

**EFFECTS OF FOREST MANAGEMENT PRACTICES
ON FOREST STRUCTURE AND
SELECTED EPIPHYTIC LICHENS IN NOVA SCOTIA**

by

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Abstract

Little is known about habitat requirements of lichens and evidence suggests that they may be negatively impacted by forestry. The purpose of this thesis is to: 1. determine if harvesting and thinning affect certain forest structural features; 2. determine if harvesting and thinning affect diversity or abundance of selected epiphytic lichen species; 3. determine habitat and forest structural features important in explaining diversity and abundance of some lichen species; and 4. examine the use of lichens as bio-indicators of forest structure.

Structural forest features and abundance on trees of 34 species of arboreal lichens were measured and compared among thirty stands in three maturity classes in central Nova Scotia including natural forests with no timber management and harvested and thinned and harvested forests.

Significant differences in forest structural features were found between natural and managed forests. Structural features found to be most correlated with lichens are tree age, crown closure and remnant trees. Natural forests had significantly greater total lichen abundance, number of lichen species and lichen diversity than managed forests. Forest management practices can be changed to improve habitat for lichens and increase biological diversity in managed forests.

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1.0 Introduction

Ecosystems are made up of complex relationships of a variety of species. However, they are impacted by human development and occupation of the land. This is evident in forests where management practices such as road building fragment the forest, silviculture alters properties of forests and timber harvesting removes large amounts of large woody material. Many forest species can be affected. One group of species which may be negatively impacted by forest management practices are epiphytic lichens. This thesis examines the relationship between forest management and lichens.

Biological systems are inherently diverse. Diversity is found within organisms, populations, communities and ecosystems. This diversity is an essential part for the continued existence of these systems. For example, genetic variability within a population is essential for continued viability of that population. Each population plays a role in ecosystem function by facilitating movement of matter and energy through various cycles or processes at different levels. Some of these processes include nutrient cycling and energy flow. There are some species groups that are essential for the functioning of these processes. No ecosystem can function without decomposers, for example. Decomposers are a critical link in nutrient cycling, carbon cycling and other processes. Without the functioning of all the essential roles within them, ecosystems would cease to function.

A diversity of organisms within an ecosystem also provides resiliency to sudden

disturbances. Change to an ecosystem may be detrimental to one or several groups of species. However, with a greater diversity of species present in a system, there is a greater probability that some organisms will survive or flourish after a disturbance. With a diversity of species in an ecosystem there is often more than one species that can fulfill a function. Therefore, ecosystem functions will continue even if a species ceases to exist in that system after a disturbance.

Natural disturbances are often common occurrences in ecosystems and can occur on many scales. Small scale disturbances in a forest ecosystem occur when a single tree dies. A gap is created in the forest canopy, increasing sunlight to the forest floor as well as adding dead wood to the forest. Larger scale disturbances in forests, such as wildfire, windthrow and insect infestations are common. These processes alter the dominance of vegetation, affect microclimate within the forest, and alter the structure and composition of forests. As a result of these disturbances, most natural forests are a mosaic of stands of trees at various stages of development often with diverse structure and composition.

The natural heterogeneity of natural forests provides a variety of habitats and as a consequence, natural forests contain a variety of species inhabiting these habitats.

Unlike natural disturbances, anthropogenic disturbances tend to reduce biological diversity. Human influenced systems are much simpler than natural systems. Agricultural systems tend to be dominated by a single plant species. Crop fields, pasture and orchards

are common examples. This results in less structural diversity and fewer habitats for species. Commercial timber management is another example of anthropogenic disturbance which tends to reduce natural heterogeneity. Forest management practices like thinning and planting promote uniformity and reduce variability. In many cases intensive forestry has reduced diversity of forest species and increased the risk of extinction of some species (Haila 1994). Managed forests with a lower density of dead and snag trees have been shown to have fewer numbers of cavity nesting birds (Scott 1979, Raphael and White 1984). Tree harvesting, in some cases, has reduced the abundance of salamanders in forests (Bury 1983, Pough 1987, Petranka 1994). Truncation of older age classes and clearcutting can result in lack of continuity of forests and may reduce the abundance of old growth dependent species of beetles, moths, bryophytes and lichens (Pettersson 1996).

Because of increasing human disturbance to natural ecosystems, there is concern among ecologists about the loss of biological diversity. A common approach to managing biological diversity is to maintain a network of natural reserves. However, there are problems with this approach for forests. Natural forests are more difficult to find as they are increasingly replaced by second growth managed forests. As a consequence of disappearing natural forests and conflicts in land use, natural reserves tend to be small in comparison to the landscapes they are meant to represent. Natural reserves are often separated from one another by roads, urban development, agricultural land and commercial forests. This results in a system of fragmented forests with small isolated patches of protected natural reserves.

The theory of island biogeography states that smaller more isolated islands tend to have lower species diversity (MacArthur and Wilson 1967). With smaller more isolated islands of natural forest in a sea of human disturbed landscapes, natural forests are likely less diverse and contain fewer species than they once did. The fragmented nature of current natural reserves may also limit dispersal of organisms. If roads, fields, urban development and plantations provide a barrier to dispersal for some species, genetic variability may be reduced within populations in natural reserves. Natural reserves may also be too small to maintain populations of some species. There should be enough resources and space within a reserve for all species to maintain a viable populations (Gilpin and Soule 1986).

It therefore becomes necessary to manage some forests for both timber production and biodiversity (Hansen 1991, Haila 1994, Keddy and Drummond 1996). There are some difficulties in attempting to integrate biodiversity management and commercial forest production. Managed forests can differ markedly from natural forests. Current forest management practices like insect and fire suppression and windthrow salvage alter or suppress natural processes. Practices such as thinning and clearcutting result in structural changes in forests (Smith 1962, Hunter 1990). Forestry has changed natural forests in three major ways: 1. changes in size, configuration and spatial distribution of forest stands (Haila 1994); 2. changes in structural features of forest stands such as amount of dead wood; and 3. changes in temporal pattern of disturbance. The first part of this study focusses on changes in structural features of forests as a result of harvesting and thinning,

where forest structure is the arrangement of material components of the forest. There is a need to understand what structural changes occur in forests as a result of forest management practices and the effects of these changes on forest dwelling species.

There is insufficient understanding of the effects of forestry on biodiversity. There is a paucity of data on the effects of forest management practices on invertebrates, amphibians, reptiles, woodpeckers, raptorial birds, forest floor plants, epiphytic plants and microorganisms in Maritime Canada (Freedman 1994). Only a few studies have examined forestry effects on epiphytic lichens (Essen and Renhorn 1996). Most of the studies have suggested significant detrimental effects.

Lichens form an important part of forest ecosystems. Lichens may be important in nutrient cycling (Tansey 1977, Pike 1978, Sendstad 1981), provide food for ungulates (Hodgeman and Bowyer 1985, Sharnoff 1994) and increase the diversity of invertebrate fauna (Frederickson 1983, Stubbs 1989, Pettersson 1996).

Structural features of forests largely determine which lichens are present. For example, *Xylographa* species inhabit only deadwood (Gowan and Brodo 1988) and therefore are likely to occur in lower abundance in forests with little deadwood. Similarly, *Lobaria pulmonaria* is found mostly on maple trees (Hale 1979) and is less likely to be found in forests with no maple component. Because forest lichens are so closely related to structure, they are likely to be affected by forest management practices and show potential

as indicators of impacts on natural forests.

In order to develop an integrated approach to forest management there is a requirement for tools to help manage forests. Indicators have been suggested as a possible tool which can measure properties of forests (Kremen 1992, Lautenschlager 1995, Keddy and Drummond 1996, Canadian Council of Forest Ministers 1997). Measured values of indicators in natural forests can be compared to managed forests to help determine changes in properties of natural forests caused by forest management practices and also serve as a measure of conservation efforts in commercial forests. Lichens have been used successfully as indicators of pollution (Richardson 1992) and forest continuity (Rose 1976, Tibell 1992, Selva 1996). Lichens show promise as potential bio-indicators for forest management because they are measurable and sensitive to structural changes in forests.

This study compares forest structural features, lichen diversity and abundance of some lichen species between natural and managed spruce forests of different maturity classes. The purposes of the study are to:

1. determine if harvesting and thinning affect certain forest structural features;
2. determine whether harvesting and thinning affect diversity or abundance of selected epiphytic lichen species;

3. **determine habitat and forest structural features important in explaining presence, abundance and diversity of some lichen species; and**
4. **assess the use of lichens as bio-indicators of forest structure.**

The report is organized into 3 main sections. The first section (2.0) examines forest structural features. This section addresses the first stated purpose of determining if harvesting and thinning affect certain forest structural features. The second section (3.0) examines the relationship of lichens to habitat and forest structural features. The section is divided into 2 parts: the first part examines how individual lichen species are affected by forest structural features; the second part examines how the softwood lichen community as a whole is affected by origin and maturity class. The second section addresses the third stated purpose in determining what habitat and forest structural features are important to lichens. The third section (4.0) examines the affects of harvesting and thinning on lichens and the use of lichens as potential biological indicators. This section addresses the second and fourth stated purpose of determining if harvesting and thinning affects lichens and examining the use of lichens as potential bio-indicators.

1.1 Study Sites

Thirty forest stands in central Nova Scotia were selected for study. These stands were located on lands of Bowater Mersey Paper Ltd. north of St. Margaret's Bay in

Halifax and Hants Counties, lands owned or managed by Kimberly-Clark Ltd. and Stora Forest Industries Ltd. in the Liscomb Game Sanctuary in Halifax and Guysborough Counties and Crown and private lands in Hants County (Appendix IV).

Study stands were at least 4 ha in size, dominated by spruce (*Picea* spp.) and had mean age greater than 40 years. Each stand selected for study is one of three types: 1. harvested and thinned stands are stands that regenerated after forest harvesting and have been thinned at least once; 2. harvested stands are stands that regenerated after harvesting but have not been thinned; 3. naturally disturbed stands are stands that regenerated after a hurricane or wildfire. Study stands were selected such that the majority (greater than 50%) of trees established after a single large disturbance (tree harvesting, hurricane or wildfire).

Potential study stands were selected in consultation with local foresters and forest technicians. Fire origin stands were found by examining fire history records of the Nova Scotia Department of Natural Resources for areas of past wildfire occurrence. The wildfire areas were then located on the ground and searched for evidence of past fire. Study sites were searched for logs or stumps with charcoal or burn scars. At least 2 soil pits were dug at each potential study site and examined for charcoal. Hurricane origin stands were evidenced by lack of stumps, presence of fallen uprooted trees and uneven ground as described by Oliver and Larson (1996). Previously harvested stands were identified by the presence of short (<1/2 m) flat topped stumps.

Study stands were selected to represent 3 maturity classes: pole, mature and climax on the basis of average tree age and stand or tree condition. Pole includes stands with trees between sapling and small saw timber size (11 cm diameter at 2.4 m from the ground) with a mean age between 40 and 45 years. Mature includes stands with the majority trees that are sufficiently developed to be harvestable (7.6 cm diameter at 2.4 m from the ground) and with a mean age between 60 to 95 years. Climax includes stands with a mean tree age greater than 100 years.

The number of study stands for each maturity class and origin type are shown in Table 1.

Table 1. Number of study sites by maturity class and origin type

Maturity Class	Origin Type		
	Naturally Disturbed	Harvested	Harvested and Thinned
Pole	6	3	3
Mature	4	4	4
Climax	3	3	0

1.2 General Methods

1.2.1 Pilot Study

A pilot study was initiated in 1996 to determine sample and plot size requirements for measuring lichen abundance using methods of McPhee (1997). Samples of lichens from tree trunks were collected at several study sites. Species were identified, dried and placed in a reference collection. A subset of 34 species of lichen from the collection was then prepared. Lichens that were reasonably easy to identify and/or were previously identified as indicators of forest continuity were chosen for the list. Only species on the list were sampled in this study to increase sampling accuracy and reduce sampling time. Identification of lichen species was aided by lichenologist Karen Casselman from the Nova Scotia Museum of Natural History. I also completed a week long intensive course taught by Dr. David Richardson on lichen identification and ecology at the Humboldt Field Research Institute in June 1997. Lichen nomenclature followed Egan (1991).

Species sample curves revealed that a minimum of 16 trees was required to detect the majority of reference lichens in the most lichen rich sites (McPhee 1997). Variation in cover estimates between observers was significant therefore McPhee (1997) suggested use of cover classes to reduce the variation and decrease sampling time. Frequencies of percent cover were then plotted to determine cover classes for the current study. Statistical testing revealed that the sampling technique used by McPhee (1997) was

sensitive enough to detect differences in lichen abundance between forest types.

1.2.2 Main Study

Transect lines were established to bisect each study stand in 1997. Six points were located at 35 m intervals along transect lines. A basal area factor 2 glass wedge prism was used at each point to identify trees to be sampled. A prism is an angle gauge made of optical glass that projects a small horizontal angle. When sighting through the prism, trees that appear larger than the projected angle are tallied and while those that appear smaller than the projected angle are not tallied. Thus, with increasing distance from the observer only larger trees are likely to be tallied. Using a prism results in sampling with probability proportional to size and assures adequate representation of the larger trees.

Twenty-three trees from each stand were selected for lichen sampling to exceed the required minimum of 16. The tree tally from each stand was divided by a number to achieve a sample of 23 (e.g. if 69 trees were tallied in a study stand, then every third tree was sampled for lichens). Percent cover of a tree by a lichen species was used as a measure of abundance. Presence of lichen species was recorded and percent cover of the tree surface for each species was estimated from ground level to 2 m up the bole of each tree on all sides of the tree. Percent cover estimate on tree boles was scored accordingly: 1 = rare <1%; 2 = occasional 1 to 2%; 3 = common 2 to 10%; and 4 = abundant >10%.

Statistical tests used in the analyses were done using S-plus version 3.3 computer software and judged significant at the 0.05 percent level.

1.2.3 Forest Structural Characteristics

Each tree in each plot was measured for diameter (cm) at breast height (DBH) using calipers. Height of a dominant or codominant tree in each plot was measured using an hypsometer and measuring tape. Heights of remaining trees in the plot were estimated to the nearest metre. Each tree was recorded by species and whether dead or alive. Crown closure was estimated to the nearest percent using a densiometer, based on one reading at the centre of each plot. An average codominant tree was selected and aged using an increment core at each plot. A codominant tree was considered a tree whose crown forms the main level of the canopy while a dominant tree was considered a tree whose crown extends beyond the main level of the canopy.

Mean crown closure and mean age were calculated for each stand. Height and diameter measurements of each tree were used to calculate tree volume using Hubers formula (Husch 1982). A mean tree volume was then calculated for each stand. The percentage of basal area of dead trees sampled was calculated for each stand.

Spacing or mean distance between trees was calculated for each plot and each stand using prism tallies for each 2 cm diameter class. Each tree tallied in a plot was

placed in a diameter class. Total basal area for each diameter class in each plot was calculated and then divided by the basal area for a single tree for that diameter class in order to obtain the number trees per hectare per diameter class. This was then used to calculate mean spacing within each plot.

The amount of remnant trees for each stand was calculated by creating linear regression equations using diameter of each tree that was aged (n=180). Scatter plots of tree diameter against tree age for trees in both thinned and unthinned forests showed a strong linear relationship (Figure 1).

Tree diameter was used as the dependent variable and age was used as the independent variable. A regression equation was created for each of the thinned and unthinned stands. Regression equation calculated for trees in unthinned forests was:

$$\text{DBH} = 3.02 + 0.27 \times \text{Age}$$

$$r^2 = 0.67, t = 13.04, p = 0.001$$

Regression equation for trees in thinned forests was:

$$\text{DBH} = 7.31 + 0.27 \times \text{Age}$$

$$r^2 = 0.42, t = 5.67, p = 0.001$$

Using each regression equation, a diameter was calculated for a 100 year old tree. The number of trees sampled greater than the diameter of a 100 year old tree for each study site was used as the basal area of remnant trees.

