ECOLOGICAL CHARACTERISTICS OF FOREST REMNANTS LEFT BY WILDFIRE

by

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THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in
NATURAL RESOURCES MANAGEMENT

THE UNIVERSITY OF NORTHERN BRITISH COLUMBIA

APRIL 1997

ABSTRACT

Increased awareness of the key ecological role of natural disturbance in maintaining ecological integrity and function coupled with forest harvesting becoming a dominant disturbance process has lead to an increasing desire to study natural disturbance at multiple scales. The eventual goal is to design harvesting regimes that achieve the ecological conditions that are maintained in nature by natural disturbance. Legacies of natural disturbance such as unburned forest remnants left by wildfire commonly occur scattered throughout large wildfires. The objective of this dissertation is to develop a better understanding of the role of unburned forest remnants in providing ecological diversity and sources of natural conifer regeneration.

Two separate studies were undertaken. The first study characterized remnant habitats and compared them to large contiguous patches of remnant free young, mature and old forest. The second study examined post-fire recruitment surrounding remnant patches of Douglas-fir.

Remnants could be discriminated from other stand types based on measures of tree and snag density. Some remnants displayed a unique unevenaged lodgepole pine regeneration structure compared to other stand types. Differences between remnants and other stand types appear to stem from the influence of the wildfire through which they survived. Remnants displayed high variability in all ecological variables examined which appears to relate to the variable influence of wildfire on them. Remnants share many ecological characteristics with old forest and thus could provide some of the same functions. Douglas-fir remnants provide a positive influence on Douglas-fir recruitment in the post fire regenerating forest.

Patches of mature forest left in managed cutovers could serve similar functions as wildfire remnants. However, selection and management criteria must be developed to ensure that the ecological characteristics of wildfire remnants are duplicated within these reserves. The alternate regeneration dynamics demonstrated by some remnants could provide a model for the development of an alternate silviculture system for lodgepole pine dominated stands.

There are many limitations to our ability to incorporate characteristics of natural disturbance into managed forests. For instance, removal of the trees to make wood products restricts our ability to leave large numbers of standing snags. However, leaving patches of trees behind which emulate the ecological characteristics of island remnants is achievable and can bring us closer towards achieving ecological sustainability in the managed forest.

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ACKNOWLEDGEMENTS

I am sincerely indebted to my thesis supervisor, Wini Kessler, for her patient and timely editing and suggestions for improving the thesis. I would also like to thank the other members of my supervisory committee, Darwyn Coxson and Ken Lertzman for their involvement in seeing it through.

I am indebted to my enthusiastic field data drones Kathi Vagt, Howard DeLong, Jenny Marsden, and any other assistants who I may have forgotten.

I am grateful to the B.C. Ministry of Forests for providing their financial support to the project and providing me with some time off to complete the thesis

To my mom, thanks for providing me with lots of opportunity to gain a love of the outdoors. To my wife, Doris, thanks for putting up with my "thesis moods" and for inspiring me to strive for academic excellence. To my kids, Michael, Janette, and Daniel thanks for providing welcome interruptions during the sometimes laborious task of completing the thesis.

DEDICATION

This thesis is dedicated to my brother and friend Lawrence Edward DeLong (1948-1986) who inspired a love of the outdoors, and encouraged me towards the study of field ecology which I love so much.

CHAPTER 1 -INTRODUCTION

1.1 BACKGROUND

Today, land managers and scientists are being asked to develop, evaluate and apply management approaches that sustain ecological function and biological diversity while maintaining a viable forest industry. The traditional approach of setting aside wilderness and other protected areas within an overall matrix of intense resource extraction was directed at preserving wilderness and natural systems. Because such protected areas were considered pristine and inviolate, management was largely restricted to emergency measures such as fire control. On the remainder of the land area a single species emphasis approach was usually applied, featuring habitat management guidelines for large game species. For example, in British Columbia, management guidelines have been developed for mule deer (*Odocoileus hemionus*) (Armleder *et. al.* 1986) and mountain caribou (*Rangifer tarandus*) (Stevensen *et. al.* 1994).

The spatially explicit management strategy of preserves and intensely managed land was deemed adequate for the provision of renewable sources of timber, recreational opportunities, and game species and met perceived public concern over the protection of alternative forest values. Today, however, the biological values of natural ecosystems such as regulation of water and nutrient flows, cycling of carbon and organic matter, are also recognized. Within this context, the protected area approach has become inappropriate. Protected areas often do not include low elevation ecosystems where net primary productivity is greatest and are generally too small to protect wide ranging large mammals (Harris and Eisenburg 1989). Prior to the more comprehensive protected areas strategies of recent years, such as the one recently adopted in British Columbia (1995), protected areas were often chosen for their visual majesty or recreation value (Götmark and Nilsson 1992). Given these and other limitations it is unlikely that maintenance of biological values will be achieved by a collection of protected areas that represent a small portion of the land base. Rather, the maintenance of biological values requires management strategies that encompass all landscapes and address multiple temporal and spatial scales (Franklin 1993).

Public criticism of past practices and better understanding of natural systems has resulted in the emergence of new ideas about forest management (Maser 1988, Franklin 1989, Hansen *et al.* 1991). One such idea is that managed disturbances should be designed to achieve the landscape patterns and habitat conditions that are maintained in nature by natural disturbance regimes. This suggestion is derived in part from emerging evidence that disturbance has a key ecological role in many forested ecosystems (Zackrisson 1977, Van Wagner 1978, Hessburg *et al.* 1994). The underlying assumption is that the biota of a forest is adapted to the conditions created by natural disturbances and thus should cope more easily with the ecological changes associated with timber harvest if the patterns created resemble those of natural disturbances (Hunter 1993, Swanson *et al.* 1993, Bunnell 1995).

Natural disturbances maintain plant and animal diversity over time and space by maintaining structural complexity within stands and by influencing the size, distribution, edge characteristics, and dispersion of stands across the landscape (Zackrisson 1977, Hansen *et al.*, 1991, Hessburg *et al.* 1994). The size, shape, and location of individual forest patches or stands profoundly affect forest community stability and productivity (Franklin and Forman 1987, Frank and McNaughton 1991). Biological legacies of natural disturbance such as old large diameter trees, snags and woody debris play a fundamental role in maintaining the long term ecological functioning of the ecosystem (Hansen *et. al.* 1991, Maser 1992, Ammaranthus 1994, Franklin 1994). The impacts of forest management appear now to exceed and confound those of natural disturbance agents (Swanson *et. al.* 1993, DeLong and Tanner 1996). Hence, understanding how forest landscape and stand elements were affected by natural disturbance is needed in order to develop alternative management systems which more closely approximate natural disturbance in their effects.

Developing an understanding of natural disturbance requires research at a variety of scales. Some progress has been made within the northern[1] forests of British Columbia in documenting particular aspects of pattern and process in natural forests all of which have relevance to this study. Two landscape level studies have been undertaken, one comparing wildfire and harvesting patterns (DeLong and Tanner 1996) and another investigating how simulated landscape mosaic patterns change under the imposition of alternative disturbance rules (Andison 1996). Both these studies determined the prominent historic role of wildfire in determining landscape pattern. Andison (1996) found that age-class distribution in his study area was unstable illustrating a dynamic temporal aspect of natural disturbance. DeLong and Tanner (1996) concluded that wildfires had more complex shapes and contained more residual structure, in the form of surviving islands of trees, when compared to harvested areas. There have also been two stand level studies, one examining the successional changes in natural forests following wildfire (Clark 1995) and another involving analysis of stand structural attributes associated with "old-growth" forests (Kneeshaw 1992). Both studies determined that succession best fit an initial floristics model with the recruitment pattern involving early invasion of lodgepole pine (*Pinus contorta)* with lesser amounts of subalpine fir (*Abies lasiocarpa)* and hybrid white spruce (*Picea glauca x engelmannii*) and a gradual shift in time to stands dominated primarily by subalpine fir and hybrid white spruce. Old growth stands were characterized by a broad range in stem diameter, negative exponential stand age structure and large numbers of large logs and snags. Clark (1995) also documented stands where understory and overstory or just understory trees had survived wildfire. Remnant islands of surviving trees have been documented in other studies and appear to be an important feature of stand replacement wildfires (Eberhart and Woodward 1987, DeLong

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[1] I will consider the term "northern forests" to be forests within the sub-boreal and boreal regions of Canada and more specifically those within British Columbia which are dominated by lodgepole pine (*Pinus contorta*) and hybrid white spruce (*Picea glauca x engelmanii*).

andTanner 1996). These "island remnants" occur scattered throughout all wildfires that have been examined and may play an important function in these forests. To date, aspects of the amount of area occupied, size and landscape pattern of island remnants has been described, but stand level characteristics of these habitats is lacking. Island remnants have been hypothesized to play an important role as wildlife habitat and as important seed sources for natural regeneration of non-serotinous species (Eberhart and Woodward 1987). This later role is of special interest with respect to Douglas-fir (*Pseudotsuga menziesii*) due to recent concern that its presence in sub-boreal landscapes of the Prince George Forest Region is at risk due to large Douglas-fir bark beetle outbreaks and lack of artificial regeneration success (Oniel *et. al.* in prep.). Examining island remnant habitats may have important management implications; specifically, what might the consequences be of not managing for equivalent habitats in future managed landscapes?

