CANOPY RESEARCH IN NORTH-CENTRAL BRITISH COLUMBIA: AN EXPLORATION OF LICHEN COMMUNITIES

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ABSTRACT

Wet temperate spruce-fir (*Picea engelmannii*/*Abies lasiocarpa*) forest communities at high elevations in east central British Columbia are host to an abundance of epiphytic lichens. The distribution and diversity of these appears to be strongly influenced by stand structure and attributes of canopy architecture. We have characterized the distribution of arboreal lichen communities along gradients in canopy structure by combining biomass estimates and subsample verification with single rope access techniques. Integrating newly developed techniques with modified existing methodology results in a reliable and objectively collected data set to describe the abundance of epiphytic lichens. Fruticose lichens respond significantly to vertical gradients separating the two fruticose functional groups (*Alectoria* and *Bryoria*) into distinct strata within the canopy. The strength of this vertical influence appears to minimize the response of fruticose lichens to other gradients in the canopy environment. The distribution of foliose lichen, in contrast, does not respond to height, but appears to be more strongly influenced by changes in the substrate availability. The most significant response of this lichen group is therefore to changes in the diameter of the host branch. Although all three functional groups (*Alectoria, Bryoria* and foliose lichen) show notable responses to gradients in stand age and size, only the two fruticose lichen groups are influenced by the clumped tree distribution of the ecosystem. The management implication of these responses to canopy architecture and stand structure have been explored.
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Chapter 1
Introduction and Literature Review

The study of organisms inhabiting the tree tops is an exciting and relatively new field of biological research. This new frontier (Erwin, 1983) was first scientifically explored thirty years ago and has diversified since to include a wide array of research activities. These activities range from quantifying carbon flux at the canopy-atmosphere boundary to documenting the abundance and diversity of epiphytic plants and animals. Observing biotic assemblages that are intrinsically different from those of terrestrial communities is exciting. Canopy research combines the physical challenge and technical rope skills of access methodology with the inspiration of studying communities that previously could only be viewed from a distance. Breakthroughs in access methodology over the past three decades have facilitated the expansion of canopy research to such an extent that the canopies of a greater variety of ecosystems are accessible to scientific study.

This thesis details the introduction of methods of canopy access to the study of epiphyte biology in northern forest ecosystems. Our research has focussed on an exploration of the epiphytic lichen communities and the architectural characteristics of the Subalpine Fir (Abies lasiocarpa) and Engelmann Spruce (Picea engelmannii) canopy.
1.1 History of Canopy Access

Documentation of epiphytic community dynamics requires the use of a safe and effective method for accessing the canopy environment. Prior to the widespread use of tree access, observations of arboreal communities were generally limited to destructive techniques such as tree felling (Forman, 1975) or to ground based work in which observations were confined to the lower branch and trunk (Stevenson, 1978). The advent of climbing technology allowed a new perspective on the dynamics of these ecosystems. The techniques range in complexity and permanence from platforms and walkways to mobile trunk climbing techniques.

Platforms and walkways have been constructed and employed in many studies (McClure, 1964; Ring and Winchester, 1996; Sugden et al., 1982). They are useful when long term research of a small sample of the canopy is required. Canopy cranes offer similar long term access opportunities, but have the added benefit of providing access to a large number of trees growing within the radius of the crane arm. The Wind River canopy crane in Washington, USA reaches the crowns of over 300 trees (Shaw, 1998). Similarly, the Smithsonian Tropical Research Institute Crane and Gondola in Panama is a 42m structure that reaches a wide circumference of dominant canopy species (Allen, 1996). Cranes and free standing towers are ideally suited for the study of the boundary between the canopy and the atmosphere (other techniques do not allow access to the outer canopy). These structures also facilitate the buildup of information about the surrounding forest when researchers share the facilities and transfer data sets (Lowman and Nadkarni, 1995).

One disadvantage of these fixed facility approaches is the initial investment of infrastructure and the subsequent operational costs that are required. When the objective of access methodology is to rapidly sample a large number of trees, less expensive, simpler
techniques are generally adopted. The simplest of these approaches uses the traditional tree climbing techniques of local inhabitants of tropical forests (Mitchell, 1982). These are extremely useful in ecosystems where the tree trunks have a small diameter but are branchless for a large distance.

More recently, the adoption of technical aids in tree climbing has allowed more widespread access to canopy environments. An arborist belt and spurs provide relatively rapid admittance to the canopy (Hinds, 1970), but this technique can easily introduce fungal infection through the spur puncture holes and is tedious to use in densely branched trees. Denison (1973) advanced this technology by using a climbing rope to reach the canopy. The first ascent involved driving lag screws into the trunk at regular intervals. Hangers and modified rope ladders were attached and the climber slowly worked up the trunk in a manner similar to mountain climbing techniques. Another person was required to belay the climber from the ground. This method was time consuming and more complicated than was necessary to ensure safety in the working environment. It was also highly injurious to the tree.

The single rope access technique, introduced by Perry (1978), can be installed and used by one person. Researchers climb a rope, tied to the trunk in the upper canopy, instead of the tree and so minimize the destructive impact. Initial rope placement is achieved by shooting a monofilament line attached to a weighted arrow from a crossbow into the upper canopy. The climbing rope is attached to this line and pulled into the tree leaving two free ends. One end is climbed while the other is securely attached to the trunk at the bottom. The rope is moved to a safer anchor location following the first ascent. This method is not as physically demanding as that of Denison (1973) and provides much more rapid access. Whitacre (1981) subsequently reported additional safety modifications to the method of Perry (1978), such as using locking
carabiners, maintaining two points of attachment to the rope at all times and carrying a back up prusik in case of ascender failure. Tucker and Powell (1991) also modified the technique by including a second rope for a belay line to increase worker safety.

The development of these various methods of canopy access has permitted detailed observation of canopy systems in a wide range of ecosystems. Access techniques should be chosen and modified to meet the safety requirements of the scientists involved, the structural features of the tree and the objectives of the study. We used the single rope technique (Perry, 1978) and will detail our successful application of this technology in studying the lichen communities of canopy ecosystems in east-central British Columbia.

1.2 Canopy Lichens

Lichens are a composite organism comprised of a fungus and a photosynthetic partner (green alga, cyanobacterium or both). The members of the two biological kingdoms make up a mutually controlled, symbiotic relationship where the alga supplies the fungus with carbohydrates, vitamins and proteins in exchange for structural support and protection (McCune and Geiser, 1997). Lichen taxonomy is based on the fungal partner. Most lichens incorporate ascomycetes as the mycobiont but the order can vary widely. In contrast, the photobiont is usually one of several alga species. The green alga, Trebouxia contributes the photobiont to approximately 40% of known lichens (for many lichens, the photobiont has not been identified to species; Honegger, 1991). Trebouxia is particularly dominant in cool, temperate regions (Rikkinen, 1995).

Canopy lichens grow on other plants, primarily trees. They use their hosts for substrate only and derive no nutritive value from them (Nadkarni, 1984b). Because epiphytes are
physically supported by other plants, they are not in direct contact with the nutrient or water
supplies that are provided through the forest floor. They must therefore depend on atmospheric
sources (Nadkarni, 1984b). The infrequent and unpredictable water and nutrient source results in
the characteristic slow growth rate of epiphytic lichens. This result is compounded by the
tendency for lichens to become dormant when the water content falls below a certain threshold
(Kershaw, 1985). This frequently occurs in the desiccating canopy environment created by strong
winds, high light intensities and extreme temperatures (Nadkarni, 1984b; Pike et al., 1975;
Sillett, 1994).

Epiphytic lichens are important components of old growth forest ecosystems in British
Columbia, both as indicators of forest health and as primary producers. As indicators, many
lichen species have associations with a narrow range of environmental conditions, such that their
presence or absence indicates the status of that ecosystem (Patton, 1987). Further, lichens require
long establishment periods in relatively undisturbed environments and are thus often used as
indicators of stable habitats or more specifically, of forest ecosystems (Pettersson, 1996).
Lichens can also indicate prior exposure to atmospheric pollution. The cation exchange
mechanism by which lichens absorb atmospheric nutrients causes significant, and often lethal,
quantities of atmospheric pollutants to be retained in the lichen matrix. This enables lichens to be
used in experimental systems for monitoring cumulative pollutant exposure.

In addition to being indicative of forest health (Duchesne, 1994; Pettersson, 1996),
epiphytic lichens are an important part of functioning ecosystems. A large proportion of the
lichen thalli is photosynthetically active when wet. In contrast, up to 80% of tree biomass is tied
up in inert, non-photosynthesizing, wood. Thus, although the biomass of lichens is small relative
to the host trees (10-20% of overall tree biomass; Pike et al., 1975), the relative contribution of
lichens to ecosystem function and nutrient cycling is larger than would be predicted by biomass alone.

Among the documented contributions of lichens to ecosystem function are their roles as forage for mountain caribou (*Rangifer tarandus caribou*; Edwards and Ritcey, 1960; Rominger and Oldemeyer, 1989), flying squirrels (*Glaucomys sabrinus*; Maser et al., 1985) and black-tailed deer (*Odocoileus hemionus columbianus*; Stevenson, 1978) or as habitat for numerous canopy dwelling arthropods (Gerson and Seaward, 1977; Seaward, 1988; Stubbs, 1989; Pettersson, 1996; Pettersson et al., 1995; Showalter, 1995). An important role of lichens in high elevation forests of western North America is as forage for mountain caribou. During the winter, when terrestrial forage becomes inaccessible because of snow pack, mountain caribou move into high elevation spruce-fir forests (Simpson et al., 1985) where they feed on the abundant supply (>3000kg/ha; Edwards et al., 1960) of epiphytic Alectorioid or fruticose lichens (Edwards and Ritcey, 1960; Rominger et al., 1994; Stevenson, 1979). Although the three-metre snow packs aid in accessibility of lichens on higher branches, a large proportion of the forage would appear out of reach to caribou. However, Terry (1994) reported that accumulation of lichen litter-fall and lichens on fallen trees are a considerable attraction for caribou, providing up to 50% of their forage intake. The growing and abundant food supply on live trees is brought into reach by strong winds and a deep snow pack (Stevenson et al., 1994).

### 1.3 Canopy Lichen Habitat

Succession, microclimate and canopy architecture of old growth environments are all believed to play formative roles in determining the distribution and abundance of epiphytic lichens (Forman, 1975; Halonen et al., 1991; Hinds, 1970; Lowman & Moffett, 1993; McCune,
The relative contribution of each of these factors to lichen habitat is, however, unknown. This uncertainty is compounded because the three variables are confounded in the canopy environment and not easily separated experimentally (McCune, 1993). Any attempt to discern the influence of one, must therefore include a discussion of others. Therefore, a study of the structural influences here is prefaced with an overview of what is known for all three variables.

1.3.1 Succession

There is a distinct sequence of epiphyte development over time that is manifested in vertical gradients within the canopy (Yarranton, 1972). In wet coastal old growth forests of the Pacific Northwest, there is a distinct dominance of bryophytes. Bryophytes are epiphytes that are most abundant in later stages of the successional sequence (McCune, 1993). Epiphytic lichens, in contrast, become established much earlier within this sequence and become richer and more abundant with age (Selva, 1994). The increase in abundance over time is likely due to the combination of the limited ability of lichens to effectively disperse and the optimal substrate that is found primarily in older trees (Sillett and Neitlich, 1996).

Although some lichens have either developed more efficient methods of reproduction or have the ability to widely disperse with small, wind borne fragments (Esseen, 1985), invasion of new substrates is generally difficult and slow. Invasion is enhanced by both spatial continuity of mature forest and by long term stability within the forest environment (Hawksworth and Hill, 1984). Large tracts of young forests have not had the time nor the proximity to the propagule sources in old forests to develop loads of lichen that are seen in more mature stands.
In addition to problems inherent in a non-specific dispersal method, the bark of young forests may be unsuitable for efficient colonization (Culberson, 1958; Hyvarinen et al., 1992). The bark of immature trees is smoother with fewer fissures and textural features than are found on older bark. These features are ideal for accepting and holding lichen propagules until they can become established (Renhorn, 1997a). The microclimate inherent in younger forests may also be less suitable for growth than that of later successional forests.

1.3.2 Microclimate

Despite the difficulty in discriminating between structural and environmental influences on epiphytic communities, there is considerable evidence documenting the importance of microclimate to epiphyte abundance (Halonen et al., 1991; Yarranton, 1972). The two most influential environmental variables affecting lichen abundance are availability of solar radiation and moisture (Boucher and Stone, 1992). Lichens are highly tolerant of frequent wetting and drying cycles and are capable of dormancy in response to moisture stress but they are only photosynthetically active when wet. Growth rate is therefore intrinsically tied to the amount of precipitation that the canopy receives (Armstrong, 1993; Renhorn and Esseen, 1995). Availability of a predictable supply of water is the most important factor limiting lichen growth (Arseneau et al., 1997; Edwards et al., 1960; Forman, 1975).

Limiting solar radiation is more deleterious to some lichen species than others. *Bryoria*, for example has a wide ecological amplitude and tends to colonize more open sites (Edwards et al., 1960). *Alectoria*, on the other hand, is tolerant of diffuse light and is commonly found in the lower canopy and in more dense forests. In general, the vertical strata of the canopy that receive maximal solar radiation (McCune et al., 1997) and trees that experience more solar radiation
(Stevenson, 1979) appear to host the most abundant and diverse lichen communities (McCune et al., 1997).