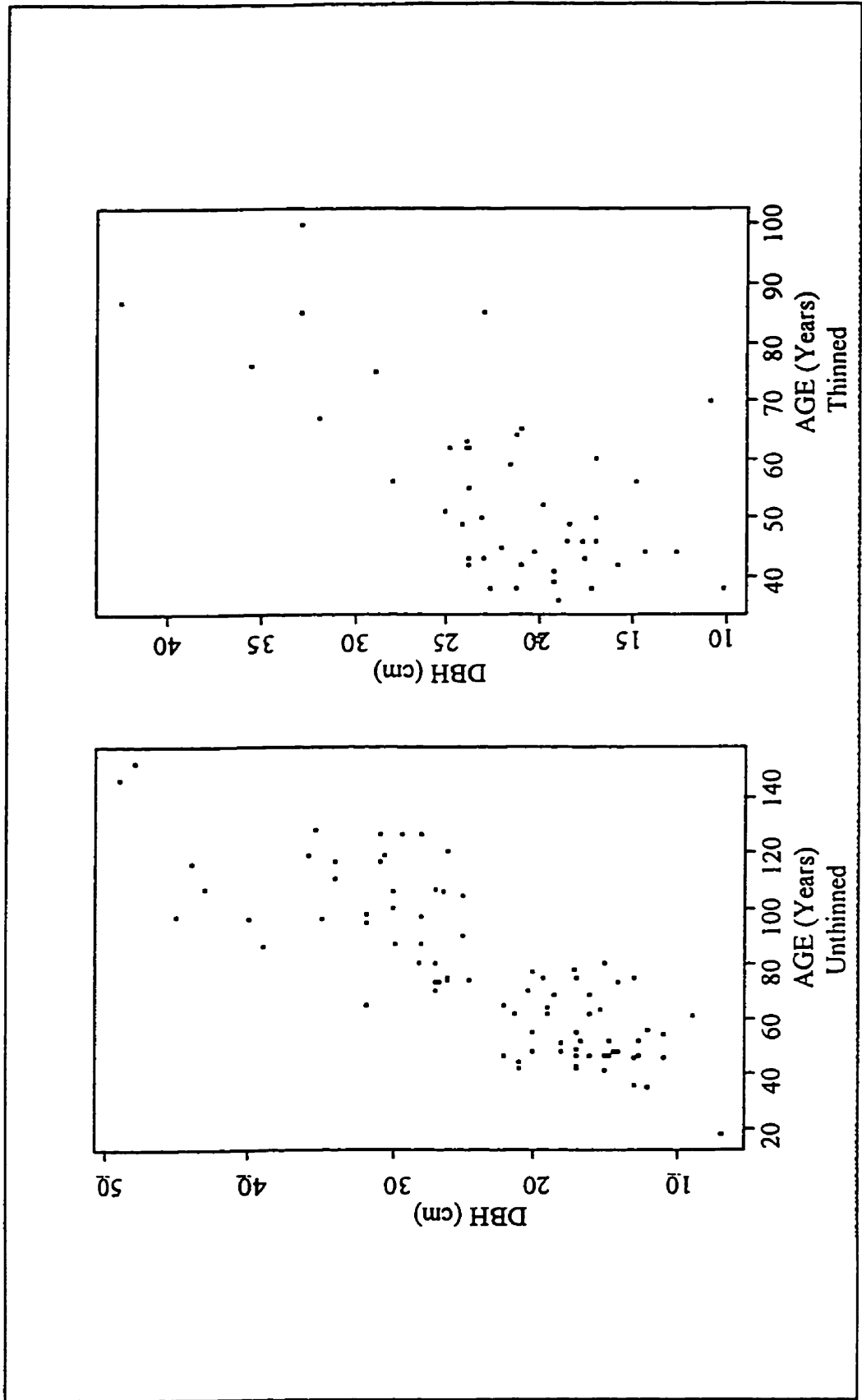


Figure 1 Scatter plots of age and diameter at breast height of trees in thinned and unthinned forests

2.0 Structure of Managed and Natural Forests in Nova Scotia

2.1 Introduction

Forest structure is an important feature in defining forest ecosystems. Clearly, the dominant feature of forests is trees. The competitive strategy of trees is to grow taller than other plants and thereby acquire necessary sunlight. As a result, forests have a vertical dimension not found in most other ecosystems. For example, tundra or prairie grassland have much less vertical stratification. Therefore, with an added vertical component, forest ecosystems become structurally complex. A useful definition of forest structure is "the various horizontal and vertical physical elements of the forest" (Dunster and Dunster 1996).

Forest structure in natural forests is a result of interactions of trees and can be somewhat anticipated (Oliver and Larson 1996). The patterns of species dominance and changes in stand structure develop through predictable stages after a large scale disturbance. The first stage in stand development occurs after a disturbance and is known as stand initiation. This stage is characterized by the appearance of new individuals and species and this usually occurs over several years. Stem exclusion stage occurs when some existing individuals die and surviving trees grow larger. The age at which this stage and the following stages occurs depends on the silvics of the tree species involved.

Understory reinitiation stage ensues as forest floor herbs, shrubs and tree regeneration appear. The final stage in stand development is known as old growth. Old growth happens much later when overstory trees die in an irregular pattern and understory trees begin to grow into the overstory.

There is a direct relationship between forest structure and biological diversity (Kimmins 1997). Some species are dependent on certain structural features. American marten (*Martes americana*) rely on vertical stem structure and downed woody debris for escape cover, thermoregulation and den sites. Marten populations are low in areas where appropriate structure is lacking (Sturtevant 1996). Red-backed salamander (*Plethodon cinereus*) are associated with depth of leaf litter (Pough 1987, DeGraaf and Rudis 1990). Cavity nesting birds rely on standing woody stems to provide nesting sites.

Forest structure also influences microclimate, which in turn influences presence of species (Hunter 1990). Light penetration to the forest floor is a function of stand density (Geiger 1980). In very dense forests only plant species that can tolerate low light levels will likely establish on the forest floor. Water vapour distribution is a function of wind speed which is affected by forest structure (Geiger 1980). Air moisture will influence presence of bryophytes and lichens (Topham 1977, Lawrey 1984).

Forest management practices change forest structure (Kouki 1994). Thinning increases spacing between trees and can change species content of a forest (Smith 1962).

Tree cutting practices can affect post cut successional structure (Hunter 1990, Keddy and Drummond 1996). For example, some studies have shown a difference in structure of forests that originated after a clearcut compared to forests originated from natural disturbances such as fire or hurricane (Heinselman 1981, Haila 1994, Haila and Kouki 1994, Syrjanen 1994, Rooney 1995).

Forest management practices tend to promote uniformity, reducing variation within stands (Haila 1994), resulting in less structural diversity than natural forests (Oliver and Larson 1996). Plantations, for example, tend to have trees of more or less the same size at equal distances apart. Further, certain structures can be reduced by forest management practices. For example, snag and cavity trees may be in short supply in managed forests (Mannon and Meslow 1984, Freedman 1994).

It has been suggested that forest management should imitate natural disturbances in order to maintain biological diversity (Hunter 1990, Hansen 1991, Rogers 1996). Because organisms have adapted to natural disturbances in forests, they may be less negatively impacted by timber harvests which resemble natural disturbances. Runkle (1991) suggested harvest openings in temperate deciduous forests be patterned after natural gaps from fallen trees. Hunter (1993) suggested that size and shape of harvest blocks in northern boreal forests be modelled after natural fires. In order to manage forests by imitating natural systems, more research is needed to determine how current forest management practices change forest structure. The objective of this section is to

determine if harvesting and thinning affect certain forest structural features.

2.2 Analyses

Principal components analyses using a correlation matrix were completed for mean crown closure, mean percent basal area of dead trees, mean tree spacing, mean stand age and mean basal area of remnant trees. Two biplots were then created using the first two principal components. The first biplot was created using all stands combined. The second biplot was created with natural climax stands excluded. Replotting without natural climax data provided better separation of other forest types.

To determine if significant differences occurred in structural variables between maturity class and stand origin, a multivariate 2 factor analysis of variance (MANOVA) was used. To determine if significant differences occurred in each structural variable, separately, between maturity class and stand origin, a series of single variate 2 factor analyses of variance (ANOVA) were used. Maturity class was one factor and stand origin was another factor in all 2 factor analysis of variance tests. To detect differences in tree volume, DBH, and tree height, a single factor analysis of variance using stand origin was used. Trees were used as the sampling unit for tests of tree volume, DBH and tree height. It is well known that there is a positive relationship between tree size and maturity. As there was no need to verify this increase statistically, a single factor test using stand origin only was used. A 2 factor ANOVA using origin and maturity class was used for all other

variables and stands were used as the sampling unit. Since dead trees per stand was calculated as a percentage, it was arcsine-square root transformed (Zar 1996). Basal area of remnants demonstrated heteroscedasticity in fitted vs residual plot and was logarithmically transformed (Zar 1996).

To compare structural variation between stand origin type, coefficients of variation were calculated for natural, harvested and harvested and thinned stands for tree height, DBH and volume.

2.3 Results

In the principal component analysis, components 1 and 2 explain 73% of the variance in forest structure (Figure 2). Component 1 provides a combination of crown closure, tree spacing, tree volume, basal area of remnant trees and tree age, with greatest loadings on the last 4 variables. Component 2 is most heavily loaded on percent basal area of dead trees and less on tree spacing, crown closure and tree age. Climax natural forests are widely separated from other forest types along component 1. Clear separation also occurs for harvested and thinned forests. This forest type is largely separated from other forest types along axis 2. This separation is largely due to the lack of dead standing trees found in harvested and thinned forests. Natural forest maturity classes show a clear separation along axis 1 indicating dead trees can distinguish maturity classes in this forest type. Natural forests show no separation in other structural variables except in the climax

stage. Both harvested and thinned and harvested forests show a separation among maturity class from lower left to upper right on the biplot (Figure 3). This indicates a combination of structural variables separate maturity classes in managed forests.

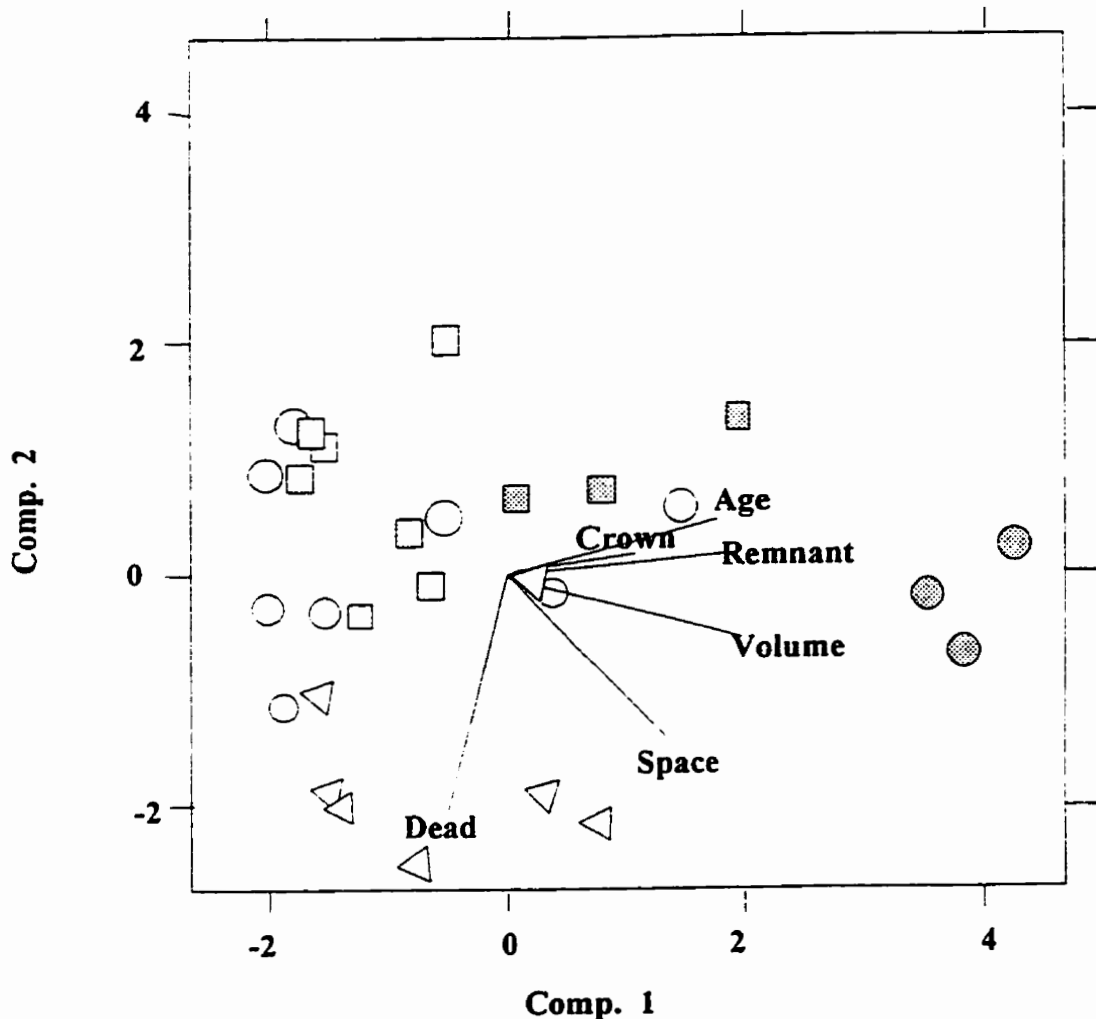


Figure 2. Biplot based on principal component analysis ordination of structural variables for all study sites. Structural variables are indicated by lines: dead=percent of basal area of dead trees, age=mean tree age, remnant=basal area of remnant trees, volume=mean tree volume, crown=mean crown closure, space=mean tree spacing. Site are indicated by symbol:
 ○ Pole stage natural forest; ○ Mature stage natural forest;
 ● Climax natural forest; □ Pole stage harvested forest;
 □ Mature stage harvested forest; ■ Climax stage harvested forest;
 ▽ Pole stage harvested and thinned forest; ▽ Mature stage harvested and thinned forest.