1.2 GOALS AND OBJECTIVES

The overall purpose of this research is to investigate whether ecological features associated with island remnants may add a dimension of ecological diversity or provide important functions beyond that provided in "remnant free" mosaics of young, mature, and old forest. Specifically, I am interested in whether aspects of stand structure, vegetation, and regeneration in island remnants are distinct in comparison to remnant free areas of young, mature, and old forest.

My approach is to characterize the stand structure and composition of island remnants and to compare these characteristics to those in large contiguous patches of young, mature and old forest. I will interpret and discuss the potential significance of any differences and examine the role of island remnants as sources of cavity trees for wildlife and seed for natural regeneration of Douglas-fir. My specific objectives are as follows:

1) To determine if island remnants differ significantly with respect to stand structure, amount and decay state of coarse woody debris and floristic composition compared to young, mature, and old large contiguous forest patches.
2) To determine if the abundance of trees containing bird-excavated cavities within island remnants is different from that in young, mature, and old large contiguous forest patches.

3) To determine if differences exist in regeneration status of island remnants compared to large contiguous forest patches of a similar age.

4) To describe the patterns of Douglas-fir regenerating in previously burned areas where remnant patches of Douglas-fir occur.

The main body of the thesis is organized into two sections (Chapters 2 and 3), each with its own introduction, methods, results and discussion. Chapter 2 examines the general hypothesis that island remnant stand structure and vegetation characteristics are significantly different from those of large contiguous forest patches on ecologically similar sites. The implications for wildlife are also discussed. Chapter 3 examines the hypothesized role of island remnants as a seed source for Douglas-fir regeneration in the surrounding forest. Overall conclusions and recommendations are presented in Chapter 4.

1.3 STUDY AREA DESCRIPTION

I conducted the study within the plateau portion of the Mossvale moist cool variant of the Sub-boreal Spruce Zone (SBSmk1)(DeLong *et. al.* 1993), which extends approximately 54°N - 55° N and 122° 30' W - 124° W and ranges 800 - 1000 m in elevation (Figure 1.1).

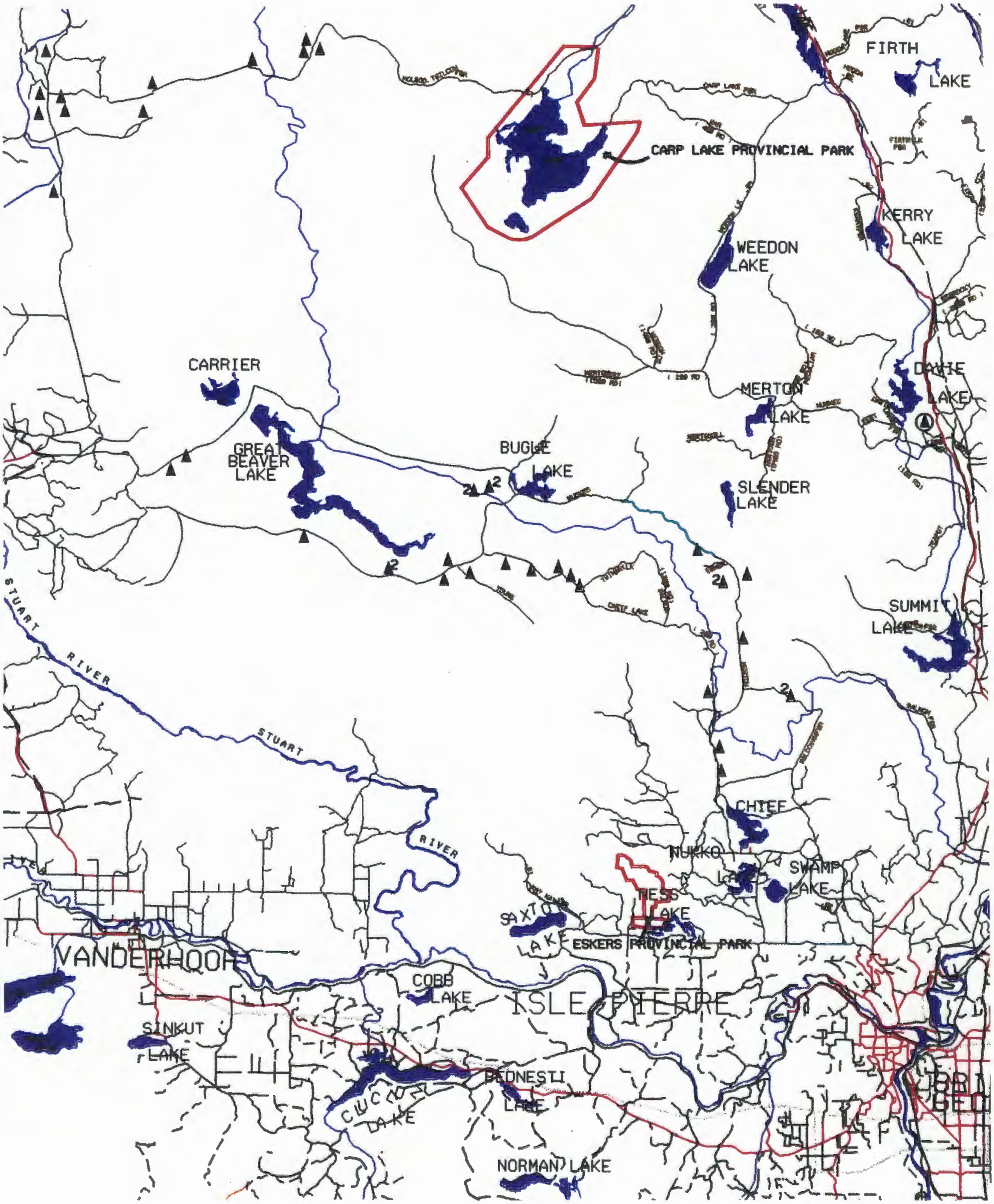

Figure 1.1. Map of study area showing plot locations (2 denotes where 2 plots are located close to one another).

The area is relatively flat with many features of heavily glaciated terrain including eskers, kettle topography and numerous well distributed wetlands. The study area covers 782 213 ha, approximately 660 000 ha of which is forested.

The study area has relatively cool, snowy winters and warm, moist summers that are short in duration (Meidinger *et. al.* 1991). The SBSmk1 has a mean annual precipitation of 727 mm and a mean annual temperature of 1.5°C (Reynolds 1989). Mean seasonal precipitation (May-Sept.) is 273 mm, mean annual snowfall 306 cm and average frost free period is 73 days (Reynolds 1989). The climate is transitional between the drier warmer portions of the Nechako plateau further south and the wetter, colder mountain slopes at higher elevation to the north.

Soils, geology and landforms

Bedrock geology in the study area is dominated by volcanic rocks of Mesozoic age, with lesser amounts of metamorphic rocks (DeLong *et. al.* 1993). Soils have developed on predominately morainal and lacustrine materials. Morainal deposits generally have gravelly loam and clay textures, associated with Gray Luvisolic soils (DeLong *et. al.* 1993). Much of the level morainal deposits are very compact at depth (> 15 cm) due to heavy glacial action. Organic soils (Fibrisols) occur in depressional sites in rolling drumlinized landscapes (DeLong *et. al.* 1993). Gray Luvisolic soils have formed on fine-textured (silty clay, clay) lacustrine deposits which occur in scattered pockets throughout the study area (DeLong *et. al.* 1993).

Vegetation

Upland forest stands are generally dominated by lodgepole pine (*Pinus contorta*) or hybrid white spruce (*Picea glauca* x *engelmannii*), with localized areas dominated by trembling aspen (*Populus tremuloides*) and scattered patches dominated by Douglas-fir (*Pseudotsuga menziesii*) or paper birch (*Betula papyrifera*). Subalpine fir (*Abies lasiocarpa*) occurs commonly in the understory of all but the driest stands and occasionally forms a significant portion of the main canopy on wetter sites. Black spruce (*Picea mariana*) commonly occurs in the understory of stands on compact till and lacustrine soils and forms the main canopy of wetland forests which are common throughout the study area. Black cottonwood (*Populus balsamifera ssp. trichocarpa*) occurs as pure stands along major water courses and as scattered individuals across the landscape where there is abundant water available in the soil.

Common shrubs on mesic sites are *Vaccinium membranaceum, Rosa acicularis, Rubus parviflorus, Lonicera involucrata*, and *Spiraea betulifolia*. On drier and poorer sites *Shepherdia canadensis and Vaccinium myrtilloides* are more prevalent whereas on wetter sites *Oplopanax horridus, Viburnum edule,* or *Lonicera involucrata* tend to dominate. Common mesic site dwarf shrubs, herbs and grasses include *Cornus canadensis, Linnaea borealis, Vaccinium caespitosum, Clintonia uniflora, Geocaulon lividum, Lycopodium annotinum, Epilobium angustifolium*, and *Aralia nudicaulis*. *Arctostaphylos uva-ursi, Oryzopsis asperifolia, Melampyrum lineare*, and *Chimaphila umbellata* are common in the herb layer of drier or poorer sites and the ferns *Gymnocarpium dryopteris, Tiarella unifoliata* and *trifoliata*, and *Athyrium filix-femina* are common on wetter sites. The feathermosses *Plerozium schreberi, Ptilium crista-castrensis, Hylocomium splendens and Dicranum polysetum* commonly dominate the forest floor except on drier sites where there can be significant lichen cover predominately composed of *Cladina* spp., *Cladonia* spp., *Peltigera* spp. and *Stereocaulon* spp. and on wetter sites where the leafy mosses *Mnium* and *Brachythecium* spp. are common. Vascular plant nomenclature follows Douglas *et. al.* (1991, 1990, 1989) and moss nomenclature follows Schofield (1992).