1.3.3 Canopy Structure

The microclimate experienced by arboreal lichens is largely determined by the structure of the tree (Halonen et al., 1991). Tree architecture plays a significant role in influencing the patterns of lichen distribution and abundance (Edwards et al., 1960) along a vertical gradient in the canopy. There are distinct vertical gradients in epiphyte abundance along which epiphyte functional groups (including bryophytes, fruticose lichens, foliose, green lichens and cyanolichens) replace one another as the most abundant in the canopy (McCune et al., 1997; Sillett and Neitlich, 1996). Most studies report that overall lichen abundance increases with increasing height above ground. There is, however, some variation in the vertical position at which peak abundances occur, depending on the ecosystem. Ahti (1977) and Edwards et al. (1960) documented the largest proportion of epiphytes within 3 and 10 metres (respectively) above the ground in central British Columbia. Others (Arseneau et al., 1977) have shown the peak to be at between 33 and 67 percent of the total height in small trees within the Gaspe-Provincial Park, Quebec. These studies are in young stands where the overall lichen biomass is expected to be lower (Forman, 1975). Similar, but more pronounced gradients, are observed in larger trees (McCune, 1990) where lichens and bryophytes seem to peak at different height intervals within the canopy (Pike et al., 1975). It is suggested that this is due to an interaction between crown height and succession (Yarranton, 1972), as each functional group becomes established at a particular time since the last disturbance.
Branch diameter, as a measure of substrate availability, also influences lichen abundance (Clement and Shaw, unpub.). Renhorn (1997a) showed that there was a strong positive relationship between branch diameter and both foliose and fruticose lichens. Variables that are less influential but significantly correlated with epiphyte abundances are branch slope and length (Clement and Shaw, unpub.; Renhorn, 1997a). Branch aspect was shown to be an important variable only in very open forests where differences in canopy gap size were appreciable (Yarranton, 1972) and variation in the amount of sunlight received could be detected. Parker (1995) reported that the proximity to the outer canopy was more important for environmental characteristics (such as photosynthetically active radiation) than other structural features. The frequency of particular lichens may also vary in response to the distance to the nearest neighbouring tree, which is reflective of the variation in the light environment (Yarranton, 1972).

1.4 Biodiversity and Conservation

Preservation of biodiversity and conservation of epiphytic communities are important considerations for many biologists. Forest biologists in particular are concerned with the loss of biological diversity resulting from the conversion of old growth forests to earlier seral stages. These earlier systems are less complex and do not display many of the characteristics of older forests. Old growth or mature forests are typically very diverse communities, providing habitat for numerous species that depend on stability and ecological continuity. Mature forest stands are generally characterized by large, dominant trees, abundant snags and dead-fall and a well-developed under-storey resulting from infrequent disturbances (Veblen, 1994). This creates a multi-layered canopy extending from the ground to the crown (Franklin and Spies, 1991). In British Columbia, old growth forest environments vary in age, structure and dynamics making it
extremely difficult to define old growth characteristics and therefore manage for the maintenance of these characteristics (Duchesne, 1994).

With intense forest management, the age class distribution of mature forests is shifted to a younger, less complex ecosystem. Prior to the 1950's, forestry activity within late successional, high elevation forests was uncommon because an abundant timber supply was available within the easily accessible and managed low elevation zones (Stevenson et al., 1994). Since then, however, harvesting has progressed into high elevation forests, bringing with it practices designed for more homogeneous, single cohort stands. Management practices can be more complicated in older forests because of the structural heterogeneity and the sensitivity of the habitats that this provides.

One of the primary considerations for forest managers working within the high elevation forests of east central British Columbia is the maintenance of arboreal lichen abundance for the mountain caribou. Mountain caribou are considered blue listed (vulnerable) by the Ministry of Environment, Land and Parks due to characteristics that make them particularly sensitive to human activity (Paquet, 1997). Traditional forest harvesting, with medium to large clear cut blocks, seems incompatible with maintaining epiphytic lichens for mountain caribou habitat. Epiphytic lichens are lost through forest harvesting, either directly through the removal of host trees or through fragmentation of lichen on neighbouring trees in the adjacent forest during harvest and as a result of increased wind scouring in the exposed canopy (Esseen et al., 1996, Fritschen, 1983). Because pendulous lichens are sensitive to fragmentation, a large proportion of existing lichens are likely lost to this process (Renhorn, 1997a). Forestry also affects lichen loading because periods of lichen growth are decreased by the shorter rotation ages (Smith, 1986) typical of traditional management (Esseen et al., 1996). Lichen biomass cannot return to previous
levels when the second harvest occurs prematurely in the successional sequence (Stevenson and Hatler, 1985). Traditional forest harvesting further prevents the effective reestablishment of epiphytes because practices do not leave mature, residual trees behind to serve as seed or propagule banks (Esseen et al., 1996). Re-colonization is also delayed by large clear cuts which prevent lichens with poor dispersal abilities from becoming established in the centre of developing forests. This is further compounded because the microclimate and substrate of new forests are generally unsuitable for lichen establishment and growth (Esseen et al., 1996). The environment in a developing forest changes too rapidly for lichen to effectively colonize the new substrate. Young second growth stands thus do not display the characteristic lichen load of the adjacent intact forest. While some species are more sensitive than others to forest harvesting as a result of fragmentation or growth and dispersal characteristics (Esseen and Renhorn, 1997), it is apparent that traditional harvesting practices are inappropriate for sensitive high elevation stands where the maintenance of diverse and abundant lichen communities is desirable.

Stevenson and Hatler (1985) recommended directing research to ascertain which partial cutting designs are least destructive to the lichen environment. Research focussed on the natural disturbance regimes of an area allows the development of harvesting practices that closely mimic natural processes (Harvey, 1994). Research into biotic diversity is also important to ensure that future actions are not destructive to the current lichen biota. Partial cutting, if conducted properly, allows for greater short-term retention of canopy lichens. Stevenson and Hatler (1985) reported that approximately 20-32% of lichen was left in a 51 cm diameter cut and residual propagule source trees were maintained for dispersal to the growing trees. Partial cutting also improved the microclimate by preventing the wind scouring that normally occurs in newly opened blocks and by opening up the canopy to allow increased light exposure (Stevenson and
Partial cutting systems, if thoroughly researched and properly managed, have the potential to sustain both timber harvesting and mountain caribou habitat, by preserving arboreal lichen abundance (Stevenson et al., 1994).

The Mountain Caribou in Managed Forests (MCMF) program began in east central British Columbia in 1988 with these goals in mind (Stevenson et al., 1994). Researchers began to gain an understanding of the ecosystem processes and attributes of biodiversity integral to caribou habitat that must be maintained in managed forests throughout the rotation. The Engelmann spruce - Subalpine fir stand at Pinkerton Mountain was studied as part of the MCMF program. Silviculture system trials were designed with the aim of maintaining epiphytic lichen biomass (g/tree) at pre-harvest levels. Levels and methods of tree removal were varied in a series of silviculture trials. The biomass of lichen both before and after these trials was documented to determine the effect of each removal mechanism on caribou habitat. The results indicated that there is a threshold of tree removal beyond which the ecosystem processes and dynamics that are favourable for lichen growth cannot be maintained (Stevenson, 1995).
1.5 Project Background and Rationale

Early investigations into high elevation forests within the Cariboo mountains in east central British Columbia revealed abundant epiphytic lichen communities (Edwards et al., 1960). The diversity of these arboreal ecosystems has remained unexplored as the difficulties of canopy access have limited research to those branches that could be observed from the ground. This project is therefore designed with the purpose of documenting the abundance of epiphytic lichens in these forest canopies. The rationale behind this project has two major components.

This is the first research endeavour into the tops of the Engelmann spruce - Subalpine fir forest ecosystem in the northern Cariboo Mountains at Pinkerton Mountain. Many of the trees comprising this old growth forest ecosystem are host to an abundance of epiphytic lichens. It has been suggested that the age of the stand is not the only factor influencing lichen abundance (Hyvarinen et al., 1992; Lang et al., 1980 Sillett, 1994; Yarranton, 1972) and that the architecture of the canopy is an important determinant. The relationship between structural factors of the canopy and the abundance of epiphytic macrolichens was investigated by characterizing the attributes of the structural environment, documenting the species composition and abundance patterns and exploring relationships and trends between these. We also investigated the influence of the distribution patterns of the trees on lichen biomass. The ecosystem at Pinkerton Mountain contains trees that grow in well developed clumps, in which the crowns of member trees significantly overlap and interact. We suggested that this clumping distribution is important for the establishment and maintenance of the large abundance of lichens.

The second aspect of the project rationale follows from the inclusion of this study into a larger research initiative concerned with producing a forest management plan that would allow for economically viable harvesting while maintaining habitat for mountain caribou. Because
timber demands have grown on low elevation ecosystems in the Bowron Valley, harvesting activities have moved into the more sensitive, high elevation, Engelmann spruce-Subalpine fir zone. Due to the mature, lichen bearing trees and the preference of mountain caribou for these ecosystems, timber harvesting has become an issue. Management with traditional clear cutting on short rotation (Smith, 1986) depletes the supply of mature trees and epiphytic lichen. A management plan that incorporates information about the dynamics of the ecosystem, including the upper canopy where the majority of forage lichens are found, is required. This project is specifically concerned with determining the key factors that influence the abundance of arboreal lichens so that informed and meaningful recommendations may be made for the responsible management of this ecosystem.
1.6 Objectives and Research Questions

I. To describe and evaluate the techniques of biomass estimation and biomass verification used in combination with single rope canopy access to study epiphytes in high elevation spruce-fir forests.

II. To describe the stand structure and canopy architecture of a representative high elevation spruce-fir forest. We will examine and document stand features such as tree age, size and distribution and the architectural characteristics of branch height, diameter, aspect, length and slope. Relationships and interactions among architectural features will be explored to gain insight into the dynamics of the canopy.

III. To quantify and describe the biomass and distribution of the epiphytic lichen functional groups; Alectoria, Bryoria and foliose lichen. Documentation of the lichen community will also include a compilation of a species list for each lichen functional group.

III. To explore relationships between stand structural and canopy architectural features and the distribution of epiphytic lichen biomass within. The response of the three functional groups to each of the canopy features will be examined to understand the determinants of lichen distribution and abundance.

IV. To discuss the implications of these results to forest management within the Pinkerton Mountain ecosystem.
Chapter 2

Site Description and Experimental Design

2.1 The Engelmann Spruce Subalpine Fir (ESSF) Biogeoclimatic Zone

The research was conducted within the Engelmann Spruce - Subalpine Fir (ESSF) biogeoclimatic zone. The ESSF Biogeoclimatic zone includes most of the high elevation forests within interior British Columbia covering in excess of 4.2 million acres of forested land (Coupé et al., 1991; Farnden, 1994). It is characterized by rugged terrain with steep valleys, sharp peaks and interior plateaus. Elevation ranges from approximately 1050 to 1500 metres at the north end of the zone. The ESSF extends from tree-line at the highest elevation to the Sub-Boreal Spruce and Interior Cedar Hemlock zones at low elevation (Coupé et al., 1991). The zone is characterized by a cold, moist continental climate with long, cold winters and short cool summers.

Unlike other forested zones, tree growth in the ESSF is not limited by the amount of available moisture. Wetter areas of the biogeoclimatic zone can receive up to 2200 mm of precipitation annually, two-thirds of which falls as snow (Coupé et al., 1991). The lower temperatures (mean annual temperature ranges from -2°C to +2°C; Coupé et al., 1991) characteristic of the upper elevation of the ESSF zone cause the large snow pack to melt much more slowly than in other zones resulting in a very small number of snow free days and even fewer frost free days each year (Farnden, 1994). The net result is a very short growing season which becomes the main factor limiting growth in the ESSF.

The ESSF is dominated by Engelmann spruce (Picea engelmannii) and Subalpine fir (Abies lasiocarpa) trees. Seral species of Lodgepole pine (Pinus contorta) and Trembling aspen (Populus tremuloides) can also be quite common. Engelmann spruce is one of the largest high elevation species reaching a maximum height of 30 metres in the ESSF. It is long lived, often reaching
maturity at 250-450 years. The crowns occupy 50-70% of the total height (Alexander, 1987) and are symmetrical and narrow. Branches are typically short and droop significantly in the lower portions of the trunk. Needles curve upward and thus appear to be crowded on the upper side of the branches. Mature spruce bark is broken into large, loose, coarse brownish scales (Farrar, 1995).

Subalpine fir grows very slowly and is susceptible to disease so trees larger than 30 metres are exceptional. The crown of Subalpine fir is narrowly conical with a much elongated and extremely narrow top which occupies 70-80% of the total height in old growth stands (Alexander, 1987). The branches are short and compact with a tendency to droop to the ground (Farrar, 1995). Needles appear nearly erect on the branches as they are long, crowded and twisted at their base. The bark in young trees is thin and smooth with blotched resin blisters. It becomes broken into irregular greyish-brown scales in maturity (Farrar, 1995).

Most climax stands in the ESSF are composed of pure Engelmann spruce or Engelmann spruce-Subalpine fir mix at lower altitudes while higher elevations are dominated almost entirely by Subalpine fir. The shift in dominance is attributed to the climate changes that are a result of topographic variation. Local differences in site conditions caused by slope, aspect, soil characteristics and elevation also help to determine the composition of the stand. Elevation is especially important as an increase in elevation of 1000 metres decreases the average daily temperature by 6°C which shortens the growing season by 30 days (Critchfield, 1974). Spruce is less tolerant of such conditions and so is unable to dominate at higher elevations.

2.2 Pinkerton Mountain

The specific study site is at Pinkerton Mountain in the Bowron Valley within the Prince George Forest Region. This site is in the Quesnel Highlands Ecosystem of the Columbia Mountains and Highlands Ecoregion. Pinkerton Mountain is approximately 90 km ESE of Prince
George, and about 2 km north of the junction of the Pinkerton, Post and Tumuch Forest Roads (N $53^\circ, 37' 52.44''$; W $121^\circ, 25' 21.23''$). The site is in a management zone designated as caribou medium in which the Ministry of Environment, Lands and Parks have requested that management (including forest harvesting) be consistent with maintaining caribou habitat and arboreal lichens. The study area is on a south facing gentle slope of the Wet Cold Cariboo variant of the ESSF (wc3) zone at approximately 1450-1475 metres in elevation. The forest stand has an average density of 572.6 stems per hectare of which 73% are Subalpine fir and 27% are Engelmann spruce. In addition, there are an average of 8 snags per hectare making up 21.8% of the total stand volume of 300.6 m$^3$/ha. Ages range from seedlings to approximately 350 years. The average diameters of live, mature (trees larger than 17 cm dbh) Engelmann spruce and Subalpine fir are 36 and 46-cm respectively. The stand is mostly composed of closely associated trees forming clumps (Fig. 2.1). Up to 62% of the trees in the stand had overlapping crowns (Coxson and Stevenson, 1996). The clumps of trees are separated by gaps in the canopy, which are approximately the same size as the clumps. Individual trees are also common. The site is a multi-cohort, uneven-aged stand with trees ranging in height from a few centimetres to a maximum of approximately 30m (Stand data compiled by Forey Management Ltd.).
Fig. 2.1  An areal photograph of the study area at Pinkerton Mountain showing the clumped nature of the ecosystem and the degree of crown overlap.
2.3 **Study Site Selection**

The research at the site is part of an ongoing silvicultural systems project (Coxson and Stevenson, 1996) so thirteen prospective study plots were chosen for this study within a four hectare plot that straddled the boundary between the prescribed cut block area and a control area that will not be disturbed to facilitate a post-harvest comparison of lichen biomass (Fig. 2.2). This initial selection was based on the following criteria:

1. An assessment of the structural makeup of the clump. Eligible clumps were composed of a taller stratum or layer of trees surrounded by an unspecified number of shorter layers.
2. A qualitative assessment of the amount of crown overlap with neighbouring trees. Eligible clumps were not aggregated with other clumps so that all were functionally distinct and the impact of other trees on the microclimate experienced by the study clump was minimized.
3. An assessment of disturbance. Eligible clumps were a sufficient distance from all clearings and landings so that minimal effects from these disturbances were experienced.
4. An assessment of safety concerns including the number, proximity and stability of neighbouring snags. None of the recommended study clumps contained large snags.
5. An assessment of site slope. Clumps were all on level ground to remove any variation due to elevation or slope.