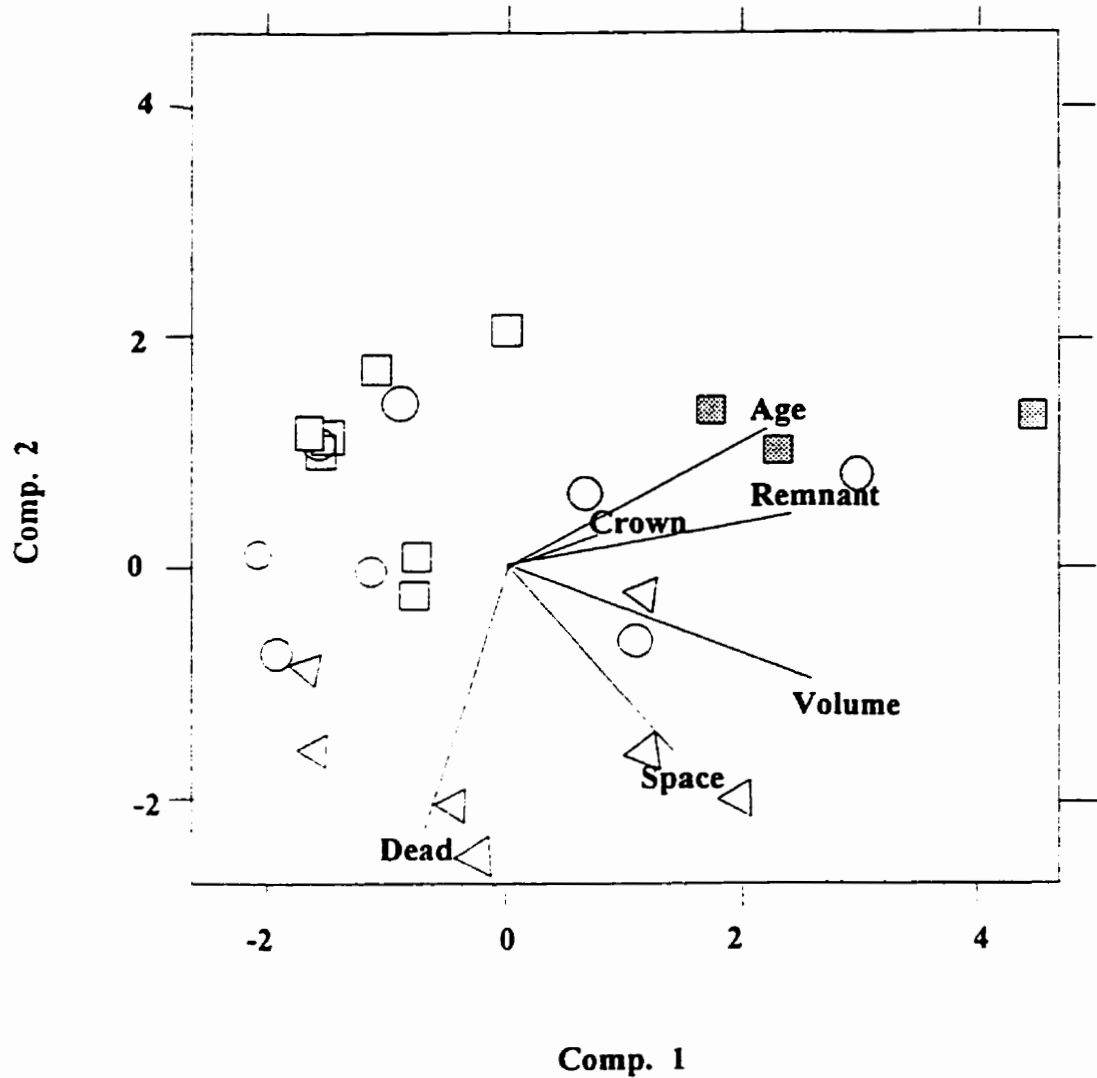


Figure 3. Biplot based on principal component analysis ordination of structural variables for all study sites except natural climax. Structural variables are indicated by lines: dead=percent of basal area of dead trees, age=mean tree age, remnant=basal area of remnant trees, volume=mean tree volume, crown=mean crown closure, space=mean tree spacing. Site are indicated by symbol:

○ Pole stage natural forest; ○ Mature stage natural forest;
 □ Pole stage harvested forest; □ Mature stage harvested forest;
 ▣ Climax stage harvested forest; ▽ Pole stage harvested and thinned forest;
 ▽ Mature stage harvested and thinned forest.

There were significant differences in stand variables between maturity classes (Pillai=0.95, $p=0.001$), and between origin type of forests (Pillai=1.07, $p=0.000$) (Table 2). Harvested and thinned forests have about half the percentage of dead trees of harvested and natural forests. Pole stage forests also have about half the percentage of dead trees as climax or mature forests. The percentage of dead trees increases with forest age although no significant difference was detected between climax and mature forests. Spacing and the number of remnants also increase with increasing maturity class although differences for spacing were not statistically significant. The amount of remnant trees had the only significant interaction between maturity class and origin type. Multiple range testing showed that climax natural forests had significantly greater basal area of remnant trees than harvested and thinned pole and natural pole forests. No other significant differences were detected between origin or maturity classes for remnant trees. Crown closure showed no significant difference between origin or maturity classes.

Table 2. Means of stand variables and results of 2 factor analyses of variance by origin type and maturity class. Ninety-five percent confidence intervals are indicated in brackets below mean values.

Variable	Origin Type			F (P)	Maturity Class			F (P)	Interaction
	Natural (n=11)	Harvested (n=10)	Harvested & Thinned (n=7)		Climax (n=6)	Mature (n=12)	Pole (n=9)		F (P)
Crown Closure	11.44 ¹ (1.5)	12.85 ¹ (1.5)	12.32 ¹ (1.5)	0.99 (0.389)	13.5 ¹ (1.9)	11.6 ¹ (1.3)	12.2 ¹ (1.6)	0.99 (0.389)	2.59 (0.090)
Dead (%)	12.3 ¹ (2.5)	11.8 ¹ (2.4)	6.4 ² (2.9)	13.65 (0.001)	13.7 ¹ (3.1)	12.1 ¹ (2.2)	7.0 ² (2.7)	11.00 (0.001)	2.78 (0.070)
Spacing (m)	2.2 ¹ (1.5)	1.7 ¹ (1.3)	3.0 ² (1.2)	10.43 (0.001)	3.8 ¹ (0.5)	2.9 ² (0.3)	3.6 ² (0.4)	0.00	0.74 (0.540)
Remnants	34.9 ¹ (10.3)	15.8 ¹ (9.7)	26.4 ¹ (11.6)	0.24 (0.793)	62.7 ¹ (12.6)	18.8 ² (8.9)	7 ³ (10.9)	12.34 (0.001)	3.85 (0.029)

^{1,2,3} indicate results of multiple range tests; results with the same superscript number (1,2 or 3) in a row indicate no significant difference.

Harvested forests had the lowest mean tree volume (Table 3), while natural and harvested and thinned forests showed no significant difference. Tree volume is a function of tree height and diameter. As there are no significant differences in tree heights between origin type, volume differences are primarily due to differences in DBH. DBH is significantly different between all origin types with harvested forests having the lowest mean value. A similar pattern is seen in spacing with harvested forests having the lowest value (Table 2). Spacing is greatest in harvested and thinned forests because these stands have been silviculturally thinned.

Table 3. Means of tree variables and results of single factor analysis of variance by origin type. All maturity classes were combined for analysis. Ninety-five percent confidence intervals are indicated in brackets below mean values.

Variable	Origin Type			F (P)
	Natural (n=252)	Harvested (n=184)	Harvested & Thinned (n=115)	
Tree Volume (cm ³)	11989 ¹ (223)	7044 ² (291)	8252 ¹ (269)	9.23 (0.000)
Tree DBH (cm)	24.9 ¹ (4.8)	20.9 ² (1.7)	23.7 ³ (2.2)	5.73 (0.003)
Tree Height (m)	14.8 ¹ (0.6)	14.7 ¹ (0.7)	14.6 ¹ (0.9)	0.057 (0.944)

^{1,2,3} indicate results of multiple range tests; results with the same superscript number (1,2 or 3) in a row indicate no significant difference.

The coefficients of variation of height, diameter and volume were greater in natural

forests than in either type of managed forest (Table 4).

Table 4. Coefficients of variation of structure variables by origin type.

Variable	Origin Type		
	Natural	Harvested	Harvested & Thinned
Tree Volume	1.38	1.03	0.91
Tree DBH	0.58	0.45	0.41
Tree Height	0.37	0.29	0.28

2.4 Discussion

Natural and managed forests have different structural features. The percentage of dead trees was significantly greater in natural forests than harvested and thinned forests. However, no significant difference in dead trees was found between natural and harvested forests. Fewer dead trees in thinned forests compared to natural forests has been previously described (Mannan and Meslow 1984, Freedman 1994). The amount of standing dead trees is reduced in thinned sites by cutting of dead, dying and diseased trees. Natural disturbances, such as wind events and fire, vary in intensity and often leave standing trees (Raphael 1983, Villard and Beninger 1993). The standing trees may be dead (killed by fire) or may die as they age and a new stand establishes. Trees scarred by fire provide a source of entry for fungi and may soon become infected and die (Oliver and

Larson 1996).

Other studies have found greater amounts of dead wood in natural forests compared to unthinned managed forests (Hansen 1991, Syrjanen 1994, Keddy and Drummond 1996). A non-significant difference in percentage of dead standing trees between natural and unthinned managed forest in this study may be a result of past cutting practices in Nova Scotia. Tree harvesting in the past was often done by selection or patch cutting in which remnants and dead trees were left (Johnson 1986). Current harvesting practices in Nova Scotia have changed and may not be fully reflected in this study.

Many forest dwelling species are dependent on dead wood. Standing dead wood is particularly important to cavity nesting birds. As snags fall to the ground they become important habitat for many other species. There has been increasing concern over the loss of dead wood in managed forests and this study supports the need to consider providing dead wood in managed forests.

Greater variation in tree size of natural forests compared to managed forests reflects greater heterogeneity of forest structure. Lesica *et al.* (1991) indicated old growth forests in Montana had greater variation in tree height and diameter than managed forests. Variation in the intensity of a natural disturbance across a landscape can result in variation in structural features. Snags and remnant trees surviving a fire provide shade, favouring regeneration (Oliver and Larson 1996). Remnants will likely be patchy in distribution

depending on how many remnants remain. Wind events also may result in some trees being left standing. Uprooting of trees after a wind storm increases nutrient release and aeration of the soil, favouring regeneration in patches (Runkle 1985). Fallen trees cause mounded microrelief, creating heterogeneity of microsite, which leads to differential growth rates (Oliver and Larson 1996). Runkle (1985) described how differential growth rates are an important feature of natural disturbance.

Forest management practices promote uniformity. A forest simulation model run by Urban and Smith (1962) showed a reduction in variation of forest structure after thinning and selective logging.

Diameter growth of trees is density dependent and is therefore affected by tree spacing. As a result, there is a similar pattern of spacing between origin types as was found for diameter. Harvested forests had the lowest mean spacing. Harvested and thinned forests have a wide spacing because they have been silviculturally thinned. Differences in spacing between natural and harvested forests may be attributed to normal variation within natural forests. The patchy nature of natural forests results in areas with high tree density and areas of low tree density. This would result in a mean spacing somewhere between densely spaced as found in harvested forests and openly spaced as found in harvested and thinned forests.

Although natural forests had the greatest number of old remnants the difference

among maturity classes were not significant. Mannon and Meslow (1984) found a greater number of old remnants in old growth forest than in managed forest in Oregon. Confidence intervals for amount of remnants in this study are very large and reflect the high variation found in forests of all origin types. Remnants, particularly in younger stands, tend to be scattered and sampling intensity may have been underestimated remnants in some study sites. Mannon and Meslow (1984) used 15 sampling points with a fixed area circular plot of 0.05 ha. They also used counts of trees rather than basal area. The six plots used in this study may be inadequate to show differences. Prism tallies provide rapid measurement, but, counts in fixed area plots may be less variable.

There was no significant difference in crown closure between forest types. Lesica *et al.* (1991) found lower crown closure in second growth than old growth forest in Montana. Thinning can reduce crown closure but this effect is only temporary. Crowns quickly expand, filling in spaces created by cut trees (Smith 1962). Crown closure can be a measure of the occupation of an area by trees (Canadian Forest Service 1995). Lesica's study may have varying degrees of occupation of area by trees. This study indicates all origin types are occupied to the same degree by trees and that this is relatively unaffected by forest management practices.

Crown closure was relatively constant across all maturity classes in all origin types. Newton and Weetman (1994) suggest black spruce in eastern Canada achieve full crown closure as early as 10 years old at a density of 15000 stems per hectare on good quality

sites. Aplet (1989) found that leaf area remained constant despite changes in size class structure in a spruce-fir forest in Colorado. As trees died, leaf area in spruce increased in the remaining trees, then to younger trees as spruce reinitiation occurred. The process of maintaining crown closure as forests mature appears unaffected by harvesting and thinning, even after tree density reducing events like silvicultural thinning.

There is a trend of increasing percentage of dead trees and spacing with increasing maturity class for all origin types. Mannan (1980) found that the number of dead trees increased with forest age in Oregon. Hansen (1991) described a study in Oregon and Washington which found snag density was negatively associated with stand age in natural forests. However, density of snags greater than 50 cm DBH was significantly greater in old growth forests than mature or young forests. Spies (1988) found the number of dead trees greatest in young and old forests and least in mature forests. Like Hansen (1991), Spies (1988) found an increase in the number of large diameter snags from young to old. Coarse woody debris in younger forests is dependent on the pre-initiation disturbance (Spies 1988). If a fire is very severe, or harvesting removes most tree stems, then fewer snags would be available in the next developing forest. Oliver (1981) describes an increasing mortality of trees from the stem exclusion stage to old growth. Then as trees die in a forest, density of trees decreases and spacing increases. This results in a trend of increasing dead trees and spacing as stands age.

Similar to the trend of increasing dead trees and spacing as forest ages, there is a

trend of increasing number of remnants from youngest to oldest forest for all origin types. Hansen (1991) indicated a positive association between abundance of large trees and forest age.

The trend of increasing percent dead, amount of remnants, and spacing from youngest to oldest forests is seen for all forest types. However, principle components analysis indicated that maturity classes separate differently depending on origin types. Natural forests change only in percentage of dead wood over time, while managed forests show differences in all structural features. Structural features other than dead wood appear to show great change only upon reaching the climax stage in natural forests. It may be that harvesting and thinning alter how forests develop as they age. Oliver and Larson (1996) suggest that the pattern of stand development is unaffected by silvicultural practices. They were addressing temperate forests in general. However, various types of temperate forests likely develop in distinct ways and therefore may be affected by forest management practices differently.

Harvesting and thinning seem to affect certain structural features. Evidence suggests that the number of dead trees, number of remnants and structural heterogeneity are reduced by harvesting and thinning. Harvesting and thinning may also alter the pattern of stand development for some forest stand types.

3.0 Occurrence of, and Habitat Features Associated with, some Species of Epiphytic Lichens in Nova Scotia

3.1 Introduction

For many forest lichens, little is known beyond the biology needed for taxonomic classification. Habitat features favoured by lichen species have received little attention. However, lichens form a significant portion of forest flora (Gustafsson and Eriksson 1995). There are estimated to be over 2500 species of lichen in Canada, many of which are associated with forest habitat (Goward 1998). Lichens were found to be a major component of forests in the Pacific Northwest (McCune 1993) and New England (Lang 1980). Culberson (1955) found that lichens and bryophytes were by far the most important component of bark vegetation in northern Wisconsin forests. McCune and Antos (1981) found that species richness was greatest in the epiphytic and bryoid layer than any other vegetation component in Swan Valley Montana.

The roles of lichens in forest ecosystems is beginning to be understood. For example, lichens are important in nutrient cycling, as a food source, and serving as habitat for other organisms. Epiphytic lichens acquire nutrients through nitrogen fixation and interception of aerosols, becoming a source of stored nutrients. Minerals are released to the forest environment by litter fall and leaching (Pike 1978). Denison (1973 in Tansey 1977) suggested that nitrogen-fixing lichens can serve as the main pathway for new

nitrogen in the ecosystem of old growth douglas-fir forests. Rock contribute to ecosystems by releasing minerals from rock weathering and soil lichens through soil development. Sendstad (1981) found that removal of lichen ground cover in Norway resulted in a decrease in the soil content of organic matter and macronutrients.

Lichens can provide an important food source for ungulates. Hodgeman and Bowyer (1985) found that arboreal lichens are an important winter forage for white-tailed deer (*Odocoileus virginianus*) in Maine. Sharnoff (1994) suggested that lichens can form a significant portion of the diet of at least 7 species of ungulates in North America.

Lichens increase the diversity of invertebrate fauna in forests by providing habitats. Pettersson (1996) found that lichen rich forest in Sweden had 3 times more spiders on tree branches than did lichen poor forests. Stubbs (1989) found significant correlation between lichen biomass and Arthropoda, Tardigrada and Rotifera abundance in oak forests in Maine.

Human impact in forest environments is increasing and natural forests are disappearing. Activities like silvicultural thinning or clearcutting change structural features of forests. Acid rain, pollution and recreational use of forests may also impact lichens. Greater understanding of occurrence and habitat features of lichens is required to aid in their conservation in managed forests.