CHAPTER 2 - COMPARISON OF ISLAND REMNANTS TO MATRIX FOREST

2.1 INTRODUCTION

"Biological legacies" of natural disturbance such as old large diameter trees, snags and woody debris play a fundamental role in maintaining the long term ecological functioning of forest ecosystems (Ammaranthus 1994; Franklin 1994; Hansen *et. al.* 1991). Remnant patches of forest, which commonly occur scattered throughout the area burned by large wildfires, are one such legacy. Studies by DeLong and Tanner (1996) in the sub-boreal forest and by Eberhart and Woodward (1987) in the boreal forest indicate that remnants comprise 3 - 15% of the total area of a wildfire and that the proportional amount of island remnant area tends to increase with the size of the wildfire. Carried over from the pre-disturbance to the post-disturbance ecosystem, these biological legacies may strongly influence the structure, function, and composition of the recovering ecosystem (Franklin 1994). They may be important for the maintenance or re-establishment of a variety of organisms.

In many forest types, wildfire has played a critical role in controlling the distribution of habitat types across the landscape and in shaping stand structure, composition and biological diversity (Agee 1993, Duchesne 1994, Whelan 1995, DeLong and Tanner 1996). Prior to fire suppression, stand replacing wildfires were the main natural disturbance shaping the forests of sub-boreal and boreal plateau landscapes dominated by lodgepole pine (*Pinus contorta)*, white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) (Rowe and Scotter 1973, Zackrisson 1977, Van Wagner 1978). Patterns of vegetation on the landscape resulted primarily from infrequent, large, highly intense fires (Johnson 1992). The overall area burned by individual stand-replacing wildfire events often exceeds 10 000 ha (Eberhart and Woodward 1987, Andison 1996) and average fire return interval ranged from 80 to 125 years (Johnson 1992, Bunnell 1995, Andison 1996). These natural fires caused extensive mortality in canopy and understory plants; and because active crown fires were so common, high levels of tree mortality was usual (Johnson 1992). Natural regeneration of burned stands was probably prompt as suggested by the vigorous and prompt natural stocking by lodgepole pine after clearcutting within the sub-boreal landscape (Eremko 1990). This leads to the relatively even-aged stands of lodgepole pine which dominate the landscape.

Although the temporal and spatial patterns generated by boreal and sub-boreal wildfires may be simpler than those generated in some natural systems, the patterns are considerably more complex than those created by current clearcut harvest disturbances (Andison 1996, DeLong and Tanner 1996). Shifts in wind and the complex internal wind patterns generated during wildfire contribute to shape complexity which increases as fire size increases (Eberhart and Woodward 1987, DeLong and Tanner 1996). In contrast, clearcuts are characterized by uniform edges and low shape complexity regardless of size (DeLong and Tanner 1996). Fires rarely if ever burn completely uniformly, and typically include unburned or lightly burned areas and trees that survive the fire (Eberhart and Woodward 1987). In contrast, up until the past few years clearcut harvest disturbances contained few or no mature trees within them (DeLong and Tanner 1996).

In northern forests remnant unburned islands commonly occur scattered throughout the burned area of large wildfires and can comprise up to 15% of the total disturbed area (DeLong and Tanner 1996). Their occurrence appears to be related to combinations of topography and soil moisture which reduce fire intensity, changes in wind during the fire, timing of burn relative to diurnal temperature and wind patterns and disruption of the horizontal continuity of the fuel bed by such factors as water bodies or rock (Foster 1983, Eberhart and Woodward 1987). Island remnants in northern forests are generally small. DeLong and Tanner (1996) found that within wildfires less than 1000 ha in total area all remnants were < 10 ha. On average, 50% of the remnants within a wildfire were less than 2 ha. The small size of these island remnants is likely to affect the microclimate within them. Edge effects on microclimate and vegetation dynamics have been demonstrated to extend at least 2 tree heights into forest patches (Oke 1978, Chen *et. al.* 1992); hence the majority of island remnants consist mostly of edge habitat.

The usefulness of wildfire remnants as wildlife habitat was demonstrated by Gasaway and DuBois (1985) in a study of the ecological impacts of large fires on moose. They found that 67% of the moose observed within a burned perimeter were located in unburned islands which represented only 15% of the total fire area. Remnants may also act as biological refugia for certain organisms. Hypogeous fungi have been demonstrated to be more abundant in remnant Douglas-fir stands than in the surrounding young forest (Ammaranthus 1994). The role of island remnants may be especially important in landscapes where dispersed residual habitat features such as scattered individual live trees or snags are uncommon. DeLong and Tanner (1996) found that within wildfires in a portion of the sub-boreal landscape there was only an average of 0.75 live and 0.26 dead dispersed remnant trees per hectare when island remnants were not considered. Since island remnants are older than the surrounding forest which regenerates around them they should typically contain habitat attributes such as larger diameter live and dead trees that are rare in the surrounding young forest. Thus, they may represent critical habitat in landscapes where the biota are adapted to conditions maintained by stand replacement wildfire.

Many studies have examined spatial and temporal dynamics in temperate forests. Current works emphasize habitat comparisons of old growth forest to younger forests (Spies and Franklin 1991, Arsenault and Bradfield 1995), gap dynamics (Collins and Pickett 1988, Mladenoff 1990; Philips and Shure 1990) and habitat change along edge gradients (Chen *et. al.* 1991). A successional chronosequence study (Clark 1995) and a study examining characteristics of old growth forest (Kneeshaw 1992) have been conducted within the sub-boreal forests of British Columbia. I have found no studies that examine habitat differences between remnants of natural disturbance and large contiguous "matrix" forest.

In this study, I examine stand structural data such as tree density, basal area, CWD volumes, presence absence and abundance of tree regeneration, and presence/absence and abundance of the understory vegetation to determine if there are differences between island remnants and contiguous forest which would suggest functional importance. Previous studies have used these same variables to investigate structural and functional relationships of old growth forests (Spies and Franklin 1991, Arsenault and Bradfield 1995).

The overall hypothesis is that island remnants constitute distinct habitats within SBS landscapes, and that their uniqueness derives from their small size and from changes caused by the wildfire that created them. My approach is to test whether selected attributes of island remnant habitats differ from those in large contiguous patches of remnant free forest of different age classes. My specific hypotheses are:

1) Island remnants can be discriminated from large contiguous forest patches of different ages on ecologically similar sites based on differences in diameter class distribution and density of live trees and snags above certain thresholds.
2) Island remnants can be discriminated from large contiguous forest patches of different ages on ecologically similar sites based on differences in volume of different decay classes of coarse woody debris.
3) Island remnants can be differentiated from large patches of old forest based on differences in presence/absence and abundance of understory tree species regeneration.
4) Island remnants are floristically different from large contiguous forest patches of different ages on ecologically similar sites.

2.2 METHODS AND ANALYSIS

In this study, an island remnant is defined as a patch of older forest surrounded by younger forest where the size of the patch is not larger than 10 hectares. The definition invokes the findings of DeLong and Tanner (1996) that wildfires less than 1000 ha in total area have remnant sizes of < 10 ha.

I used quadrat plot sampling techniques to compare various ecological attributes between island remnants and large contiguous forest patches. I used maps of stand age of the whole study area and more detailed maps of individual wildfires to identify potential sample sites. Potential island remnant sample locations were also outlined on air photos to assist in field location.

I used the following selection criteria to minimize between-site variation in my sample.

1) sites must have been mesic in moisture regime and range from poor to medium in nutrient regime;
2) sites must be classified into either the PlSb - Feathermoss site series (SBSmk1/06) or Sx - Huckleberry site series (SBSmk1/01) (DeLong *et. al.* 1993);
3) sites must occur on morainal or lacustrine soils;
4) slope position must be either level or mid-slope;
5) slope gradient must be less than 20%;
6) sites must have no evidence of prior tree cutting due to harvesting or thinning operations; and
7) sample plots must be at least one tree length (approx. 20-30m) from obvious clearings, stands of another age, or other stands not meeting these criteria.

Once a suitable stand was located a 30m by 30m plot was established in it. I placed the plot within the stand in the first available location that satisfied the selection criteria. The method of plot location approximates the relevé method which represents a compromise between complete subjectivity and complete randomness (Barbour *et. al.* 1987). I sampled a total of 40 plots, 10 each in three different age classes of fire origin stands (40-70, 71-140, 141+) and 10 in island remnants within the 40-70 year old stands. Sampling occurred between May and September in 1994 and 1995.

At each sample plot I described the site and soil according to the methods outlined in Luttmerding *et. al.* (1990). Site description included slope gradient (%), aspect (°) and slope position. I described the soils in one pit which was a minimum of 50cm into the mineral soil. For all soil layers with strongly contrasting physical characteristics, I recorded percent coarse fragment content (>2 mm) and soil texture of ≤ 2mm fraction. I also estimated effective rooting depth and identified any root restricting layers (Luttmerding *et. al.* 1990). I estimated the depth of the humus layer by measuring the depth in 5 randomly located positions within the plot. I also recorded evidence of visible damage to trees within the plot due to disturbance agents (e.g. windthrow, fire scarred trees).