From these thirteen prospective clumps, five sites were chosen for canopy study (labelled clumps 1, 2, 4, 6 and 9). These were chosen by an assessment of canopy accessibility, canopy safety, tree density (whether it was possible to get in between the trees to make observations) and the number of separate trees within the clump that would require individual access ropes (priority was given to those clumps that required no more than three ropes). Individual access ropes were generally required for trees more than 3 metres from each other.
Fig. 2.2 A map of the Pinkerton mountain research area. The map includes the logging map with both the single tree selection and group selection harvest areas. The study clumps were within a four hectare plot. This plot straddled the boundary between the group selection and control areas. Clumps 6 and 9 were within the control area and clumps 1, 2, 4, 11, 12 and 13 were chosen within the group selection area.
Of the five clumps chosen, two (clumps number 6 and 9) were in the control area where there is no planned forestry activity and three (clumps number 1, 2 and 4) were in an adjacent area where selection harvesting occurred in early spring 1998. Three additional clumps (clumps number 11, 12 and 13) were subsequently chosen in the harvest area using these same criteria, and added to the study population to increase the sample size. Stem maps of each of the study clumps and surrounding trees are given in appendix 1.

Within each of these eight study sites, an individual tree was selected so that a comparison could be made between the clump trees and the solitary trees. The solitary trees were required to be approximately as tall as the average of the clump trees. Trees were only considered as solitary if there was no contact with other trees. A pool of eligible solitary trees were chosen within a 30-m radius of the clump edge with the aforementioned safety and accessibility concerns. Often there was only one tree in the site that met all of these criteria. If more than one eligible tree was identified, then one of them was randomly selected.

2.4 Canopy Access

Methods of canopy access were chosen to suit the characteristics of the specific canopy and the safety concerns of the researchers at the site (Tucker and Powell 1991). I reviewed the existing techniques (Denison 1973; McCarthy 1988; Perry and Williams 1981; Ring and Winchester 1996; Tucker and Powell 1991) and judged that most were more complicated than was necessary to achieve a safe and reliable working environment in my study area. I selected the single rope access technique described by Perry (1978) as it was the most suitable for the requirements of my research in the subalpine canopy where the narrow crowns and dense branches create problems in manoeuvring around the trunk. Initial placement of the rope in the trees was achieved by tossing a 12-14oz sack attached to a braided nylon cord over an appropriate branch. The weighted sack was
used to increase the accuracy of the toss and to ensure that the line returned to the ground. A 10.5-
11mm static climbing rope was then attached to one end, pulled over and anchored around the base
of the tree. Ascending and descending was achieved as described by Perry (1978).

Using a single rope for ascending and descending from canopy was successful. However, it
was not possible to make detailed observations in high elevation trees from the main line. The
branch density made it difficult to reach every limb. A secondary system (lanyard) commonly used
by tree climbers was employed (Fig. 2.3). It allowed us to move around to all parts of the tree
while remaining securely attached. The system consisted of an auxiliary rope approximately 10-
20m long. One end was secured around the trunk of the tree and attached to the climbing harness.
A prusik knot (Manning, 1960; Whitacre, 1981) was tied using a small cord onto the free end of
the rope and attached to the harness. Moving the prusik along the length of the free end of the rope
allowed the climber to move horizontally and vertically through the canopy. The climber could
thus remained securely attached at all times without necessarily re-anchoring at multiple points or
depending on the main rope. This also made it possible for more than one observer to work in the
same tree. The single rope and lanyard systems were used to facilitate movement to and
observation of every branch in the trees.
The Lanyard System consists of a short line of 11mm rope (A) attached to the climbing harness (B) using both a figure eight on a bight (C) and a prusik loop (D). The prusik loop slides along the length of the short line when manually moved, but tightens and holds the climber safely in place when weighted.
2.5 Structural Variables

Each tree taller than 2m in the clump and the solitary tree were climbed (if they could not be viewed from the ground) and assessed. The clump included all the trees whose branches overlapped and those which were found underneath the main canopy. The height, age, species and diameter at breast height were recorded for each tree. Each branch greater than 2cm in diameter at the trunk was sequentially numbered from the top to the base using flagging tape. Branch basal diameter, using a hand ruler and height above ground, using a 50 m tape suspended from the top branch, were recorded for each. Branch aspect and slope, measured to the nearest degree, and length to the nearest half metre were subsequently measured on a sub-sample of branches (15% of the total branch population). The selection process is described in detail in section 2.8. Branch aspect and slope were measured to the nearest degree with a compass and length was estimated to the nearest half metre.

2.6 Canopy Lichens

Canopy lichens were divided into three functional groups (*Alectoria, Bryoria* and foliose lichen). Functional groups were used rather than taxonomic groups because of their common ecological roles which define their presence in the tree (Esseen et al., 1996, McCune, 1993). The functional groups also categorize lichens depending on the growth forms and the different species that use them as forage. Three other functional groups commonly used in epiphyte studies, that I did not include in this research, are bryophytes, cyanolichens and crustose lichens (McCune, 1993). Bryophytes and cyanolichens were not included in my research because they were rare or absent in my study area, and not considered forage lichens. Crustose lichens were excluded because of time constraints.
2.6.1 Foliose Lichens

Epiphytic foliose lichens take on a leaf like form with many lobes. They usually have differentiated upper and lower surfaces with one or many holdfasts. They are typically slow growing with broad ranging tolerance for environmental conditions and stresses (Rogers, 1990). Growth is often limited by available substrate, as expansion will rapidly cover existing branch surfaces (Stone, 1989). Thus there is the distinct possibility of competitive exclusion developing with lichen succession in a spatially limited environment (Lawrey, 1991). The role of foliose lichens (containing green algal components) as forage for wildlife is not well documented. The foliose lichen functional group includes mainly *Cetraria, Parmelia, Hypogymnia, Parmeliopsis and Platismatia* which are commonly found in the study area.

2.6.2 Fruticose Lichens

Epiphytic fruticose lichens are usually pendulous in shape, growing from a single or multiple holdfasts. The highly branched form of this lichen is species specific. Because the growth form allows rapid growth and biomass accumulation without the requirement of additional substrate (Renhorn, 1997b), fruticose lichens are able to remain unaffected by competition for space. They are, however, sensitive to stresses and have much narrower habitat tolerances. Fruticose lichens have a dispersal advantage over foliose lichens, in that they break easily into small fragments that are readily carried to new habitats in the wind. Fruticose lichens were separated into two functional groups for my study; *Alectoria* species (including *Usnea* which is rare in the study area) and *Bryoria* species.
2.7 Lichen Biomass Estimates

The biomass of Alectoria, Bryoria and foliose lichen functional groups were estimated. Development of a method of estimating the biomass of epiphytic lichens in high elevation forests was difficult because there is no standardized methodology. The tedious method of dissecting and weighing each unit in the population (branch) to obtain biomass is too time consuming to be used in an inventory study in which the entire population must be quantified (Nadkarni, 1984a). In contrast, the traditional frequency or cover estimation techniques using quadrats and transects that are generally used in terrestrial plant studies are rapid but are not easily applied or verified in a three dimensional environment (Boucher and Stone, 1992; McCune, 1990). More specialized techniques are therefore necessary to quantify or describe arboreal lichens. I used the “clump method”, developed by Stevenson (1979) for use on branches below 6 m, to estimate lichen abundance on branches throughout the canopy.

2.7.1 The Clump Method

Abundance was estimated for each fruticose lichen functional group during an initial climb of each tree by comparing the amount on a given branch to a standard “clump” of lichen of known size and weight. The amount of fruticose lichen (Alectoria and Bryoria) was estimated according to how many multiples of a standard, 2.5g (dry weight) clump of lichen, were present (Stevenson, 1978; Stevenson and Enns, 1993). Alectoria and Bryoria were subsequently separated into individual functional groups by giving an estimate of the percentage of the total fruticose lichen that was made up of Bryoria. A similar method was used for foliose lichens. The three dimensional clump of fruticose lichen was modified to a “card” of foliose lichen of known dimensions. The standard was an 8.5cm X 8cm surface which was the equivalent of approximately 1.5g of foliose lichen. The foliose lichens on each branch was then assessed according to how many multiples of
that surface area (card) it represented. In many cases foliose lichens grew in horizontal layers, forming mats. In such cases, the number of cards required to make the mat was estimated by the observer.

All biomass estimations in the same tree were made by the same researcher to minimize inter-observer error and to maintain a high level of consistency across estimates. Accuracy and precision of these methods were verified by comparing the estimates to a dissected sub-sample obtained using 3P sampling (see below) during the second climb.

2.8 Selection of Sub-samples

During a second climb of the tree, a sub-sample (15% of the total number) of branches was measured for aspect, length and slope. The branches were chosen using both stratified random sampling and three-P sampling to make up the 15%. The first method (stratified random) was used primarily to select branches to record aspect, length and slope. This selection was accomplished by dividing the vertical sampled distance (height of top branch minus height of bottom branch) into three and randomly selecting 10% of the branches within each vertical section. The second selection method, Probability Proportional to Prediction (three-P sampling), was used to select 5% of all branches within the study population (tree). We recorded aspect, length and slope and removed all of the foliose and fruticose lichens growing on this subset of branches. This biomass was removed from the branch while working in the tree when possible. When the end of the branch could not be reached, it was cut out of the tree and carefully lowered to the ground wrapped in a plastic bag. This was done to avoid any loss of collected lichen biomass through inaccessibility. Clumps number 11 and number 12 did not undergo this destructive sampling but were left as intact as possible to facilitate follow up studies.
2.8.1 Three-P Sampling for Biomass Verification

Three-P sampling occurred in three phases. Phase one involved a sequential numbering and an estimate of lichen biomass on every branch in the population (tree) as described above. Estimates of biomass were subsequently corrected for any inaccuracy with results from biomass verification. Consistency was crucial for these estimates as I required that similar values were obtained by all observers for clumps of the same size (Cochrane, 1977; Iles, 1978). The second phase involved selection of the branches for a sub-sample using a random number table and formula 2.1.

Formula 2.1

\[ K+Z = \sum_{n_e} KPI \]

Where \( K+Z \) is the top random number, \( \sum KPI \) is the sum of the estimates of fruticose lichen for the entire population and \( n_e \) is the expected sample size (5% of the total population in all of my calculations; Cochrane, 1977; Iles, 1978). Using a random number table, the estimate of fruticose lichen abundance on each branch was compared to a random number less than or equal to the top random number. The branch was selected for sampling if the estimated biomass was greater than or equal to the random number. If the calculated top random number \( (K+Z) \) was less than the lichen estimate for any one branch, then the probability of selecting that branch was greater than would be proportional to the predicted biomass. In that case, the formula was modified so that \( K+Z \) was doubled and each branch within the given population was given two chances to be sampled (compared to two random numbers). If a branch was selected by both random numbers, it was counted twice in the calculations (Stevenson, 1979). The third phase involved returning to the tree and removing the lichen from all of the selected branches for biomass measurements.
2.9 Biomass Measurements

Branches and bags of loose lichen were taken to the University of Northern British Columbia laboratory where they were separated according to functional groups and weighed. In cases where the branches were removed intact from the tree, the lichen was removed from it to be sorted and weighed. Forceps were not used in the lab to remove lichen from the branches in order to maintain a level of biomass removal that was consistent with our removal efforts while in the tree. Although care was taken to remove everything, there was a small amount of residual lichen left on the branches. Forceps were used to separate the functional groups once manually removed from the branch. Once obtained, lichen biomass was compared to the estimates recorded in the field.

2.10 Statistical Analysis

Tests for normality, independence, linearity and homoskedasticity were conducted (Tabachnick and Fidell, 1989). Lichen estimates were log (Alectoria and foliose lichen) and natural log (Bryoria) transformed to normalize and improve homogeneity of variances. Two types of transformations were used because the distribution of Bryoria was different from both Alectoria and foliose lichen and did not satisfy the requirements of normality using a base 10 log transformation. A constant (K=1) was added to all estimates prior to transformation to avoid taking the logarithm of zero (Palmer, 1998).

Most of the relationships between variables are represented by a series of box-plots. The boxes show the median line separating the two sections of each plot. The lower boundary of these sections represents the distribution of data falling within 25% of the median. The upper limit is termed the 75% quartile and the lower limit is the 25% quartile. The whiskers extending past the boxes represent the 5% to 95% range in the data. In each plot the mean is indicated by a red line.
Bar graphs were used to display the relationship of tree species and clumping to lichen biomass. Error bars represent the standard error of estimate for each group.

All averages are given as the mean plus or minus the standard deviation. All other numerical values given are accompanied by a descriptor. Identification of lichens to species was completed for clump number nine using the samples removed for biomass verification. Clump number nine was randomly chosen from the eight clumps using a random number table. The lichen biomass for the whole ecosystem was calculated by multiplying the average g/branch by the number of branches per tree (for estimates of g/tree) and by the number of trees per hectare (for the estimates of kg/ha; trees per hectare data compiled by Forey Management Ltd.) for each tree size class.