Factors affecting lichen diversity and abundance are complex (Gustafsson and Eriksson 1995). Both microhabitat and macrohabitat features have been found to affect lichen presence and abundance. For example, substrate has been indicated as important. Gustafsson and Eriksson (1995) found that tree bark chemistry was of importance to several species of lichens on aspen trees in Sweden. Flaking bark provides an unstable substrate for epiphytic lichens (Sheard and Jonescu 1974), while rough bark may increase moisture retention and provide a favourable substrate (Jesberger and Sheard 1973). Light and moisture play a significant part in determining lichen abundance. Rose (1992) suggested the growth of some canopy lichens is limited by low moisture and light in young forests. Gauslaa and Solhaug (1996) found that increased light exposure was detrimental to some forest lichens and the impact varied depending on whether the thalli were hydrated or not.

Oksanen (1988) found that habitat (next to location on tree bole) was the second most important factor in explaining variation in lichens in Finland. He found clear separation of lichens into 6 habitat types: xeric, mesic, nemoral, mire, shore and man-influenced. Oksanen also reported findings from other studies in Europe which found differences in lichens within even finer habitat classifications. In comparing lichen species in western North American forests, Eversman (1982) found different lichen species in different coniferous forest types. Sheard and Jonescu (1974) found lichen species abundance varied with forest structural characteristics such as tree density and tree size in west-central Canada. Jesberger and Sheard (1973) found lichen communities varied with

canopy closure in Saskatchewan forests. However, we are just beginning to understand lichen habitat requirements.

The purpose of this section is to document occurrence of some epiphytic lichens in temperate softwood forests and to try to determine which micro and macrohabitat features of forests that influence lichen presence or abundance. This section examines both individual lichen species and how they relate to habitat, as well as the spruce forest lichen community and how the community relates to habitat.

3.2 Lichen Species

3.2.1 Analyses

Analyses for individual lichen species were done on two levels. Tree level analysis was done relating lichen abundance per tree for each lichen species to tree variables (tree species, dead or alive, tree volume) and to plot variables (tree age, crown closure, amount of remnants, tree spacing). Stand level analysis related mean lichen abundance per stand to mean stand variables (percentage of dead trees, amount of remnants, tree spacing, crown closure, tree age, tree volume). Three stands could not be included in regression analyses, because they were harvested or partially harvested before all independent variables could be measured. *Usnea* species were combined because of low abundance of individual species. For each lichen species, the frequency of occurrence by tree and stand

were calculated. Frequency was calculated as the percent of the total number of trees (n=690) and stands (n=30).

3.2.1.1 Tree Level Analyses

One tree from each plot was selected at random for multiple linear regression analyses to determine which variables best explain the tree abundance for 14 species of lichens. Stepwise multiple linear regression with a forward selection process was used. Only 14 of the 34 lichen species surveyed had a high enough abundance to perform regression analyses (Table 6). The abundance for each species of lichen on each tree was used as the dependent variable. Tree species or tree type (*Picea* spp., *Pinus strobus*, *Abies balsamea*, *Tsuga canadensis*, hardwood), whether the tree was alive or dead, and tree volume for each selected tree, and crown closure, age, spacing and number of remnants per plot were used as independent variables. Regression analysis was repeated 5 times for each lichen species using a new randomly selected tree. Repeated regression analysis on different trees within the same plot was done to increase the probability of using representative trees.

3.2.1.2 Stand Level Analyses

Multiple linear regression was used to determine which variables best explained

total lichen abundance per stand for the same 14 species of lichen (Table 7). Stepwise multiple linear regression with a forward selection process used. Stand variables used in the regression analyses were mean tree volume, mean crown closure, percent basal area of dead trees, mean spacing, basal area of remnants and mean age per stand. Analyses were not done on the other 20 lichen species sampled because of low abundance.

3.2.2 Results

Hypogymnia physodes was the most common species in study sites (Table 5).

This species occurred in all study sites, had the highest mean percent cover and occurred on more trees than any other species. *Platismatia glauca*, *Loxospora elatina*, *Lopadium disciforme*, and *H. physodes* all occurred on over 50% of the trees surveyed and occurred in all study sites.

The least commonly occurring species was *Pseudocyphellaria crocata* which was found only once. *Chaenotheca chrysocephala*, *H. tubulosa*, *P. crocata*, *Usnea strigosa* and *Xylographa* species had tree frequency occurrences of less than 1%, or occurred on less than 6 trees.

Table 5. Tree and stand frequency for each lichen species. Frequency is percent of total number of trees (n=690) and stands (n=30). Nomenclature follows Egan (1991).

Species	Tree frequency	Stand frequency
<i>Alectoria sarmentosa</i> Ach.	15	61
<i>Bryoria capillaris</i> Ach.	11	50
<i>Bryoria furcellata</i> Fr.	16	86
<i>Bryoria fuscescens</i> Gyelnik	51	96
<i>Bryoria nadvornikiana</i> Gyelnik	29	89
<i>Bryoria trichodes</i> Michaux	9	54
<i>Calicium parvum</i> Tibell	5	39
<i>Chaenotheca chrysocephala</i> Ach.	0.6	11
<i>Hypogymnia physodes</i> Nyl.	85	100
<i>Hypogymnia krogiae</i> Ohlsson	7	39
<i>Hypogymnia tubulosa</i> Schaerer	0.7	11
<i>Lepraria finkii</i> B. de Lesd.	28	89
<i>Lobaria pulmonaria</i> Hoffm.	3	46
<i>Lobaria quercizans</i> Michaux	3	43
<i>Lobaria scrobiculata</i> Scop.	1	29

Species	Tree frequency	Stand frequency
<i>Lopadium disciforme</i> Flotow	64	100
<i>Loxospora elatina</i> Ach.	67	100
<i>Loxospora ochrophaea</i> Tuck.	49	96
<i>Mycoblastus sanguinarius</i> L.	6	29
<i>Ochrolechia androgyna</i> Hoffm.	16	79
<i>Parmelia sulcata</i> Taylor	43	89
<i>Pertusaria amara</i> Ach.	11	75
<i>Platismatia glauca</i> L.	76	100
<i>Platismatia tuckermanii</i> Oakes	16	46
<i>Pseudocyphellaria crocata</i> L.	0.1	4
<i>Ramalina thrausta</i> Ach.	3	5
<i>Sphaerophorus globosus</i> Huds.	7	25
<i>Thelotrema lepadinum</i> Ach.	3	11
<i>Usnea lapponica</i> Vainio.	4	43
<i>Usnea longissima</i> Ach.	5	25
<i>Usnea rubicunda</i> Stirton	3	29
<i>Usnea strigosa</i> Ach.	0.3	7
<i>Usnea trichodea</i> Ach.	6	39
<i>Xylographa</i> spp. Fr.	0.4	11

3.2.2.1 Tree Level Analyses

Tree age, remnant trees, tree volume, crown closure and tree spacing were selected in regression equations repeatedly for most species of lichen (Table 6). Trees species and dead trees were much less useful in predicting abundance of lichens on trees.

Table 6. Variables from regression equations that best predict abundance of 14 species of lichen on trees. Number of times a variable was selected out of 5 regression analyses and r-squared are indicated.

Species	Variable	Number of times significant	r ²
<i>Alectoria sarmentosa</i>	age	3	0.10, 0.17, 0.11
	white pine	2	0.17, 0.62
	remnants	2	0.62, 0.57
	eastern hemlock	1	0.11
<i>Bryoria fuscescens</i>	age	3	0.12, 0.16, 0.14
	volume	3	0.12, 0.16, 0.49
	hardwood	1	0.16
	crown closure	1	0.49
	remnants	1	0.57
	red spruce	1	0.14

Species	Variable	Number of times significant	r ²
<i>Bryoria nadvornikiana</i>	remnants	5	0.12, 0.13, 0.13, 0.41, 0.48
	spacing	3	0.12, 0.13, 0.13
	white pine	3	0.12, 0.13, 0.57
<i>Hypogymnia physodes</i>	hardwood	1	0.18
	crown closure	2	0.18, 0.05
	balsam fir	1	0.18
	percent dead trees	1	0.18
	red spruce	1	0.08
	age	3	0.08, 0.61, 0.60
<i>Lepraria finkii</i>	crown closure	3	0.14, 0.20, 0.12
	volume	2	0.20, 0.12
	age	1	0.14
	remnants	1	0.20
	hardwood	1	0.20
<i>Lopadimum disciforme</i>	spacing	1	0.11
	age	1	0.11
	eastern hemlock	2	0.11, 0.50
	volume	1	0.03
	crown closure	1	0.58
	remnants	1	0.50

Species	Variable	Number of times significant	r ²
<i>Loxospora elatina</i>	crown closure	5	0.14, 0.09, 0.10, 0.41, 0.49
	hardwood	2	0.14, 0.10
	red spruce	1	0.09
	white pine	1	0.49
<i>Loxospora ochrophaea</i>	crown closure	4	0.11, 0.18, 0.13, 0.61
	red spruce	2	0.18, 0.14
	age	1	0.66
	white pine	1	0.61
<i>Ochrolechia androgyna</i>	eastern hemlock	2	0.11, 0.61
	white pine	1	0.11
	age	1	0.07
	spacing	1	0.40
	crown closure	1	0.61
	volume	1	0.01
<i>Platismatia glauca</i>	hardwood	3	0.14, 0.11, 0.10
	age	4	0.14, 0.11, 0.10, 0.29
	spacing	2	0.14
	volume	1	0.14
	white pine	1	0.11
	crown closure	1	0.29
	hardwood	1	0.29

Species	Variable	Number of times significant	r^2
<i>Parmelia sulcata</i>	volume	1	0.03
	red spruce	2	0.06, 0.16
	spacing	1	0.42
	balsam fir	1	0.16
<i>Pertusaria amara</i>	volume	2	0.04, 0.06
	hardwood	1	0.06
	white pine	1	0.05
	white pine	1	0.42
<i>Usnea spp.</i>	remnants	2	0.04, 0.05
	volume	1	0.06

3.2.2.2 Stand Level Analyses

Abundance of 14 species of lichen was great enough to allow regression analyses (Table 7). Abundance of *A. sarmentosa*, *B. fuscescens*, and *Loxospora ochrophaea* increased as the percent basal area of dead trees increased in the stand. *A. sarmentosa*, *B. fuscescens*, *B. nadvornikiana* and *H. physodes* abundance increased with increasing age of trees in the stand. Basal area of remnant trees was retained as a predictor of abundance of *B. nadvornikiana*, *Lepraria finkii.*, *Mycoblastus sanguinarius*, *Ochrolechia androgyna*, and *Usnea* species. All correlations with remnant trees were positive except for *B. nadvornikiana*, which decreased in abundance as the amount of remnant trees increased in the stand. A negative correlation with crown closure and lichen abundance was found with *H. physodes*, *Loxospora elatina*, *Loxospora ochrophaea*, and *Usnea* species. No relationship was found between stand variables and abundance of *Platismatia glauca* , *Platismatia tuckermanii* and *B. furcellata*.

Table 7. Results of stand level regression analyses, showing variables that best predict abundance of lichens in stands. Included are t-value, probability, and sign for each significant variable and r^2 for the regression equation. Sign indicates whether a positive (+) or negative (-) correlation occurs between lichen abundance and the structural variable.

Species	Variable	t-value	p	sign	r^2
<i>Alectoria sarmentosa</i>	age	2.94	0.007	+	0.42
	dead	2.44	0.022	+	0.42
<i>Bryoria fuscescens</i>	age	2.89	0.008	+	0.40
	dead	2.27	0.032	+	0.40
<i>Bryoria nadvornikiana</i>	age	3.03	0.006	+	0.28
	remnants	2.08	0.048	-	0.28
<i>Hypogymnia physodes</i>	age	2.03	0.053	+	0.29
	crown	0.01	0.007	+	0.29
<i>Lepraria finkii</i>	remnants	4.96	0.000	+	0.49
<i>Loxospora elatina</i>	crown	4.40	0.000	-	0.43
<i>Loxospora ochrophaea</i>	crown	4.37	0.000	-	0.53
	dead	2.48	0.020	+	0.53
<i>Mycoblastus sanguinarius</i>	remnant	3.46	0.002	+	0.32
<i>Ochrophaeum androgyna</i>	remnant	3.71	0.014	+	0.34
<i>Pertusaria amara</i>	remnant	3.28	0.003	+	0.29
<i>Usnea spp.</i>	remnant	3.47	0.002	+	0.33
	crown	2.11	0.045	-	0.33

3.2.3 Discussion

Tree age was selected as a predictor of abundance at the stand level for *Alectoria sarmentosa*, *Bryoria fuscescens*, *B. nadvornikiana* and *Hypogymnia physodes*. All correlations show increasing abundance of lichens with increasing tree age. It has been consistently demonstrated that lichen biomass increases with increasing forest age (Lang 1980, McCune and Antos 1981, McCune 1993, Goward 1994, Sillett and Neitlich 1996). Higher diversity and biomass of lichens in older forests has been attributed to a greater diversity of structural components in older forests (Lesica *et al.* 1991). Certain species of lichens are known to be associated with certain forest successional stages (Yarranton 1972, Topham 1977, McCune 1993, Goward 1994). *Alectoria sarmentosa* was found more often in old growth forests and is likely a late successional species. Both *Alectoria sarmentosa* and *Bryoria fuscescens* were found in significantly greater abundance in older forests than younger forests in this study (Section 3.3.3).

Tree age at the plot level was also a consistent predictor of lichen abundance for many of the same lichen species as at the stand level. Repeated regression analyses using abundance of *A. sarmentosa*, *B. fuscescens*, *H. physodes* and *Platismatia glauca* resulted in tree age being selected in at least 3 regression equations for each species. All correlations are positive. The older the tree the longer the period available for colonization and growth of lichens. It is also likely that many of the factors which influence lichen abundance at the stand level, such as structural diversity, also influence

lichen abundance at the plot level.

Crown closure was selected as a predictor of abundance of several species of lichen both at the plot and stand levels. This is supported by other reports that sunlight affects many species of lichen and crown closure directly affects the amount of sunlight reaching the interior forest. Gowan and Brodo (1988) suggested that *Loxospora ochrophaea* occurs in open habitats in New Brunswick. Topham (1977) indicated that *Loxospora* species in general, out compete other lichen species for sun lit habitats. Gowan and Brodo (1988) also suggested that *Usnea lapponica*, *U. longissima*, *U. rubicunda* and *U. strigosa* all occur in open habitats in New Brunswick.

The positive association between *H. physodes* and stand abundance and crown closure, indicates *H. physodes* is found in higher abundance in shady habitat. However, *H. physodes* is cited as occurring in sunny open conditions in Sweden (Gusstafsen and Erikson 1995). Tree level regression analyses from this study also suggest *H. physodes* is found in higher abundance in open canopy habitat. However, *H. physodes* was found in greatest abundance in young forests in this study. Younger forests tended to have more uniform canopy cover and fewer openings. It is possible that the association between *H. physodes* abundance and canopy cover is reflective of *H. physodes* favouring younger stands that happen to have more dense tree canopies.

A positive correlation at the plot level between abundance of *Lepraria finkii* and

crown closure indicates that *Lepraria finkii* is found in shaded habitat. However, as no correlation was found at the stand level, *Lepraria finkii* may be more sensitive to microhabitat than macrohabitat. This is consistent with known microhabitat preferences of *Lepraria* species. Goward (1996) reported that *Lepraria* species occur on sheltered bases of tree boles. This suggests that *L. finkii* could be found in forests with a relatively open canopy provided there are sheltered micro environments suitable for *L. finkii* within the forest.