I conducted all statistical analysis using SYSTAT software (Systat Inc. Evaston, Ill) except for some of the vegetation data analysis for which PC-VTAB (B.C. Min. For. Victoria, B.C.) and DECORANA (Cornell University) were used. I used Slidewrite Plus (Advanced Graphics Software Inc. Carlsbad, CA) and Microsoft Excel (Microsoft Corp.) for all final graphics.

I assigned stands to four categories for the purposes of analysis. Assignment to the categories was first based upon stand type (remnant or matrix forest) and then stand age within matrix forest types (40-70, 71-140, >141).

I tested each variable used in Analysis of Variance (ANOVA) for homogeneity of variance using the Fmax test (Sokal and Rohlf 1969). Where noted in the results, I removed young and mature stands prior to ANOVA testing because, when included, the assumption of homogeneity of variance was violated. During ANOVA testing of the variables the residuals were saved and plotted against expected values for a normal distribution to assess normality (Wilkinson *et. al.* 1996). These plots were compared to plots of 10 different random variables plotted against expected values for a normal distribution using a feature within SYSTAT. For all cases where ANOVA results are provided the variables met the assumptions of homogeneity of variance and normality.

Overstory Stand Structure

I collected the following data for of all live and dead standing trees ≥ 7.5 d.b.h. within each 30m x 30m plot:

1) diameter (cm) at breast height (1.3m);

2) decay level (snags only): (intact, intact to partially soft, hard large pieces, small soft blocky pieces, or soft and powdery);

3) presence of cavities: (large (≥ 3cm), small (< 3cm) or both);

For the species dominating the main canopy, generally lodgepole pine, I measured heights and ages for a minimum of 6 trees from the main canopy. For other species present in the canopy I sampled a minimum of 2 trees. I selected measurement trees which were free of major defects (e.g., broken top) and represented the range of heights in the main canopy. I also measured heights and ages of all survivors from earlier disturbances present in the canopy, as indicated by fire scars or obvious larger size. I measured all heights using a Criterion laser and all ages were counted from cores extracted using an increment borer.

I computed basal area and density of trees and snags by species and 5 cm diameter classes for each sample plot. I used this data to construct plots of density by diameter class for each plot and for testing of the hypothesis relating to stand structure. I also computed average tree diameter for each plot and the number of trees containing wildlife feeding cavities. A large number of potential variables could be constructed using species, condition and diameter criteria. Therefore, I used one or more of the following criteria to decide which variables to include in analysis of variance (ANOVA) and discriminant analysis: the variable was related to a characteristic that was documented to be selected for by a particular group of bird species (e.g., snags >25cm for certain cavity nesters); the variable was likely to show sharp contrasts between some or all of the stand types (e.g., live tree density); and/or the variable could be easily measured in future in order to classify stands. Table 2.1 shows the variables selected and reasons for their inclusion. Basic statistics were computed for each selected variable. I used Analysis of Variance (ANOVA) and Tukey's pairwise multiple comparisons tests for significance testing of selected variables (Wilkinson *et. al.* 1996). All selected variables were used to conduct discriminant analysis to determine if certain stand attributes could be used to discriminate between stand types (Wilkinson *et. al.* 1996).

Table 2.1. List of attributes included in statistical analysis and reasons for inclusion.

Attribute	Reasons for Inclusion in Discriminant Analysis
> 7.5-cm-d.b.h. tree density	likely to show sharp contrasts between stand types due to high initial densities in young stands and self-thinning over time; commonly measured attribute during operational surveys
> 7.5-cm-d.b.h. basal area	likely to show sharp contrasts between stand types due to changes of basal area over time; commonly measured attribute during operational surveys
> 7.5-cm-d.b.h. snag density	likely to show sharp contrasts between stand types due to high levels of tree mortality in intermediate-aged stands; commonly measured attribute during operational surveys
> 15-cm-d.b.h. tree density	represents trees large enough to meet the requirements of certain small cavity requiring bird species[1]
> 25-cm-d.b.h. tree density	represents trees large enough to meet the requirements of certain large cavity requiring bird species
> 15-cm-d.b.h. snag density	represents snags large enough to meet the requirements of certain small cavity requiring bird species
> 25-cm-d.b.h. snag density	represents snags large enough to meet the requirements of certain large cavity requiring bird species

[1] based on tree and snag requirements for birds in Thomas *et. al.* 1979 and Neitro *et. al.* 1985).

Coarse Woody Debris

I gathered coarse woody debris (CWD) information along 90m transects using a line intercept method adapted from Trowbridge *et. al.* (1989). The first 60m of the line transect consisted of two edges of the 30m x 30m quadrat plot at right angles to one another. To complete the transect, I used a diagonal line from the plot corner, where the first 60m of transect ended, through the plot centre. I recorded the following information for each piece of woody debris ≥ 7.5cm dbh, that intersected the tape:

1) diameter (cm) at the point of interception;
2) height (cm) above the ground (measured to bottom of log);
3) decay level: (intact, intact to partially soft, hard large pieces, small soft blocky pieces, or soft and powdery);

For stems classed as soft and powdery diameter was measured both parallel and perpendicular to the ground surface. An average of these measurements was used for diameter to correct for the tendency of these logs to have become elliptical in shape.

Volume estimates by decay and 5 cm diameter class were calculated using the formula described in Lofroth (1992):

$$V = \frac{\pi^2 \Sigma d^2}{8L}$$

where V is volume in m^3/ha, d is diameter (cm) of each piece of woody debris, and L is the length (m) of the transect. I conducted a one way ANOVA to test for significant differences in woody debris volume (total, and by decay class) between stand types (Wilkinson *et. al.* 1996). This was followed by Tukey multiple comparisons procedure to contrast island remnants with the other stand types (Wilkinson *et. al.* 1996). I also conducted discriminant analysis to determine if stand type could be discriminated on the basis of total CWD volume or by volume by decay class (Wilkinson *et. al.* 1996).

Tree Species Regeneration

I sampled tree species regeneration in 5 each of the quadrat plots established within island remnants, young and old large contiguous forest patches. I established nine 3.99 m radius (50 m^2) plots using a systematic grid to assure that there were no overlaps between adjacent plots. Plot centres were established at 5, 10 and 15m along each of three lines which I established perpendicular to a plot edge at 5, 10, and 15m from that edge.

I recorded the following data for all trees $\geq$ 60 cm but $<$ 10 m: tree species, total height (cm), and current and previous years height increments (cm).

ANOVA was used to test for differences in total number by species among the stand types. A graphical comparison of lodgepole pine regeneration by height class was made between young stands and remnants.

Floristics

I identified all vascular plant species within the 30 m x 30 m plot and estimated and recorded their percent cover. I estimated to the closest 5% for species exceeding 20% cover, and to the closest 1% for species with less than 20% cover. A value of either 0.5% or 0.1% was assigned to species with less than 1% cover. My ocular estimates of percent cover were determined as the proportion of plot covered if leaf area of the species was projected vertically to the ground. Non-vascular plants were only recorded when occurring over humus.

I examined floristic similarity between stand types using coefficients of similarity and employed both a classification approach and ordination technique to examine floristic differences between stand types. I calculated average coefficient of similarity between stand types using all available methods within PC-VTAB, a vegetation classification program used in the Biogeoclimatic Ecosystem Classification for British Columbia. The four measures used are based on species presence, percent cover, prominence (% cover X sqrt(presence) and the Goldstream coefficient (presence X sqrt(% cover). For presence, I used SORENSON's presence community coefficient (SPCC):

$$IS_s = (2c/A + B) x\ 100$$

where c = number of species common to both stand types, A = total number of species in stand type A, and B = total number of species in stand type.

For the quantitative measures I used the MOTYKA quantitative modification of SPCC:

$$IS_{Mo} = 2\ Mw/MA+MB$$

where Mw = the sum of the smaller quantitative value (e.g., percent cover, prominence or Goldstream coeffecient) of species common to stand types A and B, MA = sum of quantitative values of all species in stand type A, MB = sum of quantitative values of all species in stand type B.

I generated vegetation summary tables using PC-VTAB to compare vegetation among the stand types. The summary table is a species by vegetation unit (stand type) matrix that lists mean cover and presence class for each species (row) and vegetation unit (column). Presence class is a value from I-V indicating percent presence of species in a vegetation unit where I = 1-20%, II = 21-40%, III = 41-60%, IV = 61-80%, V = 81-100%. I also computed diagnostic criteria which indicate the significance of species in a vegetation unit for differentiating it from other units using presence and species significance values (Pojar *et. al.* 1987). Species significance values are a function of percent cover where 1 = 0.4-1.0, 2 = 1.1-2.2, 3 = 2.3-5.0, 4 = 5.1-10.0, 5 = 10.1-20.0, 6 = 20.1-33.0, 7 = 33.1-50.0, 8=50.1-75.0, 9=75.1-100. The diagnostic criteria according to Pojar *et. al.* (1987) were computed as follows:

(d) Differential - Species presence class is ≥ III in a vegetation unit and at least 2 presence classes greater than in other vegetation units.