Simple regression models were calculated for each functional group to describe the relationship between the measured and estimated lichen biomass on the 5% sub-sample of branches obtained through 3P sampling. The resulting (log-log or ln-ln) regression equation was applied as a correction factor to the estimates of lichen biomass for the entire population. Estimates were converted back to g/branch by taking the anti-log/ln of the output of the regression equation. All other statistics were conducted on the corrected lichen biomass estimates.

Correlation coefficients were calculated to establish degrees of association between and within structural variables and lichen biomass estimates. Because the natural variation in biological communities can limit the applicability of correlation statistics, they were used primarily to identify possible interactions between structural variables.

Three best subsets regression tests were performed to determine which of the structural variables were important in accounting for variation in the biomass of the lichen functional groups. The variables of (branch) height, diameter, density, aspect, length and slope were included in the test for each group and the most parsimonious combination of these made up the
regression model. The dependant variables were the lichen biomass estimate for each functional group.

A Relative Pratt index (Pratt, 1987; Thomas et al., 1996) was computed using the correlation coefficients (r), standardized regression coefficients (B) and the coefficients of determination (R²) from the best subsets regression model (Formula 2.2). It was used to determine the relative importance of each of the structural variables in explaining the variation in the lichen biomass estimates.

Formula 2.2
\[ D_j = \frac{B \times r}{R^2} \]

Continuous structural variables were categorized to use as independent variables in the ANOVA’s. Height was categorized into 1-m intervals, diameter into 0.5cm intervals, length into 0.5-m intervals, slope into 10° intervals, aspect into 12 directions (N, NNE, ENE, E, ESE, SSE, S, SSW, WSW, W, WNW, NNW) and density increased by 1-branch/m at each interval.

A factorial ANOVA (analysis of variance) was conducted for each functional group. The independent factors in each model were those selected by the best subsets regression. Interactions between independent factors were included in the model. Interactions were detected by the correlation coefficients (r>0.200) and confirmed through a residual analysis (Rosenow and Rosenthal, 1995). The models used for Alectoria and Bryoria were (branch) height + diameter + length + slope + (height*length) + (height*slope) + (diameter*length) + (length*slope). The height variable was replaced by branch density in the model for foliose lichens resulting in (branch) diameter + density + length + slope + (density*slope) + (diameter*length) + (length*slope).

One way ANOVAs (analysis of variance) were used to detect significance in the relationships where both the independent and dependent variables in the model were structural variables. One way ANOVA’s were also employed in models between branch aspect (on the
solitary trees) and lichen biomass. Only solitary trees were used for this analysis to eliminate the effect of neighbouring trees on some aspects of clump trees. Tukey’s post hoc comparisons were used to detect differences between groups when variances were equal. If variances were not assumed to be equal, a less robust Dunnett’s C post hoc comparison was conducted. All statistics were conducted at a $p<0.05$ significance level.

Effect sizes were reported for each statistical test as a measure of both the size of the difference between groups being tested and as an indication of the sample sizes. A small effect size ($\eta^2 = 0.02, f^2 = 0.10$ for regression and ANOVA statistics respectively) indicated a subtle difference that may not have been detected visually, but may have been statistically significant with a large sample size. A small effect size usually indicated that there were other factors controlling the difference between groups. A medium effect size ($\eta^2 = 0.15, f^2 = 0.25$ for regression and ANOVA’s respectively) indicated that I was confident that detected differences were important and probably would have been detectable with a smaller sample size. Medium effect sizes would probably be detected by a careful observer. A large effect size ($\eta^2 = 0.35, 0.40$ for regression and ANOVA statistics respectively) suggested that the trend was easily detected visually and likely would have been significant even with a small sample size (Cohen, 1992).
A. ECOSYSTEM CHARACTERISTICS

3.1 Stand Age

The 67 trees within the eight study clumps ranged in age from 21 to 310 years with an average of 113 ± 62 years. The average age of the trees in the upper strata of the clumps was 163±50 years (Fig 3.1).

B. CANOPY ARCHITECTURE

3.2 Vertical Distribution of Canopy Architecture.

Branch height was the most easily measured structural variable against which to compare other features of the canopy environment. Thus, the following sections contain a description and statistical analysis of the distribution of each of branch diameter, density, aspect, length and slope along a gradient in crown height.

3.2.1 Branch Diameter versus Branch Height

Branch diameter was weakly, but positively correlated with branch height (r=0.151; \(\eta^2=0.076\)). Limbs (diameter of 2cm or larger) in the middle canopy were significantly larger than those in the lower canopy (\(F(24, 3717)= 12.73, p<0.001\)). The main significant difference in branch diameters was between those below 5 meters and those in the middle canopy (6-15m; Tukey’s post hoc comparison). The average branch diameter in the lower canopy (below 5m) and middle canopy was 2.96 ± 0.84 cm (n=813) and 3.37±1.14 cm (n=1965) respectively (Fig. 3.2A).
Fig. 3.1  The age distribution for 67 study trees in the Pinkerton research area. Trees below 2.0 m and trunks too small to core were not included in the population. Ages were taken at breast height.
3.2.2 Branch Density versus Branch Height

The number of branches per meter increased significantly with height above the ground ($F(24, 3717)=26.96, p<0.001, \eta^2=0.147$), with the main effects resulting from differences in branch density below 15 meters in the canopy (Tukey’s post hoc comparison). There was an increase in the average density of branches on trunk segments between five meters (6.82±4.25 branches/meter, n= 813) and ten meters (9.67±5.10 branches/meter, n=1083) in the canopy (Fig 3.2B).

3.2.3 Branch Length versus Branch Height

Mean branch length decreased significantly with each increasing 1-m height interval above the ground ($F(23, 641)=4.77, p<0.001; \eta^2=0.146$; Tukey’s post hoc comparison; Fig. 3.3A). Branches varied from 0.15-m at 25 m in height to 5 m near the lower edge of the crown.

3.2.4 Branch Slope versus Branch Height

*P. engelmannii* and *A. lasiocarpa* both had characteristically narrow crowns with branches that generally sloped steeply downward. The branches measured in this study ranged from those sloping down +80 degrees to those at a -90 degree upward slope. Branches in the top of the tree (20 to 25 m) were more horizontal or upwardly sloped (13.11±16.79°, n=275) than those in the lower canopy (25.56±19.02°, n=228). The standard deviation was high due to the range from horizontal to upwardly sloped branches in the upper canopy but the difference was nonetheless significant (n=405; $F(23, 656)=6.57, p<0.001$; Fig. 3.3B). The most noticeable changes in slope occurred below 6 metres in the canopy (Tukey’s post hoc comparison; $\eta^2=0.187$).
Fig. 3.2 Branch diameter (A) and branch density (B) in relation to increasing height above the ground. Each box-plot shows the change in diameter or density at each 5-m height interval (0-5m, 5.1-10m etc.). Numbers in parentheses are sample sizes.
Fig. 3.3 Branch length (A) and branch slope (B) in relation to branch height along a vertical transect up into the canopy. The less common upwardly sloped branches in the data were masked by the median values at each height interval and all resulting points were positive. Numbers in parentheses are sample sizes for each 5-m height interval.
3.3 Canopy Architectural Interactions

Although changes in structural variables along a gradient in height perhaps provided the most interpretable view of the dynamics of the tree crown, significant relationships did exist between other structural variables. These results are presented in the following sections.

3.3.1 Branch Length versus Branch Diameter

There was a strongly positive relationship between branch diameter and branch length ($r=0.367$). Branches with large diameters were significantly longer than those with smaller diameters ($F(11, 653)=11.50, p<0.001, \eta^2=0.162$). The main effects were between the lengths of small branches ($1.59\pm0.66$ m) and the length of branches with diameters larger than 4.0 cm ($2.39\pm0.51$ m; Tukey’s post hoc comparison). There were no significant differences in the lengths of branches within the small (2.5 -3.5 cm) and large (4.0 - 8 cm) diameter groups (Fig. 3.4).

3.3.2 Branch Diameter versus Branch Density

There was a slight but significant increase in the diameter of branches with increasing branch density ($F(21, 3720)=10.35, p<0.001, \eta^2=0.055$). The main differences were between the diameters ($3.59\pm0.82$ cm) of very dense branches (11-23 branches/metre) and the diameters ($2.92\pm0.75$ cm) of branches with low density (1-5 branches per meter; Tukey’s post hoc comparison; Fig. 3.5A).

3.3.3 Branch Length versus Branch Density

There was a weak but significant relationship between branch length and density ($r=-0.026$). Branches at a density of 3 branches/meter were significantly longer ($2.55\pm0.83$ m) than those at a density of 18 branches/meter ($1.06\pm0.61$ m; $F(21, 643)=1.59, p=0.045; \eta^2=0.049$; Tukey’s post hoc comparison; Fig. 3.5B).
Fig. 3.4 The relationship between branch length and increasing branch diameter. Sample sizes for each 1-cm diameter interval are given in parentheses.
3.3.4 Branch Slope versus Branch Density

Branches in *Picea engelmannii* and *Abies lasiocarpa* became significantly more horizontal or upwardly sloped in more dense sections of the tree (F(21, 658)=3.04, p<0.001; Fig. 3.5C). The most marked difference was between the slopes (14.80±19.70°) of moderately dense branches (12 to 13 branches per metre) and the slopes (36.51±19.30°) of less dense branches (2 to 3 branches per metre). Branches in sections where there were ≥19 branches/meter appeared to be more downwardly sloped (22.00±8.92°) than those where there were 15 to 18 branches/m, but it must be considered that there was a smaller sample size at these densities. The disparity between sample sizes contributed to the overall small effect size (η²=0.088) for this relationship.
Fig. 3.5 Changes in the branch diameter (A), length (B) and slope (C) with increasing branch density. Numbers in parentheses are the sample size for each 2-branches/m density interval.
3.3.5 Branch Length versus Branch Slope

There was a strong relationship between branch length and slope (r=0.213). Longer branches were significantly more downwardly sloped than shorter branches (F(18, 655)=5.66, p<0.001). The majority of the difference existed between the slopes of branches that were 0.5 to 2.0 metres long (18.77±19.19°) and branches that were 2.5 to 3.0 meters long (32.44±25.31°; Fig. 3.6). Again, the variation in branch slopes from the horizontal to steeply sloped contributed to both the large standard deviations and to the small effect size ($\eta^2=0.065$).
Fig. 3.6  The relationship between branch length and branch slope. The numbers in parentheses are the sample sizes for each 0.5-m interval in branch length.
C. CANOPY LICHEN COMMUNITIES

3.4 Lichen Community Composition

A lichen species list was generated by identifying all of the lichen species in the subsamples taken from clump #9 (Table 3.1). Only one clump was sorted to species due to time constraints. Although the distribution of functional groups varied along architectural gradients, the composition of those functional groups was relatively homogeneous and most species were found in the majority of dissected samples. There were no distinct trends in abundance at the species level. Both bryophytes and cyanolichens were absent from the branches in my study population (of all clumps).
Table 3.1 The lichen species list for clump number nine at Pinkerton Mountain.

<table>
<thead>
<tr>
<th>Functional Group</th>
<th>Species List</th>
</tr>
</thead>
<tbody>
<tr>
<td>Foliose Lichen</td>
<td><em>Cetraria platyphylla</em></td>
</tr>
<tr>
<td></td>
<td><em>Hypogymnia imshaugii</em></td>
</tr>
<tr>
<td></td>
<td><em>H. metaphysodes</em></td>
</tr>
<tr>
<td></td>
<td><em>H. occidentalis</em></td>
</tr>
<tr>
<td></td>
<td><em>H. physodes</em></td>
</tr>
<tr>
<td></td>
<td><em>H. rugosa</em></td>
</tr>
<tr>
<td></td>
<td><em>H. tubulosa</em></td>
</tr>
<tr>
<td></td>
<td><em>Parmelia sulcata</em></td>
</tr>
<tr>
<td></td>
<td><em>Platismatia glauca</em></td>
</tr>
<tr>
<td>Bryoria</td>
<td><em>B. capillaris</em></td>
</tr>
<tr>
<td></td>
<td><em>B. fremontii</em></td>
</tr>
<tr>
<td></td>
<td><em>B. fuscescens</em></td>
</tr>
<tr>
<td></td>
<td><em>B. glabra</em></td>
</tr>
<tr>
<td></td>
<td><em>B. pseudofuscescens</em></td>
</tr>
<tr>
<td>Alectoria</td>
<td><em>A. sarmentosa</em></td>
</tr>
<tr>
<td></td>
<td><em>Usnea lapponica</em></td>
</tr>
</tbody>
</table>
3.5 Correction of Canopy Lichen Estimates

My measurements of lichen biomass in the Pinkerton Mountain area were based on a combination of single rope access techniques, clump method estimation and verification using 3P sampling. The single rope technique made each branch in the population visible to the researchers. The clump method was evaluated by regressing a sub-population (96 branches) of estimates against the actual measured biomass (Fig. 3.7). The strong coefficients of determination, large effect sizes ($f^2$) and low standard errors of estimate (SEM) for the raw datum values (Alectoria: $R^2 = 0.68, f^2 = 2.12$, SEM=6.41, n=96; Bryoria: $R^2 = 0.76, f^2 = 3.14$, SEM=19.63, n=96; Foliose: $R^2 = 0.61, f^2 = 1.58$, SEM=7.53, n=96) indicated that the clump method was an effective tool for assessing lichens. Because there were no significant differences in the estimate efficacy on branches with low versus high abundance ($R^2$ difference test, $p<0.05$), the clump method could be effectively applied throughout the canopy. The regression equations (Alectoria: $\log Y = 0.0755 + 0.992 \log X$; Bryoria: $\ln Y = 0.790 + 1.102 \ln X$; foliose: $\log Y = 0.136 + 0.969 \log X$) were used to correct the lichen estimate data to reduce the disparity between estimates and actual biomass.
Regression lines for the clump method as an estimator of *Alectoria, Bryoria* and foliose lichen abundance. Measured lichen (Y) is the biomass of the dissected and weighed samples obtained through 3P sampling and estimated lichen (X) is the abundance of lichen estimated using the clump method on the same sample.
Estimated Alectoria Biomass (Log g/branch)

Estimated Bryoria Biomass (Ln g/branch)

Estimated Foliose Biomass (Log g/branch)
3.6 Lichen Biomass Distribution

Lichens in the three functional groups had significantly different patterns of abundance (Fig. 3.8). It was clear that *Bryoria* displayed both the greatest range in biomass and was found in the largest amounts overall. Conversely, *Alectoria* was less abundant than either *Bryoria* or foliose lichen. The entire range of *Alectoria* biomass fell well below the lowest amount of *Bryoria* and much of the foliose lichen found on any given branch. The range of foliose biomass fell within the distribution of *Bryoria*, but both the means and the median values were different. The distributions of all three functional groups were significantly different from one another (F(2, 11223)=8213.94, p<0.001).
Fig. 3.8 Lichen biomass (g/branch) for the three functional groups. The means for each functional group are indicated by the red line (n=3742 branches).
D. RESPONSE OF CANOPY LICHENS TO ECOSYSTEM CHARACTERISTICS

3.7 Response of Canopy Lichens to Tree Age

The increase in *Alectoria* biomass with increasing tree age, although subtle and variable, was significant ($F(10,3559)=38.408, p<0.001; \eta^2=0.106$; Fig. 3.9A). Trees with an average age of 238 to 263 years held a significantly greater abundance of *Alectoria* (6.69±9.32 g/branch) than did other age groups. Furthermore, younger trees (aged 38 to 113 years) had significantly less *Alectoria* biomass (0.96±1.39 g/branch) than all other aged trees.