Abundance of several species of lichen increases as the amount of remnants increased in forests both at the stand and plot level. Neitlich and McCune (1997) found 25 to 40% more epiphytic lichen species in plots with gaps or old growth remnants than in other plots in Oregon. Peck and McCune (1997) found cyanolichen biomass was positively related to the number of remnant trees present in forests in Oregon. Dispersal can be limiting for some lichen species (Sillet and Neitlich 1996). Stevenson (1988) found that establishment of some lichens was dependent on the distance to the nearest mature timber. Remnant trees with vestigial lichens from the previous forest may enhance dispersal in young forests. Presence of remnant trees may also affect microclimate in young forests, by providing shade and wind protection and reducing extremes in microclimate within the forest.

Several lichen species increased in abundance at the stand level as the amount of dead wood in the forest increased, however no relationships with amount of dead wood

were found at the plot level. Lichen species with a positive correlation with amount of dead wood (*Alectoria sarmentosa*, *Bryoria fuscescens*, *Loxospora ochrophaea*) were found occasionally on dead wood but mostly on live trees. It is likely these lichen species are responding to some features associated with dead trees in stands, such as gaps in the canopy. Neitlich and McCune (1997) found that lichen species richness correlated with occurrence of forest gaps in their study plots in Oregon. Gaps provide areas of increased sunlight, favouring species like *Loxospora ochrophaea* which inhabit sun lit areas.

Tree species was a poor predictor of epiphytic lichen abundance. Study sites were selected to be dominated by spruce and therefore had little variation in tree species on which the lichens occurred. This may be the reason for tree species being a poor predictor of lichen tree abundance.

Several structural features of forests seem to influence lichen abundance. These include tree age, crown closure, dead wood and remnant trees. Forests with older trees and gaps in the canopy are likely to have a greater diversity of lichens. Some features may favour certain species over others. For example, open canopy stands may favour *Loxospora* species while closed canopy stands may favour *Lepraria finkii*. Stands with a diversity of structural components are likely to support a higher species richness of lichens.

3.3 Lichen Communities

3.3.1 Analyses

To detect differences in abundance by origin type or maturity class for 26 lichen species or species groups (Appendix I). A 2 factor analysis of variance (ANOVA) was used. Maturity class was one factor and stand origin was another factor in the tests. Eight lichen species, of the total 34 species, did not occur frequently enough to allow testing. *Lobaria* species were combined because of low abundance of individual species. Trees were used as the sampling unit for abundance tests.

Species richness was calculated as the total number of lichen species present in each study site, of the 34 species searched for. Shannon-Wiener diversity index (Krebs 1989) was also calculated for each study site. Total lichen abundance was calculated by adding the abundances of all lichen species on all sampled trees for each site. Lichen abundance calculation does not provide an actual abundance of lichens but does provide an index of abundance.

To detect differences in species richness, Shannon-Wiener diversity index, and total lichen abundances between stand origin or maturity class, a 2 factor analysis of variance (ANOVA) was used.

Species richness and Shannon-Wiener indices were tested using stands as the sampling units as it was felt that harvesting and thinning are more likely to affect these indices at the stand level.

Three stands were removed from the 2 factor ANOVA tests because they were different from the other naturally disturbed stands: 3 of the 6 pole class naturally disturbed stands, all naturally disturbed mature class stands and at least 1 of 3 climax naturally disturbed stands were of fire origin, while the 3 rejected pole class stands were of hurricane origin.

To determine if natural disturbance type affects lichens, comparisons against hurricane origin sites were performed in a separate analysis. A single factor ANOVA was used to detect differences in species richness, Shannon-Wiener indices and lichen abundances in the pole class only. Tests were performed between hurricane origin, wildfire origin, harvested and harvested and thinned stands.

3.3.2 Results

Twenty-seven of the 34 lichen species show significantly higher abundance in, or occurred only in, natural forests compared to managed forests (Table 8, Appendix I). Seventeen of the twenty-seven, showed a significant interaction effect indicating differences between origin type vary with maturity class. Multiple range testing showed

that of the seventeen species with significant interactions, eleven species showed no significant difference between natural and harvested climax stands. Four of the seventeen with significant interaction effects, showed no significant differences between harvested and harvested and thinned stands. Two species showed no significant differences between pole class stands.

Two species (*U. strigosa*, *P. crocata*) occurred so infrequently that no trend could be discerned. No lichen species showed higher abundance in harvested and thinned forests, although 11 species showed significantly higher abundance in unthinned forests compared to thinned forests (Appendix I). *B. nadvornikiana* showed highest abundance in harvested forests.

Table 8. Lichen species with significantly greater abundance or occurring only in natural forests compared to managed forests. * indicates a lichen species that occurred only in natural forests.

<i>Alectoria sarmentosa</i>	<i>Mycoblastus sanguinarius</i>
<i>Bryoria capillaris</i>	<i>Ochrolechia androgyna</i>
<i>Bryoria furcellata</i>	<i>Parmelia sulcata</i>
<i>Bryoria fuscescens</i>	<i>Pertusaria amara</i>
<i>Bryoria tricodes</i>	<i>Platismatia tuckermanii</i>
<i>Calicium parvum</i>	<i>Ramalina thrausta</i>
<i>Chaenotheca chrysocephala</i> *	<i>Sphaerophorus globosus</i>
<i>Hypogymnia physodes</i>	<i>Usnea lapponica</i>
<i>Hypogymnia krogiae</i>	<i>Usnea longissima</i> *
<i>Hypogymnia tubulosa</i> *	<i>Usnea rubicunda</i> *
<i>Lepadium disciforme</i>	<i>Usnea tricodes</i>
<i>Loxospora elatina</i>	<i>Thelotrema lepadium</i> *
<i>Loxospora ochrophaea</i>	<i>Xylographa spp.</i> *

Eleven species of lichen showed significantly higher abundance or occurred only in climax forests (Table 9). *Bryoria furcellata*, *Parmelia sulcata* and *Platismatia tuckermanii* showed significantly greater abundance in pole forests (Appendix I). *Lobaria* spp., *Usnea lapponica*, *Usnea rubicunda*, *Platismatia glauca*, and *Lepadium disciforme* showed no association with maturity class.

Table 9. Lichen species with significantly greater abundance in, or occurring only in, climax forests compared to other maturity classes. * indicates a lichen species that occurred only in climax forests.

<i>Bryoria capillaris</i>	<i>Pertusaria amara</i>
<i>Bryoria fuscescens</i>	<i>Thelotrema lepadium</i> *
<i>Bryoria nadvornikiana</i>	<i>Ramalina thrausta</i> *
<i>Lepraria finkii</i>	<i>Sphaerophorus globosus</i>
<i>Mycoblastus sanguinarius</i>	<i>Usnea longissima</i>
<i>Ochrolechia androgyna</i>	

Natural forests had significantly greater total lichen abundance, number of lichen species and lichen diversity than either type of managed forest (Table 10). Natural forests had over twice the abundance of lichens found in harvest and thinned forests and 63 percent greater abundance than was found in harvested forests. Species richness and diversity of lichens were over 20 percent greater in natural forests compared to harvest and thinned and over 10 percent greater compared to harvested forests. Total lichen abundance and species richness showed a significant interaction affect in 2 factor ANOVA tests. Multiple range testing showed that no significant difference occurred between climax harvested and climax natural forest stands for total abundance and species richness.

Pole age forests had the lowest total abundance, number of species and diversity of lichens of the 3 maturity classes. Although, multiple range testing revealed that no significant difference occurred in total abundance between natural pole and natural climax stands. There was a 38 percent increase in species richness and a 33 percent increase in

abundance of lichens from youngest to oldest forest stands. While number of species and total lichen abundance show no significant difference between climax and mature forests, a significant difference is shown in the Shannon-Wiener diversity index.

Table 10. Mean species richness, Shannon-Wiener indices and total abundance of lichens compared in 2 factor analysis of variance by origin type and maturity class. Confidence intervals are indicated in brackets below mean values.

	Origin Type			F (P)	Maturity Class			F (P)	Interaction
	Natural	Harvested	Harvested & Thinned		Climax	Mature	Pole		F (P)
Species Richness	4.7 ¹ (0.28) n=10	4.0 ² (0.28) n=10	3.4 ³ (0.33) n=7	20.43 (0.001)	4.7 ¹ (0.36) n=6	4.3 ¹ (0.26) n=12	3.4 ² (0.30) n=9	19.21 (0.001)	4.74 (0.010)
Shannon Wiener	3.9 ¹ (0.19) n=10	3.5 ² (0.19) n=10	3.2 ² (0.23) n=7	11.90 (0.001)	4.0 ¹ (0.25) n=6	3.6 ² (0.17) n=12	3.3 ³ (0.20) n=9	11.90 (0.001)	0.22 (0.880)
Total Abundance	16.8 ¹ (0.73) n=236	10.3 ² (0.73) n=236	7.3 ³ (0.86) n=167	152.09 (0.001)	13.1 ¹ (0.94) n=141	12.9 ¹ (0.66) n=284	9.8 ² (0.76) n=214	22.09 (0.001)	16.29 (0.001)

^{1,2,3} indicate results of multiple range tests: results with the same superscript number (1,2 or 3) in a row indicate no significant difference.

No significant difference was detected in species richness and Shannon-Wiener indices between origin type in pole forests (Table 11). Total abundance was greatest in fire origin forests, followed by hurricane origin then harvested and harvested and thinned forests. Six lichen species showed no difference between hurricane and fire origin stands, although they were significantly lower in abundance in managed stands than natural stands (Appendix II). Five lichen species showed significantly greater abundance in fire than hurricane origin or managed forests. No difference was detected between hurricane origin and managed forests for these 5 species. Four species showed no preference for origin type in pole forests.

Table 11. Mean species richness, Shannon-Wiener indices and total abundance of lichens in pole class forests by origin type and results of single factor analysis of variance. Confidence intervals are indicated in brackets below mean values.

	Origin type				F (P)
	Hurricane	Fire	Harvested	Harvested & Thinned	
Species Richness	16.0 (7.1)	17.7 (7.1)	14.3 (7.1)	12.3 (7.1)	4.24 (0.356)
Shannon-Wiener	3.3 (0.7)	3.6 (0.7)	2.9 (0.7)	3.4 (0.7)	5.41 (0.144)
Total abundance	10.8 ¹ (1.3)	15.7 ² (1.3)	6.8 ³ (1.3)	5.8 ³ (1.3)	47.39 (0.000)

^{1,2,3} indicate results of multiple range tests: results with the same superscript number (1, 2 or 3) in a row indicate no significant difference.

3.3.3 Discussion

3.3.3.1 Maturity Class

Evidence from this study suggests that lichen abundance and diversity increase as forests mature. Total abundance, species richness and diversity were greater for more mature forests. Sillett and Neitlich's (1996) examination of several studies in Europe and North America led them also to conclude that epiphytic biomass and diversity increase through successional stages in forests. Other studies in North America found similar results. For example, McCune (1993) found the greatest biomass of epiphytes in older forests in Oregon and Washington. Goward (1994) suggested that certain species of lichens are likely to be found only in old growth forest in British Columbia. Reasons for greater lichen biomass and diversity in older forests are not known and the question has not been well studied. However, some authors have speculated on available evidence.

Humidity has been suggested as playing a role in lichen presence and abundance in forests. Lichens are non-vascular, obtaining water requirements from air moisture and runoff from the substrate on which they are attached. For this reason, humidity of the surrounding atmosphere is important for lichen growth. McCune and Antos (1981) and Sillett and Nietlich (1996) suggest old growth forests are much more humid than younger forests.

Sillett and Nietlich (1996) also suggest that young forests have much lower sunlight

penetration to the interior forest and that this may limit lichens. Although no difference in crown closure was found between maturity classes in this study, patchiness of the canopy was not measured and could vary between maturity classes.

Goward (1994) suggested that older forests are more stable than younger forests. Young forests are much more dynamic and always changing. Initial stages of stand development are characterized by rapid tree growth and then later, high mortality. This may result in an unstable microclimate for lichens.

A type of epiphyte succession or migration has been described by several authors (e.g. McCune 1993, Sillett and Nietlich 1996). This hypothesis suggests that in young forests certain lichen species establish and grow. As the forest ages, trees grow taller and these lichens migrate up the tree. Other lichen species then invade the lower boles. This results in a vertical stratification and a greater species richness in taller treed, older forests.

Substrate changes may also occur as trees get older. Bark chemistry and bark roughness play a role in lichen presence and abundance on trees (Sheard and Jonescu 1974, Gustafsson and Eriksson 1995) and may change as trees age.

Sillett and Nietlich (1996) suggest that dispersal limitations may result in fewer lichen species in younger forests. They cite several studies which found old growth lichen species in young forests within 10 m of an old growth forest. No old growth lichen

species were found in the interior of the young forests.

3.3.3.2 Origin Type

This study suggests that natural forests have greater diversity and abundance of lichens than managed forests. This is more evident in the younger maturity classes. Few studies have examined the effects of forest management on lichens, particularly in younger maturity classes. Okansen (1988) found variation in lichen species in man-influenced habitat compared to more natural habitat in Finland. Several other studies have found greater lichen diversity and/or biomass in old growth forests compared to second growth managed forests (Lesica *et al.* 1991, Pettersson 1996, Essen and Renhorn 1996).

Essen and Renhorn (1996) suggested that lack of substrate in managed forests may limit lichens. They found the biomass of branches was significantly less in managed forests compared to natural forests in Sweden and suggested that this provided less area for lichen colonization.

Essen and Renhorn (1996) also found that, other than branch size, there was little difference in structure between managed and natural forests. Lesica *et al.* (1991), however, found significant differences in structure between managed and old growth forest in Montana. They suggested that a greater diversity in epiphytes in old growth compared to managed second growth was due to greater structural diversity found in old

growth forests. Soderstrom (1988) also found a difference in structure between natural and managed forest in Sweden. He found that managed forests had a more uneven supply of downed logs which resulted in significant differences in epiphytes. Findings from this study suggest differences in structure of natural forests compared to managed forests (Section 1.0). How these differences may affect lichens is discussed in Section 4.0.

It has been suggested that some lichen species require a long period of time to develop. Forests with temporal continuity contain lichen species found in few other habitats (Rose 1976, Tibell 1992, Selva 1996). This may be why differences in lichen abundance and species richness were found to be less in this study in climax forests of different origin. It is also possible that natural forests in younger maturity classes provide more continuity than managed forests. Several species of lichen of continuous forests were found in significantly higher abundance in natural forests than managed forests in this study. Natural disturbances often leave undisturbed islands or standing remnants (Section 1.0). Wildfire, for example, may not burn poorly drained forested swamps or bogs. Kuusinen (1996) found that spruce swamp-forests are important for maintaining epiphytes in boreal forests in Finland. He suggested that the swamp-forest acts as a reserve and source of dispersal for lichens when the surrounding landscape is disturbed. Commercial timber harvesting, however, may remove trees from swamp-forest if they contain commercial trees. Peck and McCune (1997) and Nietlich and McCune (1997) found the abundance of some lichens was associated with remnant trees in young forests in Oregon.

The type of natural disturbance a forest undergoes appears to affect lichen abundance. Fire origin stands had a greater total abundance and greater abundance of certain lichen species than hurricane origin forest in the pole stage. Type and intensity of a disturbance will affect the structure of the regenerating forest. Low intensity fires or wind events will result in more remnant trees being retained than in high intensity disturbances. Soil is also affected by intensity and type of natural disturbance (Runkle 1985, Oliver and Larson 1996) which can affect tree growth and forest structure. Differences in structural features between disturbance type may result in differences in lichen abundance. Despite significant differences between natural disturbance types, natural disturbance sites appear to have much greater lichen abundance than managed forests.

4.0 Forest Management and Lichens

4.1 Introduction

Evidence from this study strongly suggests that harvesting and thinning affect abundance and presence of some species of lichens. Number of lichen species, diversity, and total abundance were greater in natural forests than managed forests. Twenty-six of 34 species examined either occurred solely, or in significantly higher abundance, in natural forests than managed forests. Several other studies have found higher abundances and diversity of lichens in old growth forests compared to managed forests (Lesica *et al.* 1991, Goward 1994, Essen and Renhorn 1996, Pettersson 1996). These studies compared old growth forests to much younger managed forests. Since lichen biomass is known to increase with forest age, it is unclear whether differences in lichen biomass found in these studies were attributable to forest management practices or differences in forest age. Evidence from this study suggests that differences in lichen abundance may be less when comparing natural and managed climax forest stands.