(dd) Dominant Differential - Species is not Differential in any vegetation unit, but presence class is ≥ III and species significance is 2 better than any other vegetation units.

(cd) Constant Dominant - Presence class = V in only 1 vegetation unit and species significance is ≥ 5.

(c) Constant - Presence class = V as in the (cd) criterion, but species significance is < 5.

(ic) Important companion - constant dominant or constant species but shows affinity to a particular unit as shown largely by its absence from other units under comparison; presence class ≥ II, species significance is variable.

Using this approach, a "diagnostic combination of species" (DCS), which may include any of the defined diagnostic criteria, must be exclusive for any unique vegetation unit. Generally, to be exclusive the DCS must include a differential of dominant differential species.

I generated plot summary vegetation tables for each vegetation unit using PCVTAB "long veg tables" function. These tables provide species by plot matrix for each vegetation unit.

I examined variation in species composition among stands using indirect ordination techniques. I constructed a samples by species data matrix and performed Detrended Correspondence Analysis (DCA) as described by Gauch (1980) using DECORANA to produce a stand ordination from the matrix. I examined the stand ordinations to determine if the island remnant stands could be differentiated from the other stand types based on their position along the major axis of the ordinations.

2.3 RESULTS

Overstory Stand Structure

In the young stands (40-70 yrs old), most of the lodgepole pine stems were confined to the two smallest diameter classes, thus indicating domination by a single cohort that initiated following wildfire (Fig. 2.1(a), Appendix 2). In the mature, old, and remnant stands, stems were distributed over at least 3 diameter classes and black spruce, white spruce and subalpine fir were generally more abundant (Fig. 2.1(b), Appendix 2). Lodgepole pine density fell steadily from a single peak in the majority of stands. However, in 2 of the remnants a second peak occurred in the smallest diameter class (7.5 - 12.5 cm) (Fig. 2.2), indicating the establishment of a second cohort of lodgepole pine.

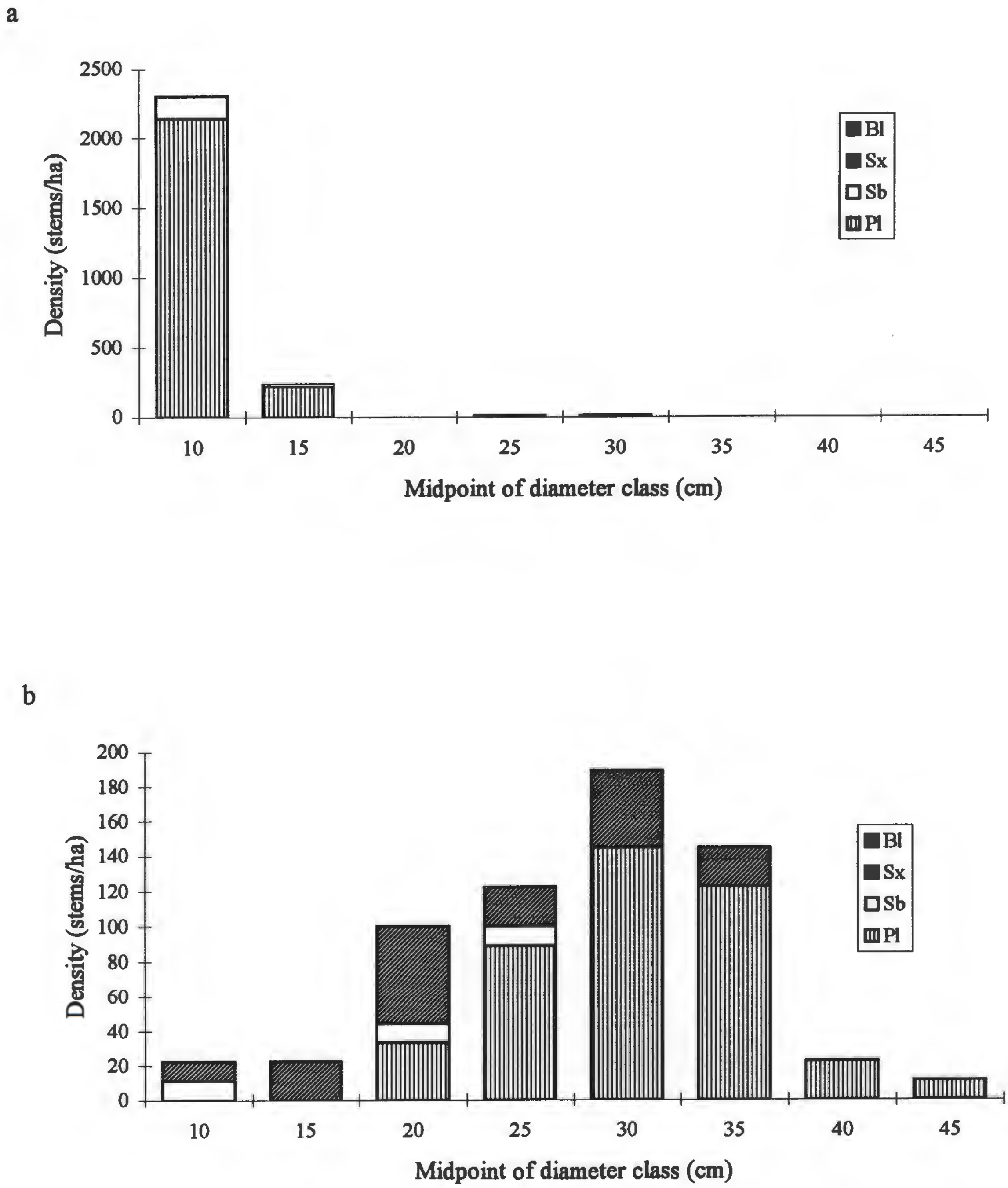

Figure 2.1. Density of live trees by diameter class for a) a young forest stand and b) an old forest stand illustrating the larger spread in diameter class distribution in older stands relative to young stands.

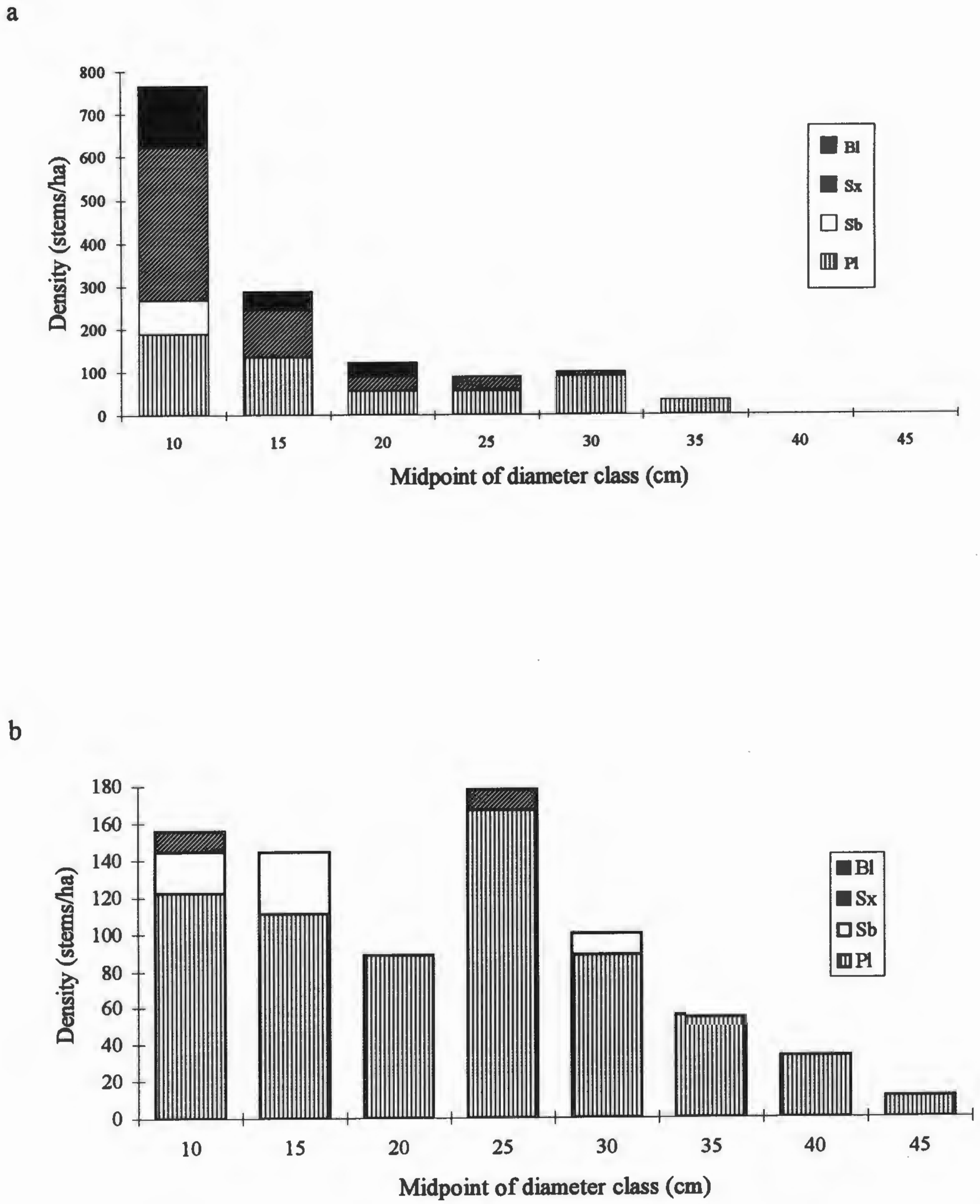

Figure 2.2 Density of live trees by diameter class for remnant plots a) 34 and b) 9319 showing two peaks of lodgepole pine density.

