38	-0.31	-0.08	-0.02	0.04
Bl.basal.area	-0.38	1.00	-0.23	0.37	0.15	0.16
Se.basal.area	-0.31	-0.23	1.00	-0.13	0.00	-0.13
decayed.wood	-0.08	0.37	-0.13	1.00	0.07	0.00
mineral.soil%	-0.02	0.15	0.00	0.07	1.00	-0.07
rock%	0.04	0.16	-0.13	0.00	-0.07	1.00
organics%	-0.05	-0.02	0.16	-0.21	-0.10	-0.05
bryoid%	0.08	-0.21	-0.07	-0.27	-0.08	-0.10
herb%	0.43	-0.45	-0.10	-0.21	-0.11	-0.19
dist.to.seed	-0.40	0.38	0.10	0.16	-0.02	0.27
shrub%	-0.43	0.26	0.31	0.09	0.02	-0.04
canopy%	-0.20	0.47	0.29	0.24	0.09	0.03
herb.ht	0.11	-0.10	0.01	-0.12	-0.14	-0.03
low.shrub.ht	-0.24	0.00	0.25	0.06	-0.03	-0.02
tall.shrub.ht	-0.05	0.15	0.01	0.07	-0.01	0.18
canopy.ht	-0.43	0.35	0.21	0.14	-0.06	0.16
duff%	-0.17	0.04	0.32	0.05	-0.03	0.09
slope%	-0.05	0.03	0.04	-0.02	-0.09	0.08

Table V.2 continued: Correlation matrix for continuous variables used in chapter 3.

	herb%	shrub%	canopy%	duff%	slope%	bryoid%
La.basal.area	0.43	-0.43	-0.20	-0.17	-0.05	0.08
Bl.basal.area	-0.45	0.26	0.47	0.04	0.03	-0.21
Se.basal.area	-0.10	0.31	0.29	0.32	0.04	-0.07
decayed.wood	-0.21	0.09	0.24	0.05	-0.02	-0.27
mineral.soil%	-0.11	0.02	0.09	-0.03	-0.09	-0.08
rock%	-0.19	-0.04	0.03	0.09	0.08	-0.10
organics%	-0.06	0.08	0.13	0.04	0.14	-0.85
bryoid%	0.21	-0.11	-0.26	-0.07	-0.13	1.00
herb%	1.00	-0.59	-0.42	-0.45	-0.26	0.21
dist.to.seed	-0.47	0.25	0.27	0.37	0.11	0.04
shrub%	-0.59	1.00	0.35	0.26	0.18	-0.11
canopy%	-0.42	0.35	1.00	0.44	0.31	-0.26
herb.ht	0.16	-0.17	-0.03	-0.14	-0.05	0.07
low.shrub.ht	-0.30	0.44	0.18	0.23	0.19	-0.01
tall.shrub.ht	-0.12	-0.05	0.27	0.15	0.09	-0.10
canopy.ht	-0.37	0.44	0.47	0.32	0.16	-0.20
duff%	-0.45	0.26	0.44	1.00	0.31	-0.07
slope%	-0.26	0.18	0.31	0.31	1.00	-0.13

	herb.ht	low.shrub.ht	tall.shrub.ht	canopy.ht	dist.to.seed	organics%
La.basal.area	0.11	-0.24	-0.05	-0.43	-0.40	-0.05
Bl.basal.area	-0.10	0.00	0.15	0.35	0.38	-0.02
Se.basal.area	0.01	0.25	0.01	0.21	0.10	0.16
decayed.wood	-0.12	0.06	0.07	0.14	0.16	-0.21
mineral.soil%	-0.14	-0.03	-0.01	-0.06	-0.02	-0.10
rock%	-0.03	-0.02	0.18	0.16	0.27	-0.05
organics%	0.04	-0.01	0.05	0.12	-0.17	1.00
bryoid%	0.07	-0.01	-0.10	-0.20	0.04	-0.85
herb%	0.16	-0.30	-0.12	-0.37	-0.47	-0.06
dist.to.seed	-0.20	0.05	-0.08	0.33	1.00	-0.17
shrub%	-0.17	0.44	-0.05	0.44	0.25	0.08
canopy%	-0.03	0.18	0.27	0.47	0.27	0.13
herb.ht	1.00	0.04	0.09	-0.19	-0.20	0.04
low.shrub.ht	0.04	1.00	-0.01	0.43	0.05	-0.01
tall.shrub.ht	0.09	-0.01	1.00	0.14	-0.08	0.05
canopy.ht	-0.19	0.43	0.14	1.00	0.33	0.12
duff%	-0.14	0.23	0.15	0.32	0.37	0.04
slope%	-0.05	0.19	0.09	0.16	0.11	0.14