However, managed forests seldom reach the climax stage. There was great difficulty in finding managed climax forest stands for this study as many stands are harvested before this stage. Rotation ages (age at which a stand reaches maximum volume and is recommended for harvesting) for spruce in Nova Scotia ranges from 50 to 100 years depending on growth capability class of the site (Nova Scotia Department of Lands and

Forests 1990). Allowing managed stands to be harvested at older age classes (over 100 years) may help lessen the impact of harvesting.

There may be many reasons why natural forests host a greater diversity and abundance of lichen species than managed forests. Tree size variation was shown to be greater in natural forests than managed forests (Section 1.0), and this may reflect a greater structural heterogeneity of natural forests compared to managed forests. Greater variation in this structure may result in greater variation in microclimate and microsites which in turn provides more niches for lichen species and hence higher lichen species richness. Greater species richness and diversity in structurally diverse habitat have been demonstrated for other species groups.

The effect of sunlight penetration in forests on lichen biomass is not clearly understood. Rominger (1994) suggested that lichen growth is less in stands of high canopy closure and low sunlight. Stevenson (1988) hypothesized that partial cutting in forests may enhance lichen growth by increasing sunlight to the lower bole and branches of trees. However, Detrick (1984, *in* Rominger 1994) suggested that reduced canopy cover and subsequent increased solar radiation may desiccate lichens and reduce growth. A more recent study by Rominger (1994) provides little more understanding. They found no significant difference in arboreal lichen biomass between partially cut and uncut forests in Idaho and British Columbia. Natural forests in this study had the greatest lichen abundance but were intermediate in tree spacing compared to thinned and unthinned managed forests.

This suggests there may be an optimum spacing for some species of lichens in which sunlight increases photosynthesis but does not desiccate lichens. This, however, may be an oversimplification of relationships between lichens, sunlight and tree canopy. It is likely that susceptibility to desiccation and ability to take advantage of increased sunlight will vary between species. *H. physodes*, *L. elatina*, *L. ochrophaea*, and *Usnea* spp. increase in abundance as crown closure decreases, indicating that these species favour increased sunlight. *L. elatina* and *L. ochrophaea* are known to increase in openings (Topham 1977). Abundance of *H. physodes* against crown closure, however, suggests a curvilinear relationship supporting the hypothesis of an optimum spacing for some species of lichens.

Presence of remnant trees in stands affects abundance of several species of lichens. Neitlich and McCune (1997) and Peck and McCune (1997) also found abundance of some lichens associated with remnant trees in young forests in Oregon. Remnant trees with vestigial lichens from the previous forest may enhance dispersal in young forests, as dispersal can be limiting for some lichen species (Sillet and Neitlich 96). Stevenson (1988) found that establishment of some lichens was dependent on the distance to the nearest mature timber. Presence of remnant trees may also affect microclimate in young forest. Remnant trees may provide shade and wind protection, reducing extremes in microclimate within the forest.

Several lichen species increased in abundance as the amount of dead wood in the forest increased. The only lichens found exclusively on dead wood were from the genus

Xylographa. This genus had a very low frequency of occurrence (Section 2.0).

Maintenance of dead wood in managed forests may be important to the survival of this genus in forests. Other species in this study found to have a positive relationship with dead wood in stands (*Alectoria sarmentosa*, *Bryoria fuscescens*, *Loxospora ochrophaea*) were occasionally found on dead wood, but mostly located on live trees. It is likely that these lichen species are responding to some features associated with dead trees in stands, such as gaps in the canopy. Neitlich and McCune (1997) found that lichen species richness correlated with percent of their study plots in forest gaps in Oregon. Gaps provide areas of increased sunlight, favouring species like *Loxospora ochrophaea* that are found more often in sunlight.

Harvesting and thinning reduce diversity and abundance of some lichen species. Changes in forest structure, including those caused by forestry, affects lichens. Remnant trees, dead wood, mean tree spacing and structural heterogeneity are important habitat components for some lichen species which are altered by forestry.

4.2 Recommendations and Conclusions

4.2.1 Forest Management Practices

Harvesting and thinning affect presence and abundance of some lichen species. Because of the roles lichens play in the forest ecosystem, forestry not only affects

biodiversity of lichens but also the biodiversity of other species and possibly ecosystem function. Forestry affects lichens at least partially through forest structural changes. It may be possible to engineer or manage the structure of managed forests to resemble natural forests (Hunter 1993). Recommendations for forest managers based on the findings of this study are:

1. leave dead wood standing and on ground wherever possible during harvest and silviculture operations;
2. leave remnant live trees standing during harvests;
3. maintain old growth reserves within landscapes;
4. leave some stands until they are 100 years before harvesting; and
5. increase structural heterogeneity within managed stands.

Guidelines for maintaining dead wood, remnant trees and old growth reserves can be found in the scientific literature as well as within publications of federal and provincial governments. Less information is available to help increase structural heterogeneity within forest stands. Much more study is required to fully determine the differences in structural heterogeneity between natural and managed forests. However, some possible guidelines

for consideration are:

1. create gaps or openings in the forest, including a variety of sizes from single tree gaps to 0.5 hectares; these gaps can be created within stands during pre-commercial and commercial thinning;
2. follow previous recommendations number 1 and 2; leaving deadwood and remnant trees;
3. leave some hardwood standing during thinning operations; and
4. vary spacing between trees during thinning operations, leaving areas of dense trees as well as areas of widely spaced trees.

Leaving deadwood and remnants already parallels forest industry practices and government guidelines. Thinning operations can be expensive, and varying spacing or leaving hardwood may reduce the effectiveness of the expenditure. It has been suggested that some areas of forests be set aside for intensive management, while other areas can be allocated to multiple use or ecological purposes. Managers will have to determine priorities in deciding whether altering thinning operations are practical in some or all cases.

There are some lichen species that occurred only in natural forests. These species

should be of particular concern to forest managers and ecologists. A landscape containing no natural forest may require special management effort in order to maintain these lichen species. These species are: *Chaenotheca chrysocephala*, *Hypogymnia tubulosa*, *Thelotrema lepadinum*, *Usnea longissima*, *Usnea rubicunda* and *Xylographa* species.

4.2.1 Lichens as Bio-indicators

Managing for certain structural features in managed forests may help to maintain certain lichen species. However, to ensure success of conservation measures, it may be useful to monitor lichens. It is unnecessary and may not be practical to monitor all lichen species in a forest. The following is a list of lichen species which would make useful indicators to reflect lichen diversity based on this study. The lichen species were selected by four criteria: 1. absence indicates some level of disturbance; 2. relatively easily identifiable; 3. not limited to a maturity class; and 4. inhabit a variety of microhabitats.

Table 12. Lichen species suitable as potential biological indicators of lichen diversity.

<i>Alectoria sarmentosa</i>	<i>Hypogymnia tubulosa</i>
<i>Bryoria furcellata</i>	<i>Platismatia tuckermanii</i>
<i>Bryoria tricodes</i>	<i>Usnea lapponica</i>
<i>Bryoria nadvornikiana</i>	<i>Usnea rubicunda</i>
<i>Calicium parvum</i>	<i>Usnea trichodea</i>
<i>Chaenotheca chrysocephala</i>	<i>Xylographa</i>
<i>Hypogymnia krogiae</i>	<i>Lapraria finkii</i> when found with
<i>Hypogymnia tubulosa</i>	<i>Loxospora</i> species

Presence of all these species in a managed forest would indicate lichen diversity and structural heterogeneity similar to natural forests. Fewer species present would indicate lower diversity and that the management area may require additional conservation management efforts. The lichen species indicated as potential biological indicators were studied in spruce forests only. Although these species may occur in other forest types, their presence may not indicate lichen diversity there. Many species of lichens are also influenced by maritime climate and may not occur or are found in very low abundance in interior forests. It is likely that the biological indicator lichens can only be used in spruce forests in northeastern North America, although further research could determine this.

More research is required to assure reliability of the indicators. Because of the low abundance of several species, specific habitat requirements are unknown. The number of

species useful as indicators is small. One way to overcome some of these difficulties is to use a suite of indicators.

Lichens appear to be useful indicators of some structural changes caused by forest management practices. However this is only one aspect of the changes that forest management can cause. To monitor other aspects of the forest ecosystem, a suite of indicators is suggested. Those that have been suggested in the literature, and show some promise, are forest floor vascular plants, bryophytes, ectomycorrhizal fungi, large carnivores, beetles and moths (Keddy and Drummond 1996). Further research is required to determine the potential of these indicators.

4.3 Further Study

After completion of the study, I found several aspects that could be improved. These improvements can provide interesting studies on their own. Also, a number of questions were generated as a result of the findings of this study. I have compiled these questions in the form of suggested further studies.

1. Many of the lichen species studied had abundances too low to measure habitat or forest structural preferences. A study designed to increase the measured abundance or occurrence would provide some insight. Logistic regression analysis may be one useful method for this type of study.

2. Most studies on forest lichen habitat have examined substrate. More study is required on larger scale habitat preferences such as forest type. This would provide better insight into why a particular lichen species occurs in a particular habitat.

3. More information on structural differences between natural and managed forests is needed. Few studies have compared natural forests to managed forests in different age classes. A larger sample size than this study, comparing remnants, dead wood and structural heterogeneity, would help determine differences. A statistically comparable measure of structural heterogeneity, rather than coefficient of variation on tree size, would be useful, as would measures of variation in tree size, tree density and tree species.

4. A variety of indicators would be useful to forest managers. More research into other possible indicators is needed.

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Appendix I Annotated List of Lichen Species

The following is a summary of occurrences and habitat associations of the 34 lichen species found in this study. Comparisons to other studies are also included. Sections are organized by genus, or by species if only one species of a genus present.

Alectoria sarmentosa

This species occurred on less than 15% of the trees surveyed in this study but was found on 61% of study sites. Casselman and Hill (1995) indicate that *A. sarmentosa* was common on their study sites in Nova Scotia. Gowan and Brodo (1988) report *A. sarmentosa* as common in Fundy National Park in New Brunswick.

A. sarmentosa abundance was found to increase with tree age in this study. McCune (1993) suggests that alectorioid lichens (mainly *A. sarmentosa*) increase in biomass with stand age. Lesica *et al.* (1991) found *A. sarmentosa* to be more common in old growth forests than younger, second growth forests in Montana. *A. sarmentosa* abundance increased as the tree remnants increased on study sites. Neitlich and McCune (1997) found *A. sarmentosa* occurred in young forest only on old remnants and was most often in old growth forests in Oregon and Washington.

A. sarmentosa association with old growth forest habitat may reflect an association

with some characteristic of individual trees rather than a structure of old growth forests. The species may be found coincidentally in older forests because these forests have older trees.

Bryoria

The most common *Bryoria* species on study sites were *B. nadvornikiana* and *B. fuscescens*, both with high frequencies of occurrence on trees and on study sites. *B. capillaris*, *B. furcellata* and *B. trichodes* all occurred on less than 16% of the trees surveyed, although most species were found on more than half the study sites. Casselman and Hill (1995) report that *B. nadvornikiana* and *B. furcellata* were common, and *B. fuscescens* were abundant on their study sites in Nova Scotia. Gowan and Brodo (1988) found *trichodes*, *capillaris*, *nadvornikiana* and *furcellata* as all common in Fundy National Park in New Brunswick. Laflamme-Levesque (1983) found *B. nadvornikiana*, *B. fuscescens*, *B. trichodes*, and *B. capillaris* all occurring frequently on the Atlantic coast of Quebec.

Selva (1996) suggested that *B. capillaris* is “faithful” to ancient forests in New England and New Brunswick. Lesica *et al.* (1991) found *B. capillaris* to be more common in old growth forests than second growth forests in Montana. *B. capillaris* abundance was significantly greater in old growth forests than younger forests in this study (Section 3). Dependence on old forests by *B. capillaris* may account for the low

occurrence found in this study.

B. fuscescens also shows significantly greater abundance in old growth forests than younger forests (Section 3.0). Dependence on old growth forests may be reflected in the positive association of *B. fuscescens* abundance with tree age.

B. nadvornikiana abundance consistently showed a positive association with number of old remnants. Neitlich and McCune (1997) reported alectorioid lichens (including *Bryoria* species) correlated with percent of the plot occupied by old growth remnant trees in Oregon and Washington. Stevenson (1988) found that *Bryoria* species colonization in second growth stands depends on distance to the nearest mature timber. This indicates that dispersal of *B. nadvornikiana* may be limited. Establishment and growth of *B. nadvornikiana* in newly established forests seems to be aided by the presence of surviving remnant trees.

The negative correlation between *B. nadvornikiana* abundance and tree spacing indicates this species favours stands of high tree density. Few studies have examined tree density effects on lichen abundance. However, Rominger (1994) found that *Bryoria* species abundance did not significantly differ between stands of different tree density. They did not examine the differences in individual species. Tree density can affect a number of microclimate variables including light intensity and humidity (Geiger 1980). It is therefore possible that *B. nadvornikiana* responds to increased humidity in dense

forests, or it may be shade tolerant and able to outcompete other species in low light conditions. There may be other factors which may play a role in the *B. nadvornikiana* relationship with tree density.

Caliciales

Calicium parvum and *Chaenotheca chrysocephala* had very low occurrences on surveyed trees and on study sites. *C. chrysocephala* was found on only 4 trees on 3 study sites. Gowan and Brodo (1988) report *C. parvum* as rare and have no record of *C. chrysocephala* in New Brunswick. Douglas (1981) indicate that *C. chrysocephala* is rare in Alberta with no record of *C. parvum*.

Selva (1996) suggests that both species are “faithful” to ancient forests in New England and New Brunswick. Rose (1976) reports *Chaenotheca* species as possible “old forest” lichens in Scotland. Dependence on old growth forests may account for low occurrences of these species in study sites. Low abundance of these species and dependence on old growth forest may also make them susceptible to anthropogenic disturbance.

Sphaerophorus globosus was relatively uncommon and was found mostly in climax forests. Selva (1996) and Goward (1994) indicate that *S. globosus* is old growth dependent. This may account for its low frequency.

Hypogymnia

H. physodes was the most commonly occurring species across genera of all lichens. *H. krogiae* was relatively uncommon, occurring on only 6.7% of trees surveyed and on 39% of study sites. *H. tubulosa* was quite rare, occurring at 3 sites on only 5 trees. Casselman and Hill (1995) indicated *H. physodes* was extremely abundant and *H. krogiae* and *H. tubulosa* as common on their study sites in Nova Scotia. Gowan and Brodo (1988) indicated *H. physodes* and *H. krogiae* were very common and *H. tubulosa* was common on their study sites in New Brunswick. Lang (1980) found a high percentage bole coverage by *H. physodes* and *H. krogiae* in balsam fir forests in New Hampshire. These species occurred in 10 out of 10 stands they studied. *H. tubulosa*, however, occurred in only 4 out of 10 stands.

Selva (1996) indicated that *H. tubulosa* is an ancient forest lichen of New England and New Brunswick. In this study *H. tubulosa* was found only in forests undisturbed by human intervention (Section 3.0). Preference for natural forests may partly account for low occurrences of *H. tubulosa* found in this study. This also suggests *H. tubulosa* may be susceptible to anthropogenic disturbance.

Only *H. physodes* had a high enough abundance to allow regression analyses. A negative association with crown closure was found for 2 of 5 regression analyses. This indicates that as crown closure increases, abundance of *H. physodes* decreases. Gustafsson

and Eriksson (1995) found *H. physodes* associated with open sunny conditions in forests in Sweden. The negative association with crown closure found in this study is likely an indication of the requirement for sunlight.