One way Analysis of Variance (ANOVA) followed by Tukey's multiple comparisons test indicated significant differences between stand types for several overstory attributes. Tree density was highest in young stands, intermediate in mature stands and lowest in remnant and old stands and snag density was higher in mature stands than other stand types (Table 2.2 & 2.3). Average density of live stems > 15cm (DL15), potentially of use to small cavity nesting species, was significantly lower in young stands than in other stand types (Table 2.2, 2.3 & Fig. 2.3a). Average density of snags >15 cm (DS15) was lower in young stands than in remnant and old stands and higher in old stands than in mature stands (Table 2.2, 2.3 & Fig. 2.3b). Average density of live stems >25cm (DL25), potentially of use to large cavity nesting species, was significantly higher in old stands than in remnants (Table 2.2, 2.3 & Fig. 2.3a). Average density of snags >25cm (DS25) was not significantly different between old and remnant stands. Trees or snags >25cm were rare or absent in young and mature stands but these stand types could not be included in the ANOVA because, when included, the assumption of homogeneity of variance was violated. DL25 was 9 and 59 s.p.h. and DS25 3 and 2 s.p.h., respectively, for young and mature stand types (Table 2.2 & Fig. 2.3). Average diameter of stems >7.5 dbh was significantly lower in young stands than other stand types and higher in old stands than in mature stands (Table 2.2 & 2.3). Greater variability in stand structure of remnants and old forest stand types compared to young and mature stands is indicated by the larger standard deviations for average tree diameter (Table 2.2).

Trees containing feeding cavities were found in all stand types and no significant differences in average number were detected between stand types. However, the mean number of trees with cavities was highest in remnants and 8 of 10 remnant plots had cavity trees versus 7, 5, and 4 for old, mature and young stands respectively.

Density of live trees greater than 25cm and overall tree density were the most effective stand structure variables tested for discriminating among stand types (Table 2.4). The discriminant functions correctly classified 34 of the 40 stands demonstrating an overall

Table 2.2. Means and standard deviations of selected stand characteristics for young, mature, remnant and old stand types and F ratio and p values for ANOVA testing (Df=3 for ANOVA where all stand types included and Df =1 where only remnant and old stands included).

Stand Characteristics	Stand Type					
	Young	Mature	Remnant	Old	F	p
Tree density	2597 (471)	1910 (780)	1165 (394)	984 (263)	24.44	0.000
Snag density	268 (198)	460 (193)	158 (78)	170 (72)	8.92	0.000
>15-cm-d.b.h. tree density	408 (273)	860 (189)	693 (171)	698 (215)	7.59	0.000
>25-cm-d.b.h. tree density	9 (11) ni[1]	59 (55) ni	221 (90)	334 (99)	7.23	0.015
>15-cm-d.b.h. snag density	12 (17)	59 (52)	73 (45)	126 (54)	11.29	0.000
> 25-cm-d.b.h. snag density	3 (5) ni	2 (5) ni	15 (17)	31 (27)	2.38	0.140
# of cavities/ha	13 (18)	9 (11)	30 (34)	18 (20)	1.68	0.189
Average tree d.b.h. (cm)	11.3 (1.2)	15.4 (1.9)	17.7 (3.7)	20.8 (3.3)	24.31	0.000

[1] stand type not inlcuded in ANOVA due to assumption of homogeneity of variance being violated when included.

Table 2.3. p values for Tukey pairwise comparisons for stand characteristics where all stand types were included in the analysis and where ANOVA was significant at <0.05.

Stand Characteristics	Stand Type Pairwise Combinations					
	Y-M[1]	Y-R	Y-O	M-R	M-O	R-O
Tree density	0.003	0.000	0.000	0.020	0.002	0.822
Snag density	0.030	0.358	0.461	0.000	0.001	0.998
>15-cm-d.b.h. tree density	0.000	0.027	0.024	0.325	0.348	1.000
>15-cm-d.b.h. snag density	0.105	0.020	0.000	0.885	0.008	0.051
Average tree d.b.h. (cm)	0.012	0.000	0.000	0.055	0.000	0.162

[1] Stand types (Y=young, M=mature, R=remnant, O=old)

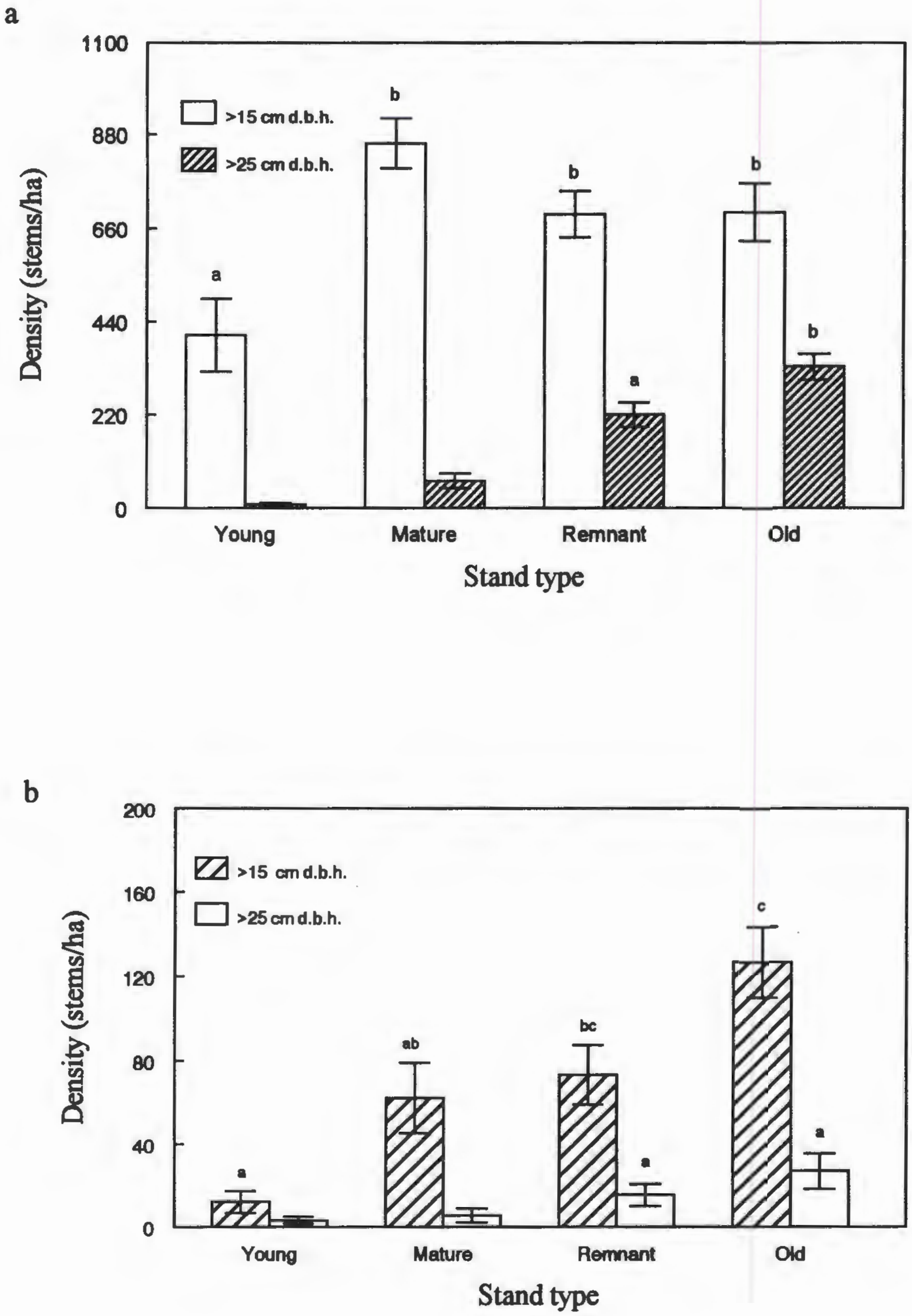

Figure 2.3. Density of a) live trees and b) snags >15 cm d.b.h. and >25 cm d.bh. in young, mature, remnant and old stands. (error bars equal ±1 SE, different letter above bar signifies difference at p<0.05, no letter indicates stand type not included in ANOVA).

Table 2.4. Overstory stand structure variables and their F, p and canaonical coefficient values for discriminant analysis of stand types.

Stand Variables	F	p	Canonical Coefficients[1]
>25-cm-d.b.h. tree density	42.7	0.000	-0.730, -0.181, 0.298
Tree density	24.4	0.000	0.581, -0.317, 0.559
> 15-cm-d.b.h. snag density	11.3	0.000	-0.304, 0.194, 0.436
Snag density	8.9	0.000	0.119, 0.645, 0.595
> 15-cm-d.b.h. tree density	7.6	0.000	0.015, 0.728, -0.245
> 25-cm-d.b.h. snag density	6.8	0.001	-0.123, 0.036, 0.297

[1] dependent variable canonical coefficients standardized by conditional (within groups) standard deviation for 3 discriminant factors with canonical correlations 0.933, 0.702, and 0.392.