*Bryoria* also responded to tree age ($r=0.377$; Fig. 3.9B) and increased in abundance with increasing tree age ($F(10,3559)=33.819, p<0.001$; Tukey's post hoc comparison; $\eta^2=0.285$). The increase in *Bryoria* was highly significant and approximately ten times greater than the corresponding increase in *Alectoria* biomass.

Age also had a significant influence on the distribution of foliose lichens ($F(10,3559)=12.416, p<0.001; \eta^2=0.134$). This effect of tree age on foliose lichen was greater than the corresponding response of *Alectoria* but less than the response of *Bryoria*. The abundance of foliose lichens was greater in trees with an average age of 38 years (7.66±6.73 g/branch) than in trees averaging 263 years (8.00±6.07 g/branch; Fig. 3.9C).

3.8 The Response of Canopy Lichens to Host Tree Species

*Alectoria, Bryoria* and foliose lichens were all significantly more abundant on *Picea engelmannii* branches than on *Abies lasiocarpa* branches (*Alectoria*: $F(1.2065)=8.49, p=0.004$, $\eta^2=0.003$; *Bryoria*: $F(1.2065)=73.57, p<0.001$, $\eta^2=0.034$; foliose: $F(1.2065)=60.12, p<0.001$, $\eta^2=0.028$; Fig. 3.10).
Fig. 3.9 The distribution of *Alectororia* (A), *Bryoria* (B) and foliose lichen (C) biomass along a gradient in age between 38 and 310 years. Numbers in parentheses are sample sizes for each 50 year interval.
Fig. 3.10 The average biomass of each functional group in both *Picea engelmannii* and *Abies lasiocarpa*. Significance is indicated with a star and sample sizes are given in parentheses.
3.9 **Response of Canopy Lichens to Tree Size.**

The biomass of *Alectoria* in the lower canopy zone (0-5m) of large trees (greater than 15 m tall) was significantly larger than in any other zone (2.64±4.66 g/branch; F(5, 3736)=230.65, p<0.001, \(\eta^2=0.309\)). The least biomass was found in the upper canopy of large trees (0.41±0.85 g/branch) and in trees shorter than 5m (0.67±0.99 g/branch; Fig. 3.11A). *Alectoria* constituted only a very small proportion (12.0%; 0.67±0.99 g/branch) of the total lichen in small trees and its contribution to the total lichen in medium and large trees was even less. *Alectoria* made up only 10.6%(1.90±3.18g/branch) of lichen in medium trees and 7.7%(2.61±4.40g/branch) of total lichen in large trees.

The total lichen biomass for small, medium and large trees was 5.57±5.19g/branch, 14.95±15.66g/branch and 25.04±21.20g/branch respectively. These datum, when extrapolated to the ecosystem level, resulted in approximately 2kg/ha (46 g/tree), 9kg/ha (72 g/tree) and 29kg/ha (331 g/tree) of *Alectoria* in small, medium and large trees respectively (Fig. 3.12). Although visually dominant in some trees due to its pigmentation, *Alectoria* was the least abundant of the three functional groups, contributing to only 8.3% of the total lichen biomass. This contribution remained consistently low over the height classes, irrespective of tree size. There was a decrease in the percent contribution of *Alectoria* to the total abundance of the ecosystem along increasing height zones (18.5%, 11.7% and 1.3% in low, middle and upper height classes respectively).

The greatest biomass of *Bryoria* was found in the upper canopy of ecosystem dominants (25.51±23.63 g/branch). The middle canopy of both large (15.11±14.22 g/branch) and medium (7.35±9.70 g/branch) trees also held significantly more *Bryoria* than the lower canopy in any size tree (F(5, 3736)=540.67, p<0.001; \(\eta^2=0.420\)). Small trees, less than 5 metres tall carried less than 10% of the *Bryoria* that was found in the upper canopy of large trees (Fig. 3.11B). Although the
total biomass in small trees was low relative to larger size classes, *Bryoria* accounted for 40.9% (2.28±2.92 g/branch) of lichen biomass. It also made up 42.7% (5.47±7.88 g/branch) and 66.7% (15.20±15.60 g/branch) of total lichen biomass in medium and large trees, respectively. The contribution of *Bryoria* to the total lichen biomass of the ecosystem was increased with tree size from approximately 7 kg/ha (19 g/tree) in small trees, to 33 kg/ha (265 g/tree) in medium sized trees and to 206 kg/ha (2742 g/tree) in large trees (Fig. 3.12). The total biomass and relative contribution of *Bryoria* to lichen biomass also increased as I went from lower (27.9%) to the upper crown (82.9%).

There was significantly less foliose lichen in small trees than any other zone (F(5, 3736)=69.75, p<0.001, η²=0.085; Fig. 3.11C). The largest biomass was in the lower canopy of medium sized trees (9.17±11.66 g/branch, 5-15 m tall) and the middle canopy of large trees (9.42±8.91 g/branch). Small trees held significantly less foliose lichen (2.62±3.42 g/branch) biomass than either large or medium trees. Despite the low biomass, foliose lichen still contributed up to 47.0% of the total lichen in small trees and nearly half of the total lichen in medium trees (7.59±9.39 g/branch). There were, on average, 7.23±7.34 g/branch of foliose lichen in large study trees, which although greater than the biomass in other size classes, made up only 25.5% of the total. The total foliose lichen biomass in the ecosystem was approximately 8 kg/ha (22 g/tree), 38 kg/ha (308 g/tree) and 80 kg/ha (1072 g/tree) in small, medium and large trees respectively (Fig. 3.12). There was a general decrease in the contribution of the foliose functional group to the total lichen with increasing height zone (from 53.5% in the lower canopy to 15.8% in the upper canopy).

The total lichen loading for the whole ecosystem was much greater in large trees than in small or medium trees. The biomass was approximately 87 g/tree for small trees, 655 g/tree for
medium sized trees and 4145 g/tree in large trees.

3.10 Response of canopy lichens to the Clumped Tree Distribution

*Alectoria* and *Bryoria* were significantly more abundant in clumped trees than in solitary (non clumped) trees (*Alectoria*: $F(1, 2007)=53.73$, $p<0.001$, $\eta^2=0.026$; *Bryoria*: $F(1, 3740)=26.58$, $p<0.001$, $\eta^2=0.013$). Foliose lichens showed no significant difference in abundance between clumped and solitary trees (Fig. 3.13).
The average biomass (g/branch) of the Alectoria (A), Bryoria (B) and foliose lichen (C) functional groups at the lower (0-5 m), mid (5.1-15 m) and upper (15.1+ m) canopy zones in small, medium and large study trees. Size class was categorized according to total height. Small trees were shorter than 5 m, medium trees were 5.1 to 15 m tall and large trees were 15.1 m or taller. Sample sizes were 184 (small/low), 285 (medium/low), 739 (medium/middle), 154 (large/low), 1270 (large/middle) and 1110 (large/high).
The contribution of each functional group to the total biomass of the ecosystem in each of small, medium and large tree classes.

Fig. 3.12
Fig. 3.13  The average biomass per branch of each functional group in both clumped and non clumped trees. Significance is indicated with a star.
E. RESPONSE OF CANOPY LICHENS TO CANOPY ARCHITECTURE

3.11 Multiple Regression

The resultant group of explanatory variables in the regression equation for the fruticose lichens (*Alectorina* and *Bryoria*) was (branch) height, diameter, aspect, length and slope. The model for foliose lichen included (branch) diameter, density, aspect, length and slope. An $R^2$ difference test (between regression equations containing height, diameter, density, aspect, length and slope and those without either branch density (fruticose) or height (foliose) for each functional group revealed that the sixth variable did not account for any additional variance in the lichen biomass (*Alectorina* $F(1, 658)=0$, $p>0.05$; *Bryoria* $F(1, 658)=0$, $p>0.05$; Foliose $F(1, 658)=0.942$, $p>0.05$). Thus the more parsimonious model was selected in each case (Table 3.2). The regression model was significant for all three functional groups but did not explain much of the variance in *Alectorina* and foliose lichen biomass.
Table 3.2  Multiple regression for each of *Alectoria* (Al), *Bryoria* (Br) and foliose lichen (Fo) functional groups. Independent variables are branch height (He), density (De), diameter (Di), aspect (As), length (Le) and slope (Sl).

<table>
<thead>
<tr>
<th>Regression Equation</th>
<th>$R^2$</th>
<th>Effect size</th>
<th>Analysis of variance</th>
</tr>
</thead>
<tbody>
<tr>
<td>LogAl = -0.573 - 0.036Ht + 0.134Di +0.001As + 0.127Le - 0.002Sl</td>
<td>0.22</td>
<td>0.284</td>
<td>F(5, 658)= 37.23, p=0.00</td>
</tr>
<tr>
<td>LnBr = -0.561+ 0.130Ht + 0.304Di - 0.0004As + 0.154Le - 0.003Sl</td>
<td>0.64</td>
<td>1.762</td>
<td>F(5,658)=231.72, p=0.00</td>
</tr>
<tr>
<td>LogFo = -0.509 + 0.041De + 0.186Di +0.001As + 0.114Le - 0.001Sl</td>
<td>0.30</td>
<td>0.435</td>
<td>F(5, 658)= 56.97, p=0.00</td>
</tr>
</tbody>
</table>
3.12 Relative Pratt Index

The order of importance for the structural variables in describing the variation in *Alectoria* abundance was (branch) height, diameter, length, aspect and slope (Table 3.3). The large index value (D,) for branch height emphasized the importance of this variable. The negative index value for branch slope indicated a possible collinearity with the other explanatory variables. The impact of collinearity was reduced in this case because the value was very low relative to the other indices and the variance inflation factor (VIF=1.2) was not large (Chaterjee and Yilmaz, 1992).

The Pratt index for *Bryoria* resulted in a similar order of importance (Table 3.4). Branch height, again, had a very large index value followed by (branch) diameter, slope, length and aspect. The low values for branch aspect, length and slope indicated that these variables did not strongly influence the distribution of *Bryoria* in the ESSF canopy.

The resulting order of importance for foliose lichen was (branch) diameter, length, aspect, density and slope (Table 3.5). It is evident that branch diameter was a key determinant of foliose lichen biomass.
Table 3.3  Computation of the relative Pratt index for *Alectoria*. B is the standardized regression coefficient for each explanatory variable, r is the correlation coefficient between the structural variable and the lichen biomass, $R^2$ is the coefficient of determination from the regression model and $D_j$ is the index total.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>B</th>
<th>r</th>
<th>$R^2$</th>
<th>$D_j$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height</td>
<td>-0.366</td>
<td>-0.443</td>
<td>0.22</td>
<td>0.734</td>
</tr>
<tr>
<td>Diameter</td>
<td>0.238</td>
<td>0.192</td>
<td>0.22</td>
<td>0.207</td>
</tr>
<tr>
<td>Aspect</td>
<td>0.154</td>
<td>0.157</td>
<td>0.22</td>
<td>0.109</td>
</tr>
<tr>
<td>Length</td>
<td>0.158</td>
<td>0.301</td>
<td>0.22</td>
<td>0.215</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.086</td>
<td>0.059</td>
<td>0.22</td>
<td>-0.023</td>
</tr>
</tbody>
</table>
Table 3.4  Computation of the relative Pratt index for *Bryoria*. B is the standardized regression coefficient for each structural variable, r is the correlation coefficient between the structural variables and *Bryoria* biomass, $R^2$ is the coefficient of determination from the regression model and $D_j$ is the index total.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>B</th>
<th>r</th>
<th>$R^2$</th>
<th>$D_j$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height</td>
<td>0.682</td>
<td>0.643</td>
<td>0.64</td>
<td>0.687</td>
</tr>
<tr>
<td>Diameter</td>
<td>0.278</td>
<td>0.442</td>
<td>0.64</td>
<td>0.193</td>
</tr>
<tr>
<td>Aspect</td>
<td>-0.034</td>
<td>-0.051</td>
<td>0.64</td>
<td>0.003</td>
</tr>
<tr>
<td>Length</td>
<td>0.099</td>
<td>0.032</td>
<td>0.64</td>
<td>0.005</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.055</td>
<td>-0.270</td>
<td>0.64</td>
<td>0.023</td>
</tr>
</tbody>
</table>
Table 3.5 Computation of the relative Pratt index for foliose lichen. B is the standardized regression coefficient for each explanatory variable in the regression model, r is the correlation coefficient between foliose lichen and each structural variable, $R^2$ is the coefficient of determination for the model chosen in the best subsets regression and $D_j$ is the index total.