Lepraria finkii

Lepraria finkii was a common lichen on study sites, found in all but 3 sites. Brodo (1988) in Ottawa and Gowan and Brodo (1988) in New Brunswick indicate that *L. finkii* was common on their study sites.

The most consistent variables to explain abundance were crown closure and tree volume. Both relationships are positive indicating that greatest abundance of *L. finkii* occurs on large trees in areas of low light (high crown closure). *L. finkii* is often cited as occurring on tree bases (Brodo 1988, Geiser 1994). Goward (1994) indicated that *Lepraria* species inhabit sheltered boles of trees where sunlight is minimal. Tree size may be an indication of tree age, however, tree age was used as a variable in regression analyses. Sheard and Jonescu (1974) suggested tree size associations with some species of lichens are related to bark roughness. Bark roughness has been shown to influence lichen abundance mainly by the increased water retention ability of rough bark. Sheltered boles of trees are less likely to receive rain water directly. *L. finkii* may have to rely more on atmospheric humidity, and water run off from tree boles.

Lepadium disciforme

L. disciforme was a very common lichen on study sites. It occurred on all study sites and on 64.2% of trees surveyed. Eastern hemlock was the only variable retained more than once during regression analyses. Gowan and Brodo (1988) found *L. disciforme* very common on *Picea* species on their study sites in New Brunswick. *L. disciforme* is likely a habitat generalist, inhabiting many sites in spruce dominated forests.

Lobaria

All *Lobaria* species were relatively uncommon on study sites. *L. scrobiculata* was the least common, occurring on only 9 trees in 8 sites. *L. pulmonaria* and *L. quercizans* had similar frequencies for both tree occurrence and site occurrence and tended to be found together. Gowan and Brodo (1988) and Casselman and Hill (1995) found all 3 *Lobaria* species to be abundant or common on their study sites in Maritime Canada. All 3 *Lobaria* species are found most often on *Acer* (Gowan and Brodo 1988, Brodo 1988). Preference for *Acer* substrate reduces the probability of finding these species on the spruce dominated forests in this study, and is likely partially responsible for the low frequencies.

Selva (1996) suggested that *L. pulmonaria* and *L. quercizans* are faithful to ancient forests in New England and New Brunswick. Rose (1976) indicated that *L. pulmonaria* and *L. scrobiculata* are lichens of old growth in Britain. Hale (1979)

suggested that *L. pulmonaria* and *L. scrobiculata* were common in mature forests but rare in second growth. *Lobaria* species were found more often in mature or climax sites than pole forests in this study. Commercial use of forests in eastern North America will likely reduce suitable habitat for these species.

Loxospora

Both *L. elatina* and *L. ochrophaea* were common on study sites. *L. elatina* was found on all study sites while *L. ochrophaea* was found on all but one study site. Mean abundance of both *Loxospora* species was high relative to other lichen species examined in this study. Gowan and Brodo (1988) found both species to be common on balsam fir and spruce on their study sites in New Brunswick.

Regression analyses twice demonstrated a negative relationship between *L. elatina* abundance and hardwood. *L. ochrophaea* twice showed a positive relationship with red spruce. This is consistent with substrate preferences demonstrated by these species.

Crown closure was retained in all regression analyses for *L. elatina* and in 4 out of 5 regression analyses for *L. ochrophaea*. Crown closure was negatively associated with abundance for both species, indicating that both species prefer open light conditions. Gowan and Brodo (1988) indicate that *L. ochrophaea* is often found on forest edges and openings. Topham (1977) indicated that *Haematoma* species (some of which now classed

as *Loxospora*), outcompete other lichen species for light. It may be possible that these species outcompete other lichens for sites with optimum sunlight and therefore have high abundance on trees in open conditions.

Mycoblastus sanguinarius

M. sanguinarius was relatively uncommon on study sites, found on 6% of trees surveyed. It occurred on 8 sites and most of these were old growth or mature forest types. *M. sanguinarius* has been little studied. However, Lang (1980) found *M. sanguinarius* in 3 out of 10 study sites in New Hampshire. He found mean cover on tree boles of 0.02%, which is much less than 0.12% found in this study. Gowan and Brodo (1988) indicate that *M. sanguinarius* is common on spruce and balsam fir on their study sites in New Brunswick.

Ochrolechia androgyna

O. androgyna was found on almost 80% of study sites and on 16% of the trees surveyed. Gowan and Brodo (1988) indicated *O. androgyna* was very common on their study sites in New Brunswick. *O. androgyna* is also widespread in other parts of Canada (Brodo 1988) and Sweden (Tibell 1992).

Eastern hemlock was the only variable retained in more than one regression

equation for this species. *O. androgyna* is known to occur on a wide variety of substrates (Brodo 1991, Tibell 1992). Although it was found on a variety of tree species within this study, results of regression analyses may indicate a slight preference for eastern hemlock.

O. androgyna was found in relatively high abundance in a variety of habitat types and conditions, indicating that this species is a habitat generalist.

Parmelia sulcata

P. sulcata is a very common species on study sites, with a high percentage coverage on boles. Casselman and Hill (1995) indicated *P. sulcata* was extremely abundant in their study sites in Nova Scotia and Gowan and Brodo (1988) found *P. sulcata* to be common on their study sites in New Brunswick. This is in contrast to Lang (1980) who found *P. sulcata* in only 2 of 10 stands in balsam fir forests in New Hampshire, with 0.09 mean percent cover of tree boles. This study found *P. sulcata* in 25 of 28 stands with a mean percent bole cover of 0.89%.

No variables were retained more than once for the regression analyses with the exception of red spruce being retained in 2 regression analyses. Stone (1986) indicates *P. sulcata* has high growth rates in exposed sites, is light limited in closed stands and is adapted to early successional habitats. It was found in this study that *P. sulcata* abundance was significantly greater in pole forests than mature or old growth forests

(Section 3.0). No relationship with crown closure was retained in any of the regression analyses for *P. sulcata*, to indicate any preference for open sites. Nor was tree age retained in any regression analyses, which might indicate a preference for younger trees. This indicates *P. sulcata* is responding to some other habitat feature of younger forests. *P. sulcata* appears to establish and grow rapidly in early successional stages of forest development. The species declines in abundance as the forest ages, but still maintains a significant abundance even in old growth forests.

Pertusaria amara

P. amara was relatively common on study sites. Other studies have found *P. amara* to be common or abundant in eastern North America (Casselman and Hill 1995, Gowan and Brodo 1988). The only variable retained more than once during regression analyses was tree volume. This was a positive relationship, indicating *P. amara* abundance increases with increasing tree size. This is likely a reflection of some feature such as bark roughness changes with tree size rather than tree age. Tree age was a variable used in the regression analysis and not found to be significant. Tree bark often becomes rougher as the tree ages and becomes bigger. The rough bark is better able to trap moisture and therefore may be more favourable for *P. amara*.

Platismatia

P. glauca was the second most commonly occurring lichen on trees and was found at all sites in relatively high abundance. *P. tuckermanii* was much less common, having been found on only 16% of trees surveyed and less than half of the study sites. Other studies in eastern North America have found similar results (Lang 1980, Gowan and Brodo 1988, Casselman and Hill 1995).

P. tuckermanii abundance was too low to allow regression analyses, however 3 variables were retained more than once for *P. glauca*. The negative association between *P. glauca* and hardwood indicates that *P. glauca* prefers conifer trees. Gowan and Brodo (1988) reported *P. glauca* occurring on conifer and hardwood trees. Gustafsson and Eriksson (1995) found *P. glauca* occurring on aspen on their study sites in Sweden, although abundance was relatively low compared to other lichens studied. Hale (1979) found *P. glauca* as occurring on conifers. Geiser (1994) described *P. glauca* as being found most often on conifers and less often on deciduous shrubs. *P. glauca* can be found on hardwood trees but seems to prefer conifers.

P. glauca abundance was positively associated with tree age. Lesica *et al.* (1991) found a greater abundance of *P. glauca* in old growth forests than in second growth forest in Montana. However, *P. glauca* was not significantly more abundant in older forests than in younger forests in this study. It seems unlikely that the association between *P. glauca*

abundance and tree age is related to a preference for old growth forests. *P. glauca* is found in abundance in a variety of habitats. Increasing abundance with tree age may simply be related to length of time *P. glauca* has to grow. If *P. glauca* becomes established early in the life of a tree, abundance will likely increase as the tree ages. Tree bark characteristics also change with tree age and *P. glauca* may be responding to this change.

Ramalina thrausta

Ramalina thrausta is relatively rare on my study sites, occurring on only 2.9% of the trees surveyed, and at only 5 sites. Gowan and Brodo (1988) found *R. thrausta* to be common on their study sites in New Brunswick. Lesica *et al.* (1991) found *R. thrausta* on trunks in 5 of 10 stands surveyed in Montana. Percent cover on tree trunks ranged from 0.01 to 0.02 in their study which compares to 0.02 found in this study. Neitlich and McCune (1997) found frequency of *R. thrausta* ranged between 6 to 28% in Oregon, which is much higher than the 2.9% found in this study.

R. thrausta was found only in old growth forests in this study. Selva (1996) and Kuusinen (1996) indicated that *R. thrausta* is an old growth dependent lichen, which may be a factor in its low abundance and frequency found in this study.

Pseudocyphellaria crocata

P. crocata was found only once on a large diameter *Acer rubrum* in an harvested and thinned mature forest. Gowan and Brodo (1988) found *P. crocata* was rare on their study sites in New Brunswick. They found this species occurring on *Acer saccharum* in hardwood forests. Preference for hardwood substrate would account for its rarity in our softwood dominated study sites.

Thelotrema lepadinum

This was another uncommon to rare lichen on my study sites. It was found in only 3 sites, all of them old growth forests. Rose (1976) indicated that *T. lepadinum* is a lichen of old growth forests in Britain. This species is declining in Europe because of air pollution and habitat disturbance, mainly by forestry practices (Purvis 1992). *T. lepadinum* may also be in danger of declining in North America as forestry operations increase and area of old growth forest decreases.

Usnea

Each individual species of *Usnea* surveyed occurred in less than 50% of the study sites and on less than 10% of trees. *Usnea strigosa* was most rare, occurring on only 2 trees in 2 sites. Casselman and Hill (1995) indicated that *Usnea strigosa* was abundant on their study sites in Nova Scotia. Gowan and Brodo (1988) reported *U. lapponica*, *U. rubicunda*, *U. strigosa* and *U. trichodea* to be rare in New Brunswick. Laflamme-Levesque (1983) found *U. trichodea* only once in their study sites in Quebec. They also found *U. longissima* to be much less common than most other lichens they studied.

Stevenson (1988) indicated that *U. lapponica*, *U. longissima* and *U. rubicunda* are old growth dependent lichens. *U. trichodea* abundance was highest in old growth forests in this study. If these *Usnea* species are old growth dependant this may explain their rarity in this study. However, none of these species were found exclusively in old growth forest. All *Usnea* species surveyed in this study, except *U. strigosa*, were found in higher abundance, or exclusively in, naturally disturbed forests (Section 3.0). Gowan and Brodo (1988) suggested *U. strigosa* occurs most often on *Acer rubrum*, hence lack of suitable substrate in my study sites may also account for its rarity.

Number of old remnants was retained twice after repeated regression analyses using *Usnea* species abundance. Neitlich and McCune (1997) found the diversity and abundance of alectorioid lichens was correlated with percent of the study plot occupied by

old growth remnant trees in Oregon. Peck and McCune (1997) found the biomass of alectorioid lichens was greater in mid-elevation sites with remnant trees than without in Oregon. Dispersal ability of *Usnea* species may be limited, and establishment and growth of this genus in second growth forests may be aided by the retention of remnants from the previous stand. This may have important implications for conservation management in commercial forests.

Xylographa

Xylographa species were found on 3 trees on 3 different sites. All individuals occurred on dead wood. The dependence on dead wood by this genus will likely affect its abundance in forests. Forest management practices reduce the amount of dead wood (Section 1.0) and could endanger the continued existence of this genus, at least in forest habitats.

Appendix II. Mean cover for each lichen species by origin type and maturity class and results of 2 factor ANOVA
 Lichens species with cover too low to test are indicated last. Ninety-five percent confidence intervals are indicated in brackets below mean values. N= number of trees.

Species	Origin Type			F (P)	Maturity Class			F (P)	Interaction F (P)
	Natural n=230	Harvested n=230	Harvested &Thinned n=161		Climax n=138	Mature n=276	Pole n=207		
<i>Alectoria sarmientosa</i>	0.41 ¹ (0.15)	0.41 ² (0.15)	0.00 ³	27.80 (0.00)	0.34 ¹ (0.20)	0.31 ¹ (0.14)	0.02 ² (0.16)	21.67 (0.00)	21.05 (0.000)
<i>Bryoria capillaris</i>	0.32 ¹ (0.07)	0.14 ² (0.07)	0.04 ² (0.09)	11.49 (0.00)	0.28 ¹ (0.08)	0.14 ² (0.05)	0.00 ³	10.46 (0.00)	2.90 (0.09)
<i>Bryoria furcellata</i>	0.43 ¹ (0.06)	0.10 ² (0.06)	0.07 ² (0.15)	42.63 (0.00)	0.13 ¹ (0.07)	0.11 ¹ (0.05)	0.42 ² (0.06)	31.82 (0.00)	52.33 (0.00)
<i>Bryoria fuscescens</i>	1.60 ¹ (0.13)	0.95 ² (0.13)	0.47 ³ (0.15)	66.07 (0.00)	1.73 ¹ (0.16)	1.08 ² (0.12)	0.60 ³ (0.13)	59.11 (0.00)	26.07 (0.00)
<i>Bryoria nadvornikiana</i>	0.43 ¹ (0.09)	0.59 ² (0.09)	0.16 ³ (0.10)	19.76 (0.00)	0.61 ¹ (0.11)	0.44 ² (0.08)	0.25 ³ (0.09)	12.81 (0.00)	5.53 (0.00)
<i>Bryoria trichodes</i>	0.31 ¹ (0.06)	0.04 ² (0.06)	0.06 ³ (0.08)	20.99 (0.00)	0.19 ¹ (0.08)	0.21 ¹ (0.06)	0.03 ² (0.07)	8.49 (0.00)	6.55 (0.00)
<i>Calicium parvum</i>	0.12 ¹ (0.04)	0.04 ² (0.04)	0.02 ² (0.04)	6.71 (0.00)	0.05 ¹ (0.05)	0.11 ² (0.03)	0.01 ¹ (0.04)	8.12 (0.00)	11.53 (0.00)

^{1,2,3} indicate results of multiple range tests; results with the same superscript number (1,2 or 3) indicate no significant difference.