Table 2.5. Summary of discriminant classifications of stand type based on stand characteristics.

	# of plots classified into each stand type by discriminant function			
Stand type	Young	Mature	Remnant	Old
Young (n=10)	**8**	2	0	0
Mature (n=10)	0	**10**	0	0
Remnant (n=10)	0	1	**7**	2
Old (n=10)	0	0	1	**9**

misclassification rate of 15% (Table 2.5). Seven of the ten remnant stands were classified as remnants while two were classified as old forest and one as mature forest. Of the two remnant plots missclassified as old forest, one was the largest remnant sampled (approx. 10 ha.), while the other was the oldest remnant sampled (i.e., 200 yrs old). The remnant plot classified as mature forest was the youngest remnant sampled (i.e., 90 yrs old). The discriminant analysis produced equations which can be used to assign new stands to stand type based on the stand structural criteria on which the equations are based (Table 2.6).

In summary, remnant stands can generally be discriminated from young and mature stands based on a number of overstory stand structure variables. Using ANOVA, only average density of live stems >25cm was significantly different between remnants and old forest. However, discriminant analysis indicated that remnants can generally be discriminated from old stands based on overstory stand structure characteristics. The data generally support the hypothesis that remnants can be discriminated from other stand types based on overstory stand structural characteristics. The presence of a second cohort of lodgepole pine in 2 of the 10 stands was the only unique characteristic demonstrated by remnants.

Table 2.6. Discriminant functions for predicting stand type membership. New case is assigned to the stand type with the largest function value for the case.

Stand type	Function[1]
Young forest	$0.013x_1 + 0.012x_2 + 0.014x_3 - 0.006x_4 - 0.031x_5 + 0.176x_6 - 23.288$
Mature forest	$0.010x_1 + 0.019x_2 + 0.023x_3 + 0.002x_4 - 0.015x_5 + 0.193x_6 - 24.372$
Remnant	$0.006x_1 + 0.008x_2 + 0.018x_3 + 0.033x_4 - 0.006x_5 + 0.198x_6 - 24.372$
Old forest	$0.005x_1 + 0.011x_2 + 0.016x_3 + 0.057x_4 - 0.018x_5 + 0.231x_6 - 24.847$

[1] discriminant function where x_1 = live tree density, x_2 = snag density, x_3 = > 15 cm d.b.h. tree density, x_4 = > 25 cm d.b.h. tree density, x_5 = > 15 cm d.b.h. snag density, and x_6 = > 25 cm d.b.h. snag density.

Coarse Woody Debris

No significant differences in average total volume of coarse woody debris (CWD) >7.5cm in diameter were found among stand types. ANOVA followed by Tukey multiple comparisons indicated average volume of larger diameter (>22.5 cm) CWD in decay class 1 (i.e., recently downed) was significantly higher ($n=10$, $p<0.05$) in old stands than in young and mature stands but not significantly higher in old stands than remnants. Nine out of 10 remnant stands had CWD in piece sizes >22.5 cm in diameter compared to only 6, 5, and 4 out of 10 for young, old and mature stands respectively. An average of 71% of the volume of CWD in young stands was in diameter classes >17.5 cm, indicating that a high proportion of the CWD originated from the pre-disturbance stand (Table 2.7).

In young and mature stands, CWD volume was concentrated in the most decayed states (i.e., decay class 4 & 5) (Figure 2.4). In old and remnant stands, CWD was more evenly distributed, with a higher proportion of total CWD volume attributed to decay classes 1, 2 and 3 (Figure 2.4).

Discriminant analysis using CWD variables indicated that no one decay class was important for discriminating between stand types as no decay class showed a high correlation with the discriminant factors (Table 2.8). Discriminant analysis using these variables correctly classified only 24 out of the 40 stands (Table 2.9). Only 5 of the 10 remnants was correctly classified. The inability for CWD variables to correctly classify stand types is likely related to the wide variation in CWD volume within different stand types. The widest variation was in young stands, where volume varied from 1.6 to 590 m^3/ha, but all stand types showed considerable variation (Table 2.7).

In summary, remnants can generally be differentiated from young and mature stands by having a higher proportion of CWD in less decayed states but there are no detectable differences between remnant and old stands. Variation in the CWD attributes examined is high for all stand types.

Table 2.8. CWD variables and their F, p and canonical coefficient values for discriminant analysis of stand types.

CWD Variables	F	p	Canonical coefficients[1]
Decay class 1 volume	2.89	0.049	2.52, 1.98, 2.23
Decay class 2 volume	2.92	0.047	5.51, 3.35, 6.76
Decay class 3 volume	3.75	0.019	4.91, 2.26, 6.38
Decay class 4 volume	3.62	0.022	5.08, 4.21, 8.33
Decay class 5 volume	1.48	0.236	11.66, 8.71, 16.69
Total volume	1.92	0.143	-17.12, -12.12, -23.96
Decay class 5/decay class 1 volume	2.41	0.083	-0.22, -0.25, 0.34

[1] dependent variable canonical coefficients standardized by conditional (within groups) standard deviation for 3 discriminant factors with canonical correlations of 0.692, 0.566, and 0.221.

Table 2.9. Summary of discriminant classifications of stand type based on CWD attributes.

	# of plots classified into each stand type by discriminant function			
Stand type	Young	Mature	Remnant	Old
Young (n=10)	**5**	3	2	0
Mature (n=10)	1	**9**	0	0
Remnant (n=10)	1	1	**5**	3
Old (n=10)	0	3	2	**5**

Table 2.7. Summary statistics for CWD volume for different stand types (n = 10).

	Total			< 17.5 d.b.h.		>17.5 d.b.h.	
Stand type	Mean	Range	SD	Mean	SD	Mean	SD
Young	261.8	5.6 - 590.3	201.3	76	54.7	188.5	177.3
Remnant	229.2	33 - 393.4	116.4	104.8	46.7	124.2	86.5
Mature	174.4	23.4 - 283.3	90.5	71.8	37.5	84.1	74.6
Old	192.6	38.6 - 286	78.7	82.5	37.6	112.8	61.5

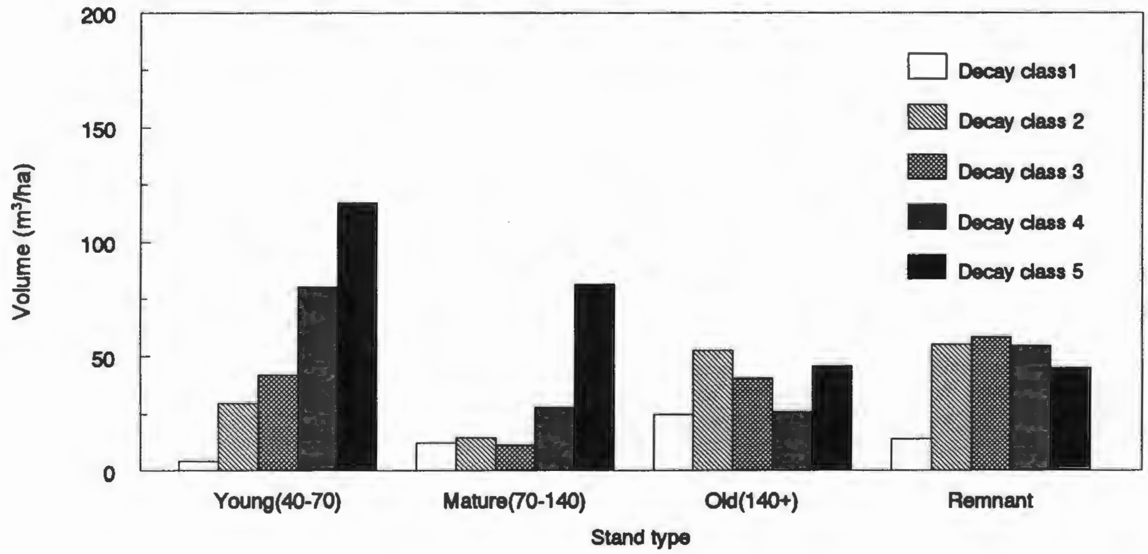

Figure 2.4. Distribution of CWD volume in five decay classes for young, mature, remnant and old stand types.

Tree Species Regeneration

I found some distinct differences between remnants and old forest with respect to the regeneration layer (0.6-10 m in height). Lodgepole pine was present in the regeneration layer of 3 of 5 of the remnants sampled, but was absent from all 5 old forest stands. Using ANOVA, I found weak evidence for statistical differences in density of hybrid white spruce (n=5, F=4.16, p=0.076) and black spruce density (n=5, F=4.73, p=0.061) between the stand types while there was no statistical difference for subalpine fir density (Table 2.10 & Fig 2.5).

In remnants having a lodgepole pine component, there were up to 20 stems of lodgepole pine within a single 0.005 ha subplot (4000 stems per hectare) and an average of 8 stems (1600 stems per hectare). The height of this < 10 m regeneration layer ranged between 0.6 m and 6 m, with an average height of 1.6 m. Much of the regeneration was in smaller height classes with the distribution approaching a negative exponential (Fig. 2.6). In contrast, most of the fire-initiated lodgepole pine in the stands surrounding the remnants exceeded 10 m in height. There was a maximum of 8 stems <10 m within a single 0.005 ha subplot (1600 stems per hectare) and an average of 3 stems (1600 stems per hectare.). Average height was 7.5 m and most stems were in the taller height classes (Fig. 2.7).