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>B</th>
<th>r</th>
<th>$R^2$</th>
<th>$D_j$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter</td>
<td>0.410</td>
<td>0.451</td>
<td>0.30</td>
<td>0.613</td>
</tr>
<tr>
<td>Density</td>
<td>0.138</td>
<td>0.111</td>
<td>0.30</td>
<td>0.051</td>
</tr>
<tr>
<td>Aspect</td>
<td>0.193</td>
<td>0.169</td>
<td>0.30</td>
<td>0.108</td>
</tr>
<tr>
<td>Length</td>
<td>0.176</td>
<td>0.286</td>
<td>0.30</td>
<td>0.167</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.046</td>
<td>-0.080</td>
<td>0.30</td>
<td>0.012</td>
</tr>
</tbody>
</table>
3.13 Factorial ANOVA

The statistics resulting from the factorial ANOVA for each functional group are reported in section 3.13, but the main effects of the variables are investigated more closely in subsequent sections.

The model was significant and accounted for 76.0% of the variance in *Alectoria* abundance in the ESSF canopy (F(337, 286)=1.819, p<0.001; $\eta^2=0.760$). Branch height was the only structural variable that contributed significant main effects to the ANOVA for *Alectoria* (Table 3.6).

The factorial ANOVA for *Bryoria* biomass considered all of the main effects and the interactions outlined in the description for *Alectoria*. The resulting model was strongly significant at a $p=0.05$ level (F(377,286)=4.760, p<0.001; $\eta^2=0.863$) and accounted for 86.3% of the variation in *Bryoria* biomass in the crowns of study trees. Main effects resulted from both branch height and branch length for *Bryoria* biomass (Table 3.7).

The factorial ANOVA model was significant and explained 64.3% of the variation in foliose lichen (F(270, 393)= 2.620, p<0.001; $\eta^2=0.643$; Table 3.9). There were significant main effects for diameter, density and slope and the interactions of (diameter*length), (density*slope) and (length*slope) within the model for foliose lichens.
Table 3.6  The factorial ANOVA results for the influence of structural variables on *Alectoria* biomass. The model was \( \text{Log } Alectoria = \text{intercept} + (\text{branch}) \text{ height} + \text{diameter} + \text{aspect} + \text{length} + \text{slope} + (\text{height}*\text{length}) + (\text{height}*\text{slope}) + (\text{diameter}*\text{length}) + (\text{length}*\text{slope}). \) The F statistics and effect sizes are given for each factor and interaction.

<table>
<thead>
<tr>
<th>Factor</th>
<th>ANOVA</th>
<th>Effect size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Factorial Model</td>
<td>( \text{F}(337, 286)= 1.819, p&lt;0.001 )</td>
<td>0.76</td>
</tr>
<tr>
<td>Height</td>
<td>( \text{F}(23, 286)= 2.682, p&lt;0.001 )</td>
<td>0.177</td>
</tr>
<tr>
<td>Diameter</td>
<td>( \text{F}(10, 286)= 1.632, p=0.097 )</td>
<td>0.054</td>
</tr>
<tr>
<td>Length</td>
<td>( \text{F}(6, 286)= 0.644, p=0.695 )</td>
<td>0.013</td>
</tr>
<tr>
<td>Slope</td>
<td>( \text{F}(12, 286)= 0.832, p=0.627 )</td>
<td>0.033</td>
</tr>
<tr>
<td>Height*Length</td>
<td>( \text{F}(83, 286)= 1.246, p=0.095 )</td>
<td>0.268</td>
</tr>
<tr>
<td>Height*Slope</td>
<td>( \text{F}(140, 286)=1.082, p=0.288 )</td>
<td>0.346</td>
</tr>
<tr>
<td>Diameter*Length</td>
<td>( \text{F}(35, 286)=1.020, p=0.443 )</td>
<td>0.111</td>
</tr>
<tr>
<td>Length*Slope</td>
<td>( \text{F}(39, 664)=0.670, p=0.935 )</td>
<td>0.084</td>
</tr>
</tbody>
</table>
The factorial ANOVA statistics for Ln *Bryoria* biomass. The model included the main effects of height, diameter, aspect, length and slope as well as interactions between (height*length), (height*slope), (diameter*length) and (length*slope). The F statistics and effect sizes are given for each factor and interaction.

<table>
<thead>
<tr>
<th>Factor</th>
<th>ANOVA</th>
<th>Effect size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Factorial Model</td>
<td>$F(377, 286) = 4.760, p&lt;0.001$</td>
<td>0.863</td>
</tr>
<tr>
<td>Height</td>
<td>$F(23, 286) = 6.821, p&lt;0.001$</td>
<td>0.354</td>
</tr>
<tr>
<td>Diameter</td>
<td>$F(10, 286) = 1.780, p=0.064$</td>
<td>0.059</td>
</tr>
<tr>
<td>Length</td>
<td>$F(6, 286) = 2.331, p=0.033$</td>
<td>0.047</td>
</tr>
<tr>
<td>Slope</td>
<td>$F(12, 286) = 1.666, p=0.074$</td>
<td>0.065</td>
</tr>
<tr>
<td>Height*Length</td>
<td>$F(83, 286) = 1.309, p=0.055$</td>
<td>0.278</td>
</tr>
<tr>
<td>Height*Slope</td>
<td>$F(140, 286)=1.175, p=0.129$</td>
<td>0.365</td>
</tr>
<tr>
<td>Diameter*Length</td>
<td>$F(35, 286)=1.034, p=0.421$</td>
<td>0.112</td>
</tr>
<tr>
<td>Length*Slope</td>
<td>$F(39, 286)=1.109, p=0.310$</td>
<td>0.131</td>
</tr>
</tbody>
</table>
The factorial ANOVA statistics for Log foliose lichen biomass. The model included the main effects of diameter, density, length and slope as well as interactions between diameter*length, density*slope and length*slope. The F statistics and effect sizes are given for each factor and interaction.

<table>
<thead>
<tr>
<th>Factor</th>
<th>ANOVA</th>
<th>Effect size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Factorial Model</td>
<td>F(270, 393)= 2.620, p=0.000</td>
<td>0.643</td>
</tr>
<tr>
<td>Diameter</td>
<td>F(10, 393)= 7.007, p=0.000</td>
<td>0.151</td>
</tr>
<tr>
<td>Density</td>
<td>F(21, 286)= 2.642, p=0.000</td>
<td>0.124</td>
</tr>
<tr>
<td>Length</td>
<td>F(6, 393)= 1.367, p=0.227</td>
<td>0.02</td>
</tr>
<tr>
<td>Slope</td>
<td>F(12, 286)= 1.803, p=0.046</td>
<td>0.052</td>
</tr>
<tr>
<td>Diameter*Length</td>
<td>F(38, 393)= 1.537, p=0.025</td>
<td>0.129</td>
</tr>
<tr>
<td>Density*Slope</td>
<td>F(125, 393)= 1.407, p=0.007</td>
<td>0.309</td>
</tr>
<tr>
<td>Length*Slope</td>
<td>F(48, 393)= 1.885, p=0.001</td>
<td>0.187</td>
</tr>
</tbody>
</table>
3.14 Response of Canopy Lichens to Branch Height

There was a strong main effect of branch height on *Alectoria* abundance (F(23,286)=2.682, p<0.001, η²=0.117). *Alectoria* biomass reached peak abundance at approximately 6m (and decreased with increasing height above ground; Fig. 3.14A). This was in sharp contrast to *Bryoria* which increased steadily over the same range in height. The inverse relationship between height and *Alectoria* had a strong correlation coefficient of -0.443. Branches ranged from a maximum *Alectoria* biomass of 46.36 g/branch at 6.8m to a minimum of 0.19g/branch on most branches above 20 metres. The average *Alectoria* biomass was significantly greater at 3 - 10 meters (3.30±5.42 g/branch) than at 1-2 meters (0.95±1.41g/branch) or 11-25 meters (0.65±1.08 g/branch; Dunnett’s C post hoc comparison, p<0.05).

Branch height also had a significant mean effect on the biomass of *Bryoria* (F(23,286)=6.821, p=0.000, η²= 0.354). Average *Bryoria* biomass increased significantly with increasing height above ground. The functional group ranged from a minimum value of 1.20 g/branch to a maximum of 335 g/branch at 21.90 metres. *Bryoria* biomass below 5 metres (3.30±6.24 g/branch) was significantly lower than the biomass at 6 to 8 metres (7.28±7.81 g/branch) which in turn was less than the biomass at 10 - 24 metres (22.56±19.11 g/branch; Dunnett’s C post hoc comparison; p<0.05; Fig. 3.14B). The relationship between branch height and *Bryoria* biomass was among the strongest and most significant in this study (r=0.643). There was no visible difference in the biomass of foliose lichen along a vertical gradient and branch height was not found to be a significant determinant for this functional group (Fig. 3.14C).
The response of *Alectoria* (A), *Bryoria* (B) and foliose lichen (C) to an increase in the height of the branch above the ground. Numbers in parentheses indicate sample size for each 2-m height interval.
3.15  **Response of Canopy Lichens to Branch Diameter**

There was no observable or significant difference in the distribution of *Alectoria* biomass with branch diameter (Fig. 3.15A). In contrast, there appeared to be an increase in *Bryoria* biomass with increasing branch diameter (Fig. 3.15B), however this trend was found to be non-significant within the confines of the overall ANOVA model. Foliose lichen biomass responded significantly to branch diameter \( (F(10, 393)=7.007, p<0.001, \eta^2=0.151) \). There was an increase in foliose lichen with each 0.5cm increase in branch diameter (up to 4.0cm). Foliose lichen biomass reached a plateau at 14.44±9.61 g/branch on branches between 4.5 and 6.5 cm (Fig. 3.15C).

3.16  **Response of Canopy Lichens to Branch Density**

The biomass of *Alectoria* remained consistently low over the entire range of branch densities and there was no identifiable trend or significant influence of density on *Alectoria* biomass (Fig. 3.16A). Although *Bryoria* biomass fluctuated from 26.90±14.03 g/branch at a density of 18 branches/m to 4.64±8.90 g/branch at a density of 1 branch/m (Fig. 3.16B), differences were not significant given the variation in biomass at each density. Unlike the fruticose lichens, foliose lichen biomass was significantly effected by branch density \( (F(21,393)=2.642, p<0.001, \eta^2=0.124) \). There was a larger amount of foliose lichen in sections where there were 7-9 (16.69±21.44 g/branch) or 18 (26.90±14.03g/branch) branches per meter than at all other branch densities (Dunnett’s C post hoc comparison, \( p<0.05 \); Fig. 3.16C).
Fig. 3.15 The response of Alectoria (A), Bryoria (B) and foliose lichen (C) to increasing branch diameter. Numbers in parentheses indicate sample size for each 0.5-cm diameter increment.
Fig 3.16  The response of *Alectoria* (A), *Bryoria* (B) and foliose lichen (C) to an increasing gradient in branch density. Numbers in parentheses indicate the sample size for each 2-branch/m increase in branch density.
3.17 Response of Canopy Lichens to Branch Length

There appeared to be an increase in *Alectoria* biomass over a gradient of increasingly longer branches (Fig. 3.17A). However, this increase was not significant within the ANOVA. In contrast, although *Bryoria* biomass did not appear to be influenced by the length of the branch (Fig. 3.17B), the response of *Bryoria* to branch length was significant ($F(6, 286)=2.331, p=0.033, \eta^2= 0.047$). There was significantly more *Bryoria* on branches 3.0 to 3.5-m long ($31.45\pm56.35$ g/branch) than on any other branches. The small effect size was likely due to the variation in *Bryoria* biomass at each branch length and to the fact that the biomass increase did not occur steadily along a gradient in branch length.

Foliose lichen biomass had a direct linear relationship with branch length ($r=0.286$) and increased in proportion with increasing length (Fig 3.17C). The differences in foliose lichen abundances on branches of various sizes were not, however, statistically significant. The interaction of both branch diameter and branch slope with the length of the branch produced significant main effects in describing foliose lichen abundance. It cannot be assumed, therefore, that branch length is completely without influence on the distribution of this lichen functional group.
The response of *Alectoria* (A), *Bryoria* (B) and foliose lichen (C) abundance to a gradient in branch length. Numbers in parentheses are branch sample sizes for each 0.5-m increase in branch length.
3.18 **Response of Canopy Lichens to Branch Slope**

Branch slope did not significantly affect the abundance of *Alectoria* biomass. *Alectoria* remained consistently low (Fig. 3.18A) while branch slope varied from $-20^\circ$ (upward sloping) to $+60^\circ$ (steeply downward sloping). Similarly, *Bryoria* biomass was not influenced significantly by the slope of the branch. This non-significance, despite the apparent decrease in biomass with increasingly downward sloping branches (Fig. 3.18B), was likely due to the variation in the functional group at each slope category. Conversely, while the distribution of foliose lichen appeared independent of branch slope (Fig. 3.18C), slope was a significant determinant of foliose lichen biomass ($F(12, 393)=1.803, p=0.046; \eta^2=0.052$).

3.19 **Response of Canopy Lichens to Branch Aspect**

Branch aspect did not significantly influence the distribution of *Alectoria, Bryoria* or foliose lichen biomass in the solitary study trees (Fig. 3.19).
Fig. 3.18  The response of *Alectoria* (A), *Bryoria* (B) and foliose lichen (C) to a gradient in branch slope. Numbers in parentheses are branch sample sizes for each 10° change in branch slope.
The response of *Alectoria* (A), *Bryoria* (B) and foliose lichen (C) to the aspect of branches in the solitary trees (*N* = 838).
Chapter 4

Discussion

4.1 Evaluation of Methods Development

The single rope technique was very successful in the high elevation forests of east-central British Columbia. The equipment used was relatively inexpensive and readily available from many outdoor equipment stores. It could be carried and easily assembled by one person and afforded rapid access compared to other techniques where a first ascent might take up to a full day for an experienced climber (Mitchell, 1982).

The single rope technique provided access to most of the tree crown. This allowed us to apply the clump method to each branch individually with high confidence in the visual estimates. Stevenson (1979) applied the clump method to both highly visible and poorly visible branches and found that coefficients of variation ranged from 15% to 85%. Coefficients were lowest for branches that were more easily observed and not concealed by others. Combining the clump method with tree climbing techniques ensured that nearly every branch was visible and thus resulted in a low standard error of estimate for this study.