Appendix II Continued

Species	Origin Type		F (P)		Maturity Class			F (P)	Interaction F (P)
	Natural n=230	Harveste d n=230	Harveste d &Thinne d n=161	Harveste d	Climax n=138	Mature n=276	Pole n=207		
<i>Hypogymnia krogiae</i>	0.23 ¹ (0.06)	0.11 ² (0.06)	0.03 ³ (0.08)	7.85 (0.00)	0.00 ¹	0.24 ² (0.06)	0.07 ¹ (0.07)	13.98 (0.00)	5.65 (0.00)
<i>Hypogymnia physodes</i>	2.50 ¹ (0.12)	1.44 ² (0.12)	1.42 ² (0.15)	90.66 (0.00)	1.78 ^{1,2} (0.16)	1.73 ¹ (0.11)	2.0 ² (0.13)	4.94 (0.01)	35.32 (0.00)
<i>Lepraria finkii</i>	0.45 ¹ (0.08)	0.55 ² (0.08)	0.26 ¹ (0.11)	7.31 (0.00)	0.81 ¹ (0.12)	0.42 ² (0.09)	0.22 ³ (0.10)	30.41 (0.00)	8.78 (0.00)
<i>Lobaria spp.</i>	0.06 ¹ (0.07)	0.16 ^{1,2} (0.07)	0.23 ² (0.08)	4.75 (0.01)	0.17 (0.09)	0.18 (0.06)	0.07 (0.07)	2.76 (0.06)	1.98 (0.12)
<i>Lopadium disciforme</i>	1.28 ¹ (0.14)	1.23 ² (0.14)	0.97 ³ (0.16)	4.50 (0.01)	1.00 ¹ (0.18)	1.42 ² (0.12)	0.99 ¹ (0.14)	13.87 (0.00)	5.23 (0.00)
<i>Loxospora elatina</i>	1.62 ¹ (0.13)	1.20 ² (0.13)	1.06 ² (0.16)	16.33 (0.00)	1.12 ¹ (0.17)	1.56 ² (0.10)	1.14 ¹ (0.14)	13.45 (0.00)	23.07 (0.00)
<i>Loxospora ochrophaea</i>	1.74 ¹ (0.16)	1.25 ² (0.16)	0.75 ³ (0.19)	31.93 (0.00)	1.06 ¹ (0.20)	1.87 ² (0.14)	0.71 ³ (0.16)	57.92 (0.00)	29.88 (0.00)

Appendix II Continued

Species	Origin Type			F (P)			Maturity Class			F (P)	Interaction F (P)
	Natural n=230	Harvested		F	(P)	Climax n=138	Mature		Pole n=207		
		n=230	n=161				n=276	n=207			
<i>Mykoblastus sanguinarius</i>	0.27 ¹ (0.05)	0.04 ² (0.05)	0.01 ² (0.06)	25.11 (0.00)	0.27 ¹ (0.07)	0.11 ² (0.05)	0.03 ³ (0.06)	15.24 (0.00)	3.90 (0.01)		
<i>Ochrolechia androgyna</i>	0.35 ¹ (0.07)	0.24 ² (0.07)	0.06 ³ (0.09)	11.83 (0.00)	0.44 ¹ (0.10)	0.21 ² (0.07)	0.13 ³ (0.08)	13.61 (0.00)	4.24 (0.01)		
<i>Parmelia sulcata</i>	1.24 ¹ (0.12)	0.58 ² (0.12)	0.45 ² (0.14)	42.39 (0.00)	0.64 ¹ (0.16)	0.65 ¹ (0.11)	1.07 ² (0.13)	14.60 (0.00)	14.98 (0.00)		
<i>Pertusaria amara</i>	0.20 ¹ (0.05)	0.12 ² (0.05)	0.09 ² (0.06)	4.36 (0.01)	0.24 ¹ (0.07)	0.12 ² (0.05)	0.11 ² (0.06)	5.59 (0.00)	2.32 (0.07)		
<i>Platismatia glauca</i>	1.69 ¹ (0.12)	1.32 ¹ (0.12)	1.05 ¹ (0.14)	23.23 (0.00)	1.43 ¹ (0.17)	1.38 ¹ (0.11)	1.37 ¹ (0.13)	0.23 (0.79)	0.31 (0.82)		
<i>Platismatia tuckermannii</i>	0.53 ¹ (0.06)	0.05 ² (0.06)	0.04 ² (0.07)	74.68 (0.00)	0.04 ¹ (0.08)	0.17 ² (0.06)	0.48 ³ (0.06)	58.45 (0.00)	60.30 (0.00)		
<i>Ramalina thrausia</i>	0.04 ¹ (0.02)	0.01 ² (0.02)	0.00	5.48 (0.00)	0.07 (0.02)	0.00	0.00	19.26 (0.00)	5.20 (0.00)		
<i>Sphaerophorus globosus</i>	0.38 ¹ (0.07)	0.01 ² (0.02)	0.00	39.15 (0.00)	0.46 ¹ (0.09)	0.09 ² (0.06)	0.01 ³ (0.07)	39.18 (0.00)	22.28 (0.00)		

Species	Origin Type			F (P)	Maturity Class			F (P)	Interaction F (P)
	Natural n=230	Harvested n=230	Harvested & Thinned n=161		Climax n=138	Mature n=276	Pole n=207		
<i>Usnea lapponica</i>	0.10 ¹ (0.03)	0.01 ³ (0.03)	0.00	18.80 (0.00)	0.04 (0.03)	0.04 (0.02)	0.05 (0.03)	0.19 (0.83)	0.86 (0.46)
<i>Usnea longissima</i>	0.15 (0.03)	0.00	0.00	31.47 (0.00)	0.15 ¹ (0.02)	0.05 ² (0.03)	0.02 ² (0.03)	15.99 (0.00)	9.20 (0.00)
<i>Usnea trichodea</i>	0.21 ¹ (0.04)	0.01 ² (0.04)	0.00	30.66 (0.00)	0.14 ¹ (0.04)	0.08 ^{1,2} (0.04)	0.05 ² (0.04)	3.93 (0.20)	3.81 (0.01)
<i>Chaenotheca chrysocephala</i>	0.01	0.00	0.00		0.01	0.01	0.00		
<i>Hypogymnia tubulosa</i>	0.02	0.00	0.00		0.01	0.01	0.004		
<i>Pseudocyphellaria crocata</i>	0.00	0.004	0.00		0.00	0.004	0.00		
<i>Thelotrema lepadinum</i>	0.07	0.00	0.00		0.12	0.00	0.00		
<i>Usnea strigosa</i>	0.004	0.004	0.00		0.00	0.004	0.004		
<i>Xylographa spp.</i>	0.01	0.00	0.00		0.001	0.004	0.00		

Appendix III Mean cover for each lichen species by origin type in pole class forests and results of single factor analysis of variance. Confidence intervals are indicated in brackets below mean values.

Species	Hurricane n=72	Fire n=72	Harvested n=70	Harvested & Thinned n=71	F (P)
<i>Alectoria sarmentosa</i>	0.22 ¹ (0.31)	0.35 ² (0.31)	0.00 ³	0.00 ³	5.36 (0.00)
<i>Bryoria furcellata</i>	0.10 ¹ (0.13)	1.09 ² (0.13)	0.07 ¹ (0.13)	0.06 ¹ (0.13)	59.7 (0.00)
<i>Bryoria fuscescens</i>	0.29 ¹ (0.16)	1.23 ² (0.16)	0.23 ¹ (0.16)	0.16 ¹ (0.16)	37.42 (0.00)
<i>Bryoria nadvornikiana</i>	0.29 (0.14)	0.33 (0.14)	0.48 (0.14)	0.22 (0.14)	2.26 (0.08)
<i>Hypogymnia physodes</i>	1.58 ¹ (0.22)	3.19 ² (0.22)	1.03 ¹ (0.22)	1.65 ² (0.22)	64.24 (0.00)
<i>Lepraria finkii</i>	0.67 ¹ (0.17)	0.00	0.45 ¹ (0.17)	0.14 ² (0.17)	8.71 (0.00)
<i>Lobaria spp.</i>	0.09 (0.10)	0.00 (0.10)	0.13 (0.10)	0.10 (0.10)	0.184 (0.832)
<i>Lopadium disciforme</i>	2.0 ¹ (0.26)	0.94 ² (0.26)	1.29 ² (0.26)	0.67 ² (0.26)	18.16 (0.00)
<i>Loxospora elatina</i>	1.54 ¹ (0.25)	1.59 ¹ (0.25)	0.94 ² (0.25)	0.81 ² (0.25)	9.58 (0.00)
<i>Loxospora ochrophaea</i>	0.36 ¹ (0.26)	1.12 ² (0.26)	0.59 ¹ (0.26)	0.26 ¹ (0.26)	8.06 (0.00)
<i>Ochrolechia androgyna</i>	0.20 (0.10)	0.13 (0.10)	0.03 (0.10)	0.19 (0.10)	2.27 (0.08)
<i>Parmelia sulcata</i>	1.28 ¹ (0.23)	2.03 ² (0.23)	0.70 ¹ (0.23)	0.39 ¹ (0.23)	38.60 (0.00)
<i>Pertusaria amara</i>	0.14 ¹ (0.08)	0.20 ² (0.08)	0.10 ¹ (0.08)	0.01 ³ (0.08)	3.59 (0.00)

^{1,2,3} indicate results of multiple range tests; results with the same superscript number (1,2 or 3) in a row indicate no significant difference.

Appendix III Continued

Species	Hurricane n=72	Fire n=72	Harvested n=70	Harvested & Thinned n=71	F (P)
<i>Platismatia glauca</i>	1.65 ¹ (0.23)	1.73 ¹ (0.23)	1.29 ² (0.23)	0.99 ² (0.23)	8.27 (0.00)
<i>Platismatia tuckermanii</i>	0.07 ¹ (0.13)	1.32 ² (0.13)	0.01 ¹ (0.13)	0.06 ¹ (0.13)	89.90 (0.00)
<i>Usnea trichodea</i>	0.09 ¹ (0.05)	0.10 ¹ (0.05)	0.00 ²	0.01 ¹ (0.05)	3.30 (0.02)

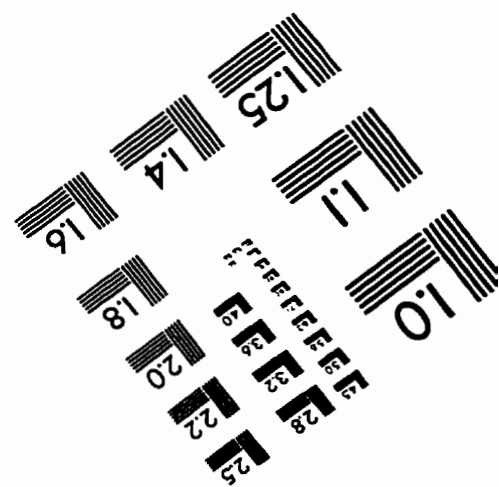
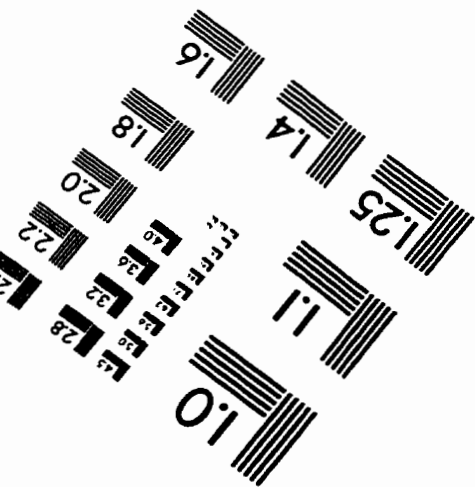
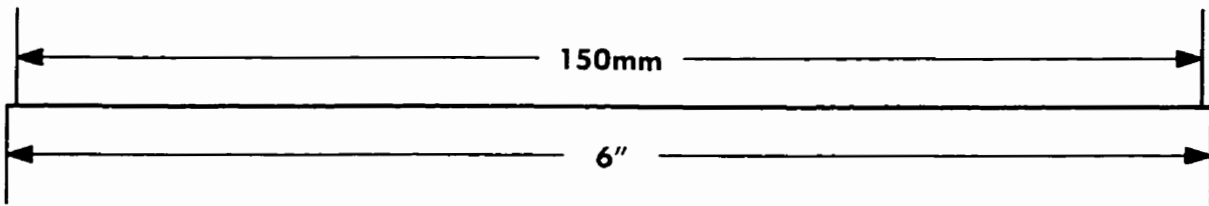
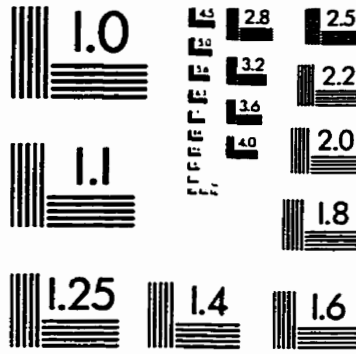
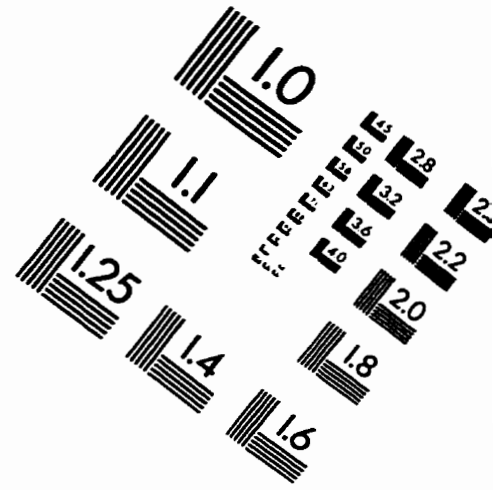
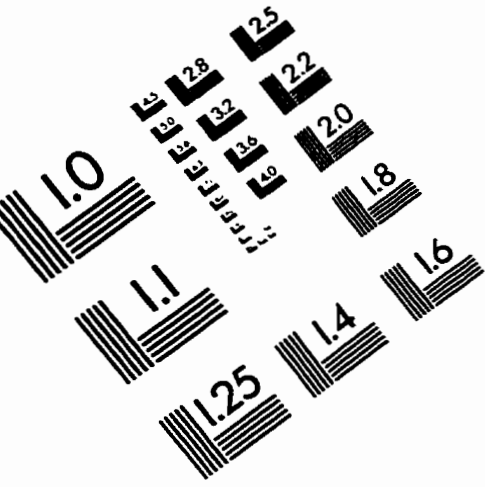
Appendix IV. Study sites and their locations.

Site Name	Origin	Maturity Class	General Location	Latitude		Longitude	
				degrees	minutes	degrees	minutes
Panuke Edna	natural	pole	Panuke Lake	44	48	64	18
Panuke	natural	climax	Panuke Lake	44	47	64	06
Dam Road	harvest	pole	Campbell Hill	44	46	63	54
Pockwock	harvest	mature	Campbell Hill	44	48	63	53
S Road	harvest	mature	Panuke Lake	44	45	64	06
Indian Lake	harvest	climax	Sandy Lake	44	45	63	55
Dam Two	thinned	pole	Campbell Hill	44	66	63	54
Pockwock 2	thinned	pole	Campbell Hill	44	48	63	53
Pockwock 3	thinned	mature	Campbell Hill	44	48	63	53
Main Road	natural	pole	Dayspring	45	14	62	36
Sloan Road	natural	pole	Seloam Lake	45	09	62	31
Antidam	natural	mature	Antidam Lake	45	06	62	30
Rocky Lake	natural	mature	Rocky Lake	45	14	62	33
Abraham Lake	natural	climax	Abraham Lake	45	09	62	38
West River	harvest	pole	West River	45	06	62	30

Appendix IV. Continued.

Site Name	Origin	Maturity Class	General Location	Latitude		Longitude	
				degrees	minutes	degrees	minutes
Grassy Lake	harvest	pole	Grassy Lake	45	11	62	34
Governor Lake	harvest	mature	Lake Little	45	10	62	40
Dayspring 2	harvest	mature	Dayspring	45	13	62	35
12 Mile Stream	harvest	climax	Governor Lake	45	09	62	40
Malay Lake	thinned	pole	Malay Lake	45	06	62	14
Malay 2	thinned	mature	Malay Lake	45	06	62	14
Sloan Road	thinned	mature	Seloam Lake	45	11	62	29
Sandy Lake	thinned	mature	Sandy Lake	44	44	63	55
Asa Laffin	thinned	climax	Northfield	45	15	63	39
Blois Road	natural	pole	Nine Mile River	45	02	63	33
Nine Mile River	natural	pole	Nine Mile River	45	02	63	31
Shanks	natural	mature	Armstrong Lake	44	49	64	09
Armstrong	natural	mature	Armstrong Lake	44	49	64	11
Card Lake	natural	climax	Card Lake	44	45	64	16
George Road	natural	pole	George Lake	45	06	62	16

IMAGE EVALUATION TEST TARGET (QA-3)



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