As with most canopy studies evaluation of the entire tree crown was prevented because the very top of each tree was beyond a safe climbing range (Pike et al., 1977). However, since many of the branches in the upper two to three metres were young and had a diameter below the cutoff of my study (2cm) they would not have been included in the sample regardless. This omission thus only slightly affected my overall lichen biomass estimates for the stand. In addition, since the vast majority of lichen in that portion of the tree was Bryoria, the impact of excluding these branches on Alectoria and foliose lichen biomass was negligible.
The clump method was ideally suited for the community structure and composition of the Pinkerton mountain study site. It provided a rapid estimate of lichens on each of the branches in the study population. This was necessary both because a large number of branches were to be assessed as part of a biomass inventory and because verification was achieved using 3P sampling, which stipulates that the entire population must be assessed for calculation of the sub-sample (Stevenson and Enns, 1993). The clump method was also well suited to the ecosystem at Pinkerton mountain because the lichen community was fairly homogeneous in composition and abundance. We could therefore adjust our estimates to the single standard much more easily and remain more consistent than in situations where large variation in abundance dictates the use of several standards.

Although my study sites required only one size standard for the clump method, the fact that the standard clump can be tailored in size makes this method applicable to a wide range of ecosystems provided that verification is conducted in each different study area. I did find, however, that using the card as a standard for foliose lichen was most reliable when the abundance was low and the branches were small and easily seen.

Combining our estimates of the entire population obtained using the clump method with known biomass of the sub-sample resulted in a reasonably accurate and objectively collected data set. There was some variation in the size of the measured lichen biomass for each estimate. This variation is a weakness in any epiphytic lichen estimation technique that occurs because it is not logistically possible to directly measure every branch in the population. The clump method resulted in a relationship between measured and estimated lichen biomass that was comparable to those resulting from many of the existing techniques.
The coefficients of determination from the regression between estimated and measured lichen biomass varied from 76.1% for *Bryoria* to 61.3% for foliose lichen. This were comparable to other biomass estimators. McCune (1990) estimated lichen biomass using a variety of estimators. Resulting coefficients of determination were $0.58 < R^2 < 0.91$, $0.30 < R^2 < 0.96$ and $0.33 < R^2 < 0.91$ using cover classes (an estimate of the amount of branch covered by lichen), maximum thallus length and maximum thallus width respectively. Although the clump method resulted in estimates that were not as closely related to actual lichen biomass as in the best cases with previously used estimators, it is uncertain whether cover classes and maximum measures for each functional group would be easily applied in ecosystems where *Alectoria* and *Bryoria* thalli are abundant and extremely intertwined (Stevenson and Enns, 1993).

The efficacy of the clump method as an estimator varied among the lichen functional groups. There are two reasons for this variation. First, the standard clump was large and therefore more easily compared to lichen in large amounts. *Bryoria* makes up the bulk of epiphyte abundance and is therefore more accurately estimated using a large standard than either of the less abundant functional groups. Second, the 3P sampling was calculated based on the estimates of total fruticose lichen (*Alectoria* and *Bryoria* combined), the majority of which is *Bryoria*. In essence, then, the selection of sub-samples was based on the sum of estimates of *Bryoria* and therefore had a larger proportion of branches heavily laden with *Bryoria* than those with large loads of either *Alectoria* or foliose lichen. The larger coefficient of determination for *Bryoria* reflects this bias. Sampling according to *Bryoria* abundances is, however, still a reasonable estimator of both *Alectoria* ($R^2 = 67.9\%$) and foliose lichens ($R^2 = 61.3\%$). It appears advantageous to select branches for sampling according to the most important or most abundant attribute in the context of the study (ie caribou forage lichen). If all attributes are equally
important, it is perhaps advisable to select a different sampling scheme such as 3P sampling based on estimates of each functional group separately would become time consuming and expensive.

Regressions, rather than ratios (Pike, 1981), were used in my study to compare the estimates with the sub-sampled biomass. Stevenson (1979) used ratios to compare estimated and measured biomass. She required a sub-sample of 25-33% to maintain the confidence intervals within reasonable limits. By using regression statistics, we could have a smaller, more manageable sample size. The data for the entire population was pooled to maintain a statistically viable sample size of 96 branches. Combining 3P sampling (rather than sequential, systematic or random sampling) with the regression statistics minimized the sub-sample without jeopardizing the statistical reliability of the sub-sampling procedure (Cochrane, 1977).

Measurements of architectural features introduced a similar dilemma to that resolved with techniques of lichen estimation. I wanted to represent the dynamics of the entire crown and yet time constraints precluded the measurement of every characteristic on all branches. The fifteen percent sub-sample within each of the three height zones for branch aspect, length and slope represented my efforts to fulfill two requirements. It gave me a representative sub-sample throughout the canopy while decreasing the actual time spent in an, often uncomfortable, climbing harness. While this method provided a large enough sample to conduct statistical tests over the entire ecosystem, it was not large enough to facilitate direct tree to tree comparisons of branch length, slope and aspect.

The methods presented in this thesis represent both my desire for confidence in the structural measurements and lichen estimates (so they may be used in place of direct biomass sampling on every branch) and my need to quantify the lichen and document architectural
characteristics on a large and varied population. Such a population is required to be confident both in my conclusions about the determinants of lichen abundance and in any subsequent management recommendations that will be made for the ecosystem using the results of this study.

4.2 Stand Structure and Canopy Architecture

The stand at Pinkerton mountain is considered old growth, with a maximum tree age of up to 350 years. Stand structure of the forest is typical of many high elevation ecosystems in that the tree distribution patterns are not regular, but instead form clumps of highly associated trees (Arno and Hammerly, 1984). This characteristic response is due to the extreme climatic conditions of higher elevation forest communities (Aplet et al., 1988). Long, cold winters with a heavy snow pack coupled with short, wet and cool summers limit the growing season (Farnden, 1994). At Pinkerton mountain, the maximum tree height was approximately 30 metres, in contrast to trees in a forest of similar age at a lower elevation, that often exceed 50m in height (Clement and Shaw, unpub.; Pike et al., 1977; Pike et al., 1975).

I have described the morphological features of branches within the ESSF canopy with the dual purpose of characterizing the canopy architecture and documenting the response of epiphytic lichens to it. The literature describing canopy architecture is incomplete (Parker, 1995), which prevents a thorough comparison of my findings. However, the existing information pool has been expanded by characterizing branch morphology relative to gradients in other structural features of the canopy at Pinkerton mountain.
4.3 Distribution of Lichen Functional Groups

Sillett and Neitlich (1996), McCune (1993) and McCune et al. (1997) discussed a vertical gradient in epiphyte biomass that is intrinsically tied to epiphyte succession. The successional sequence of epiphytes is a result of the size of the host tree. Therefore it is understandable that the pattern of epiphyte succession in the ESSF ecosystem is different from those seen in coastal ecosystems where the trees are often twice the height seen at Pinkerton mountain. The lichen distribution at Pinkerton mountain corresponds with the earlier successional stages detailed in the literature. Foliose lichens are the first to colonize (Stone, 1989), followed by Alectoroid lichens (*Alectoria* and *Bryoria*). These are displaced to the higher canopy zones by the later successional cyanolichens and epiphytic bryophytes. The resulting distribution of Alectoroid and foliose lichen in my ecosystem resembles that of the 30 to 60 metre zone in the literature (McCune et al., 1997). *Alectoria* and *Bryoria* dominate this zone, foliose lichens exhibit a less obvious distribution with height above ground and cyanolichens and bryophytes are essentially absent. McCune (1994) showed that *Alectoria sarmentosa* and *Bryoria* spp. were present in all age categories, but reached maximal abundance in the medium aged class forest. Certain foliose lichens were also most abundant in the early mature forests considered in that study. The ESSF lichen communities at Pinkerton mountain display a successional stage that is normally found earlier in the successional sequence of lower elevation forests. This difference, given the age of the stand at Pinkerton mountain, is more likely a result of the harsh environmental conditions than tree age.

The separation of *Alectoria* and *Bryoria* into individual strata within a vertical gradient is documented in this study. *Bryoria* dominated the upper canopy and was gradually separated at approximately 7 metres from *Alectoria*, which increased in abundance from there to the lowest
branches. Arseneau et al. (1997) and Rominger et al. (1994) described separate responses for *Alectoria* and *Bryoria* to the vertical gradient but did not provide reasons for why it exists.

One hypothesis considers the more shade tolerant nature of *Alectoria* (Arseneau et al., 1997; Edwards et al., 1960), and indicates that *Bryoria* colonizes the upper canopy where it has better access to solar radiation. Another theory, along these same lines, suggests that *Bryoria* is more adept at tolerating the frequent wetting and drying cycles in the upper canopy, created by alternating light rains or dew with drought like conditions. *Alectoria*, in contrast, requires the steady humid conditions of the lower canopy where neither the rain nor daily drying occurs frequently, and moisture is obtained from through-fall after a heavy rain event (Arseneau et al., 1997; Pike et al., 1975). This explanation is supported by the observation that more xeric sites often have markedly less *Alectoria* than sites where moisture availability is not a limiting factor (Edward et al., 1960). The response of arboreal lichens to moisture availability is related to both stand age and tree size class. The canopy of older tree stands is generally a multi-cohort stand in which the trees are irregularly spaced. These stands are typically more moist than younger stands where sunlight and desiccating wind can penetrate the canopy more deeply (McCune, 1993). Thus the lichen communities that are abundant in each of the size and age classes are possibly a reflection of the moisture regimes to which they are specifically adapted (Rogers, 1990). The influence of tree age and size on lichen biomass will be discussed more fully in the following sections.

The distinct zones of abundance for *Alectoria* and *Bryoria* might also be due to competition between lichens. Malanowski (1911, 1912, cited in Hawksworth and Chater, 1979) observed examples of thallus overgrowth, indicating that competitive exclusion between fruticose lichens is a possibility. More recently, photographic evidence provides support for
competitive causes of lichen abundance patterns (Hawksworth and Chater, 1979). It has been suggested that *Alectoria* is the stronger competitor, as *Bryoria* will occupy branches in remnant trees following a harvest, only after the branches have been vacated by the more light sensitive *Alectoria* (Rominger et al., 1994). Stone (1989) found evidence for competitive release also, but concluded that competition was a less influential factor than the physical environment. Thus, while it may be valid to attribute part of the distribution patterns to competition for beneficial habitat within the moisture and light regimes, much of the vertical threshold where *Alectoria* is replaced by a more abundant *Bryoria* must still be explained by the changing physical environment of a growing tree. Microclimatic observations are currently being collected in the Pinkerton mountain ecosystem in an attempt to elucidate the causal factors of this lichen distribution pattern (Coxson and Stevenson, unpublished data).

There were five different *Bryoria* species, six *Hypogymnia* species and three other foliose lichen species identified in this study. These were all distributed throughout the vertical canopy. The homogeneity of the foliose lichens was not wholly unexpected, as there were few vertical differences within the group as a whole. I was surprised, however, that there was no vertical stratification within the *Bryoria* species. Personal observations within the canopy led me to expect that the different pigments in these groups would have separated them out along a gradient from the lower canopy where the light yellow-green *Alectoria* was abundant to the upper crown where the dark brown-black *Bryoria* functional group predominates. For example, *B. capillaris* has a light olive pigmentation that may result in the requirement of a sunlight and moisture regime similar to that of *Alectoria*. I would therefore have expected to find more of this species on branches that were closer to the lower canopy zone. These results may have been due more to sampling methodology than to actual community composition. The observed
homogeneity in lichen species distribution may have been an artifact of identifying only one clump to the species level. In addition, Pike (1973) indicated that the species assemblages on tree branches were quite homogeneous in comparison to the great epiphyte diversity found growing on the trunk. Any species level response to tree height might therefore have been missed by omitting trunk sampling. The exclusion of trunk lichens from the study would have very little impact on the lichen biomass and relative abundance of the functional groups since the lichen biomass on the trunk was small compared to on the branches. Also, because my methods allowed close examination of every branch in the population (where the majority of lichens are found), our estimates are likely to be closer to the actual biomass than traditional ground level estimates of lichen biomass. These results are therefore intended to make conclusions about the distribution and abundance of functional groups and should not be used to describe lichen diversity in the Pinkerton mountain ecosystem.

4.4 Stand Level Determinants of Lichen Abundance

Many of the responses of canopy lichens in this study were documented in reference to a vertical gradient. Because branch height is an easily measured variable that is representative of changes in stand age and tree size (Esseen et al., 1996; Parker, 1995), lichen abundance patterns were specifically examined along a gradient in both tree age and size class.

It is well documented (Edwards et al., 1960; Esseen et al., 1996; Hinds, 1970; McCune, 1994) that stand age has a positive effect on the abundance and the diversity of lichen communities. Similarly, my study found that all three lichen functional groups were significantly more abundant in trees at the upper end of the age distribution. I also found that the degree of response differed across the functional groups. *Bryoria* appeared to benefit more from increasing
tree age than either foliose lichen or *Alectoria*. This is an important fact to consider when designing strategies for the maintenance of forage lichens in managed forests.

Edwards et al. (1960) found that young trees in the ESSF had approximately 50 g/tree, intermediate aged trees held 100 to 1600 g/tree and older trees had between 3100 and 8600 g/tree. Biomass values at Pinkerton mountain for small (87 g/tree), medium (655 g/tree) and large trees (4145 g/tree) fall within these intervals, indicating that the size class intervals used in this study correspond with the age classes described by Edwards et al. (1960). It also shows that Pinkerton mountain holds an abundance of arboreal lichens that is comparable to other study areas.

While arboreal lichens are found more abundantly in older forests, the age of the tree is often a misleading criterion on which to base this conclusion. Trees respond to differing climatic conditions by growing at different rates and so the age of the tree is not always well represented by its size (Aplet et al., 1988). In addition, because succession with tree age and the architectural environment are often confounded (McCune, 1993), it is perhaps better to consider lichen abundances along a scale combining age with height. I termed this interaction the "size class".

All functional groups become more abundant along a gradient in size class from the lower canopy of small trees to the upper canopy of large trees. It appears that small trees do not make suitable habitat for arboreal lichens (Forman, 1975; Lang et al., 1980). Large trees within my study area hosted so much more lichen that, as others have found (Lang et al., 1980), it was difficult to summarize the lichen biomass on different size trees in one graph. The lichen biomass in large trees was so great that it rendered the lichen biomass in small trees insignificant and unreadable. Although the overall abundance in large trees was greater than in small or medium trees, there appeared to be a similar gradient with height in all three. There were, however, large
disparities in each of the three functional groups, both relative to each other and relative to different size classes. *Alectoria* was consistently less abundant than either foliose lichen or *Bryoria*, but steadily increased across tree sizes. Foliose biomass similarly became more abundant with tree size, but much of this difference was manifested in the change from small to large trees rather than along the corresponding height increase. This again, gives supporting evidence for the inconsequential influence of height on the abundance of foliose lichen. It would appear that foliose lichen operates according to different ecological roles than either of the fruticose lichens. *Bryoria*, in contrast, produced only minor increases in biomass from small to medium trees and from low to middle canopy but nearly tripled in abundance from medium to large trees. Maximal levels of *Bryoria* were therefore found only in upper canopy of large trees.

The cause of the dominance of *Bryoria* in the upper canopy of large trees is unexplored in this ecosystem. However, it seems that, given the poor response of *Bryoria* to branch diameter, the preference for this upper zone is probably not due to an increase in substrate availability, but instead to changes in the microclimate experienced by *Bryoria* in the upper canopy. These results reinforce the importance of large trees in a healthy, lichen bearing ecosystem.

Pendulous forage lichens appeared to respond positively to the irregular clumping distribution of the trees at Pinkerton mountain. *Alectoria* and *Bryoria* exhibited greater abundance per branch in clumped trees than in solitary trees of corresponding size in nearby canopy gaps. There are several possible explanations for this, all of which likely play a role in determining the abundance of lichens in clumped trees. The first is that the crown perimeter of clump trees join together to form in essence, a “mega tree”. This “mega tree” may confer a microenvironment on its member trees that is similar in nature to late successional, lower elevation forests. The micro-environment is more conducive to lichen growth and establishment.
The second, and somewhat related hypothesis takes into consideration the suitability of substrate in young trees for lichen development. Young trees that become established under the canopy of large clump trees experience slower growth rates and have a different morphology than similar aged trees developing in canopy gaps due to competition for sunlight (Aplet et al., 1988). Young trees developing in the open provide poor habitat for lichen establishment. They grow quickly and because branches are continually being shaded out by the growing canopy, a constantly changing microhabitat is created. Lichen dispersal and establishment is too slow a process to adapt to this unstable environment and so lichens typically do not become abundant in small trees (Sillett and Neitlich, 1996). In contrast, young trees within the clump environment have a markedly slower growth rate that is more conducive to the establishment of arboreal lichens. In addition, these trees often have extremely long branches, relative to their total height, that reach out from under the clump canopy. This facilitates maximal absorption of solar radiation by both the tree foliage and by the epiphyte community growing there. Greater biomass in clumped trees may also be due to increased and more efficient dispersal from a nearer propagule source to young trees growing under larger clump trees. Regardless of the causal factors, the fact that clumped trees may carry more epiphytic lichens has significant implications to forest management.

4.5 Canopy Architecture Determinants of Lichen Abundance

The distribution of *Alectoria* and *Bryoria* biomass is largely determined by the height of the tree branch on which it grows. Branch height was the most important variable describing the abundance trends within these functional groups. Edwards et al. (1960) suggested that the most important factor limiting the abundance of *Alectoria* and *Bryoria* was the size of the branches. In
contrast, I found that branch diameter was not a main determinant of fruticose lichen biomass. The pendulous growth form of these lichens allow them to become attached to the host by a single holdfast. Substrate availability would therefore not seem to limit Aleoctorioid lichen growth after initial colonization (Stone, 1989; Renhorn, 1997a).

An increase in branch length, on the other hand, would seem to satisfy the substrate requirements for both *Alectoria* and *Bryoria*. Increasing branch length would also provide access to the outer crown where solar radiation is more readily available. Branch length and *Alectoria* abundance are both negatively correlated with branch height. It would thus seem intuitive that longer branches would host greater abundances of *Alectoria* simply by virtue of being in the lower canopy. It was therefore surprising that branch length was not a major determinant of *Alectoria* abundance. It was, however, important in determining the distribution of *Bryoria* biomass which likely results from the increase in substrate that longer branches provide for this pendulous lichen. The fact that branch length was negatively correlated with branch height and *Bryoria* increases only up to a certain length threshold suggest that the response of *Bryoria* to limb length is counteracted by the stronger influence of branch height at that point. The fact that length was a significant determinant of *Bryoria* biomass but not of *Alectoria* biomass is perhaps explained by the weakly significant probability value and the small effect size for *Bryoria*. The influence of branch length on fruticose lichens requires further investigation before conclusions can be made.

The ranking of structural determinants of foliose lichen were different from those of the fruticose lichen functional groups. Height, arguably the most important variable in a canopy environment, as it represents a proxy measure for age and succession (Yarranton, 1972), was not even included in the explanatory models for foliose lichen. There were no distinct vertical zones
of maximum and minimum foliose abundance as there were with the other two functional
groups. Foliose appeared, instead, to be strongly influenced by the diameter of the branch on
which it was found. The increase in foliose lichen with branch diameter corresponds with earlier
literature which reported that foliose lichen distribution is strongly limited by competition for
suitable substrate (Stone, 1989). The interaction between diameter and length also represents an
overall increase in the size of the host branch, which has been shown to be a positive influence
on foliose lichen biomass (Clement and Shaw, unpub.; Edwards et al., 1960; Renhorn, 1997a). It
is interesting to note that while the interaction between these two variables was a key
determinant, branch length alone did not influence foliose lichen with any significance. This is
likely because foliose lichen appears to prefer the axis of branches (Pike et al., 1977) over parts
of the branch on which large amounts of foliage are found. Branch diameter is an important
factor determining how much branch axis is available for colonization. Increased branch length,
on the other hand, is likely a measure of branch foliage rather than the more readily colonized
branch axis (Pike et al., 1977). Future measurements should monitor the response of foliose
lichen to variations in the axis to foliage ratio of branches in this canopy.

Length interacted with the inclination angle of branches to determine how much of the
branch, and therefore, lichen, is exposed to sunlight. The interaction had a significant influence
on foliose lichen and while length was uninfluential, branch slope turned out to be important.
This is puzzling, given that slope did not have an influence on Bryoria biomass, which showed a
far greater increase over the range of branch slopes than did foliose lichen. Yet foliose lichen was
significantly influenced by branch slope despite the constancy of lichen biomass with varying
slope. The weakly significant probability value and the small effect size indicate that branch
slope was not as influential as branch diameter and density in determining foliose biomass
distributions. Density is a very important variable to consider also when describing the abundance of foliose lichens. This may be due to facilitation of dispersal from branch to branch coupled with a dampening of the effects of wind scouring and desiccation that would be a result of increased branch density (Armstrong, 1993). The influence of branch aspect on all three lichen functional groups was insignificant. This was consistent with the results of Halonen et al. (1991), who suspected that differences in lichen cover at various exposures would only be significant in very open forests.

4.6 Management Implications

The final objective of this study was to consider the key determinants of lichen abundance in light of the silvicultural trials that have been and will be conducted at Pinkerton mountain. Characterizing the structural characteristics of the trees and documenting the abundance patterns of epiphytic lichens within has increased the available information about the dynamics of this ecosystem. It is hoped that this information will be expanded upon to develop management strategies for the maintenance of lichen biomass in this ecosystem.

There were four major management implications that resulted from a combination of this study, other research currently being conducted at Pinkerton mountain (Coxson and Stevenson, unpublished data), and the existing literature.

1. Large tree remnants: One of the dominant impressions that this study leaves is the importance of large trees in maintaining lichen biomass levels. Maintaining canopy dominants in managed forests is necessary for several reasons.

   A. Studies (including this one) have shown that small trees do not exhibit the abundance of arboreal lichens that are present in larger, canopy dominants
(Arseneau et al., 1997; Forman, 1975; Lang et al., 1980). This is especially true with *Bryoria*, which does not begin to become abundant until trees reach a threshold of approximately 15 metres in height. Maintenance of *Bryoria* biomass is of paramount importance because it is the primary forage lichen for the mountain caribou.

B. Large trees provide a broader spectrum of microclimates and habitats than do smaller trees (Franklin and Spies, 1991). This facilitates use by a greater diversity of flora and fauna which greatly increases the biological value of the ecosystem.

C. The presence of large trees defines the canopy structure, by moderating the effects of sunlight and wind on both the understorey and canopy plant communities.

D. Canopy dominants are also integral to the regeneration of the forest ecosystem. They provide a seed and lichen propagule source for dispersal into the developing forest. It has been suggested that leaving large trees well dispersed in a cut block increases the dispersal capabilities and thus enhances the speed at which the new ecosystem develops (Muir and Rambo, personal communication).

2. Uneven stand structure: It is imperative that large trees be left during selection harvesting and it is equally necessary to maintain an uneven stand structure in the remaining forest patches. Short rotation periods between logging events may allow for the development of relatively large trees as in an early mature forest (Smith, 1986), but they do not generally allocate enough time for the stand to develop the uneven age structure characteristic of later maturity (Lefsky, 1997). The uneven aged structure is important as it provides a larger realm of possible habitat use by a larger variety of biological organisms (Jull, 1992). The stratified canopy also enhances the abundance of epiphytic lichens. In fact, in
some forest ecosystems, stand structure is a larger determinant of lichen abundance than is the absolute age of the stand (Pipp, 1998).

3. Clumped structure: Maximal lichen abundance appears to result from maintaining the clumped structure of the ecosystem at Pinkerton mountain.

4. Finally, thorough investigations should be conducted into the dynamics of the whole ecosystem, including the previously overlooked canopy. Traditionally, pre-harvest research on lichen distribution and abundance has been conducted using ground based techniques. This is inappropriate because the upper canopy is host to an abundance of forage lichens which are neither well represented by the lower canopy nor readily apparent from the ground.
Literature Cited


The nearest neighbours of all clump trees were mapped using the Nikon Total Station Survey system. The station reported the distance, horizontal angle and vertical angle to each tree from one, two or three set reference points. The reference points were back-sighted to each other to obtain a zero horizontal angle with which to reference all other horizontal angles. All trees within qualitative assessment of a sphere of influence (trees within 14-m of the clump were considered influential; Moeur, 1993) were measured and mapped. Large trees (10m or taller), between 14-m and 50-m from the clump were also mapped. This criteria ensured that larger trees, behind smaller trees that played smaller roles in influencing microclimate, would not be ignored. The height of all surrounding trees, included in the map was measured or estimated in reference to a neighbouring, measured, tree (Lesica et al., 1991). The clump or solitary numbers, if applicable, were also given and shown on the maps.

The distribution of stems was similar in all study sites. Minor differences are generally due to topographic features of the study site in general. For example, the larger gaps surrounding clump 1 were due to the bog-like characteristic of the forest immediately surrounding. The maps clearly show the clumped nature of the ecosystem.
Fig. 1a The stem map of clump 1. The solitary and seven clump trees and the 177 surrounding trees are shown.
Stem Map for Clump 1

CLUMP TREES
- CT1-1
- CT1-2
- CT1-4
- CT1-5
- CT1-6
- CT1-7
- CT1-8
- CT1-sol

STEM HEIGHTS (m)
- 0 - 5
- 5.01 - 10
- 10.01 - 15
- 15.01 - 20
- 20.01 - 25
Fig. 1b  The stem map of clump 2. The solitary and five clump trees and the 176 surrounding trees are shown.
Stem Map for Clump 2

CLUMP TREES
- CT2-1
- CT2-10
- CT2-2
- CT2-3
- CT2-9
- CT2-Sol

STEM HEIGHTS (m)
- 0 - 5
- 5.01 - 10
- 10.01 - 15
- 15.01 - 20
- 20.01 - 25
Fig. 1c  The stem map of clump 4. The solitary and nine clump trees and the 144 surrounding trees are shown.
Stem Map for Clump 4

- CLUMP TREES
  - CT4-1
  - CT4-11
  - CT4-12
  - CT4-13
  - CT4-2
  - CT4-3
  - CT4-4
  - CT4-5
  - CT4-6
  - CT4-7
  - CT4-9
  - CT4-sol

- STEM HEIGHTS (m)
  - 0 - 5
  - 5.01 - 10
  - 10.01 - 15
  - 15.01 - 20
  - 20.01 - 25
Fig. 1d  The stem map of clump 6. The solitary and eight clump trees and the 177 surrounding trees are shown.
Stem Map for Clump 6
The stem map of clump 9. The solitary and ten clump trees the 173 surrounding trees are shown. There were no trees immediately surrounding the solitary tree on the south east side.
Stem Map for Clump 9
Fig. 1f  
The stem map of clump 11. The solitary and twelve clump trees and the 152 surrounding trees are shown.
Stem Map for Clump 11

CLUMP TREES
- CT11-1
- CT11-10
- CT11-11
- CT11-2
- CT11-3
- CT11-4
- CT11-5
- CT11-6
- CT11-7
- CT11-8
- CT12-9
- CT11-sol
- CT11-sol

STEM HEIGHTS (m)
- 0 - 5
- 5.01 - 10
- 10.01 - 15
- 15.01 - 20
- 20.01 - 25
Fig. 1g  The stem map of clump 12. The solitary and eleven clump trees and the 157 surrounding trees are shown. The north-east side of the clump faced into a large gap in the canopy and thus fewer stems are shown at that aspect.
Stem Map for Clump 12

CLUMP TREES
CT12-1  CT12-10  CT12-11  CT12-12  CT12-2  CT12-3  CT12-4  CT12-5  CT12-6  CT12-7

STEM HEIGHTS (m)
5.01 - 10  10.01 - 15  15.01 - 20  20.01 - 25
The stem map of clump 13. The twenty clump trees are shown in the centre of the map. This clump has a larger number of trees in it due to the inordinate amount of advanced regeneration below the canopy of the clump dominants. No single tree was assessed in conjunction with this clump due to access difficulties. The 201 surrounding trees are mapped.
Stem Map for Clump 13

STEM HEIGHTS (m)
- 0 - 5
- 5.01 - 10
- 10.01 - 15
- 15.01 - 20
- 20.01 - 25

CLUMP TREES
- CT13-1
- CT13-10
- CT13-11
- CT13-12
- CT13-13
- CT13-14
- CT13-15
- CT13-16
- CT13-17
- CT13-18
- CT13-19
- CT13-2
- CT13-20
- CT13-3
- CT13-4
- CT13-5
- CT13-6
- CT13-7
- CT13-8
- CT13-9