I failed to find statistical differences in height growth between the stand types for any of the tree species present.

In summary, the absence of lodgepole pine and lesser amounts of black and hybrid white spruce in old forest stands provide support for the hypothesis that there are differences in regeneration attributes between these stands and remnants. The height class distribution of lodgepole pine regeneration within remnants is distinct from that of the surrounding young forest.

Table 2.10. Mean and standard error and results of nested ANOVA for density of regeneration > 0.6-10m in height in remnant and old stands.

Species	Remnant Mean density (stems/ha)	Remnant SE	Old Mean density (stems/ha)	Old SE	F	P
Lodgepole pine	449	145	0		na	na
Black spruce	1116	214	160	47	4.73	0.061
Hybrid white spruce	240	45	49	20	4.16	0.076
Subalpine fir	596	155	800	193	0.107	0.752

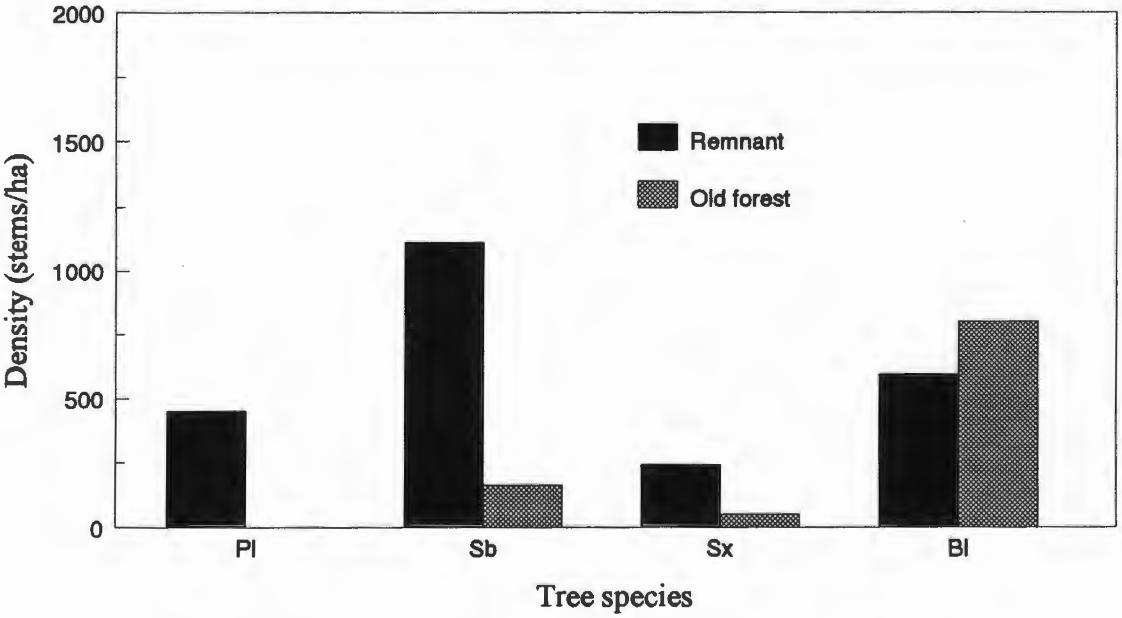

Figure 2.5. Density of live trees 0.6-10m in height for different species within remnants and old forests.

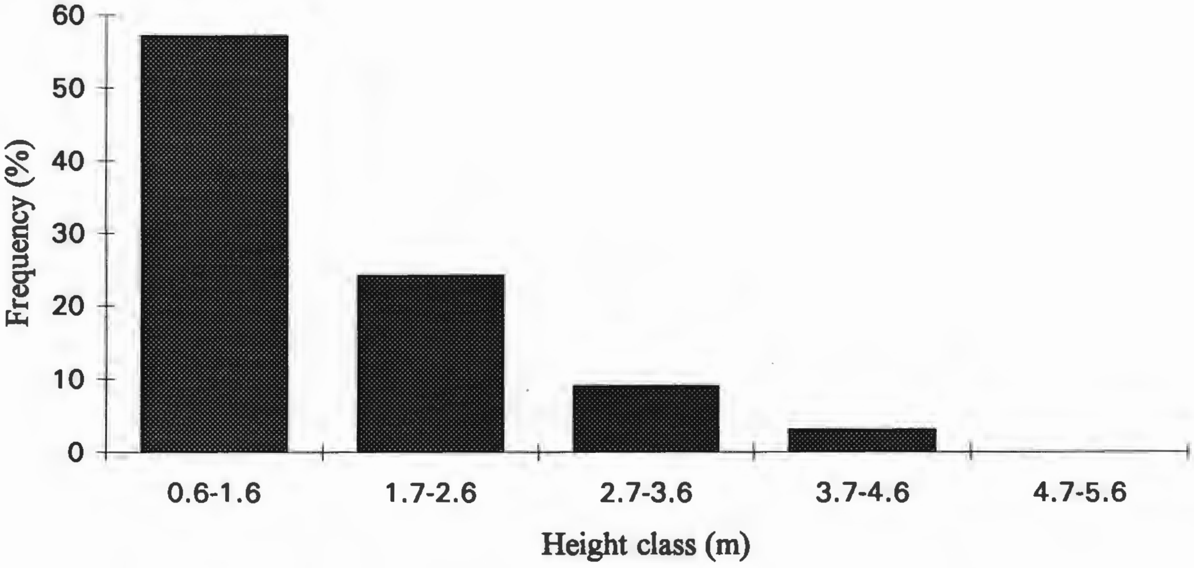

Figure 2.6. Frequency of lodgepole pine regeneration within 5 height classes in remnant plots.

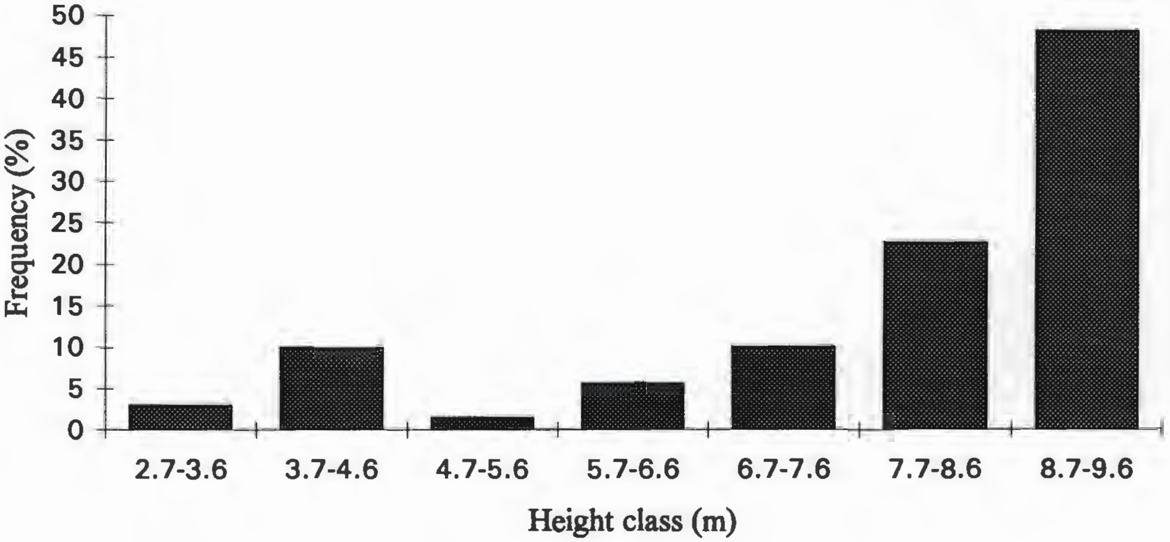

Figure 2.7. Frequency of lodgepole pine regeneration within 7 height classes in young stands.

Floristics

Species composition of understory vegetation was similar among stand types. Of 141 species present within the total sample of 40 stands, 64 species were represented in all the stand types. Of the 64, 29 were present in at least 50% of the plots within each stand type. Similarity coefficients based on four different criteria (presence absence, species percent cover, species prominence, and Goldstream values) averaged above 70% between different stand types with a minimum value of 66.1% between young and old forest (Table 2.11). Remnants were similar to all other stand types (Table 2.11). The lowest similarity was 69.9 between remnants and young stands. Basesd on species presence remnants were most similar to old forest but based on all quantitative values remnants were most similar to mature stands (Table 2.11).

Most of the floristic differences between stand types were associated with differences between old forest and all other stand types. Old forest was the only stand type to have a unique diagnostic combination of species (DCS). No other stand types had differential species which are required to form a DCS. According to the diagnostic criteria used, there were 3 species classed as differential (*Listera caurina*, *Smilacina racemosa*, *Spiraea pyrimidata*), 2 as constants (*Calamagrostis canadensis*, *Clintonia uniflora*), 1 as a constant dominant (*Ptilium crista-castrensis*), and 1 as an important companion (*Sorbus scopulina*) for the old forest type (Table 2.12, Appendix 3). Old forest was also characterized by a lack of lichens within the genera *Cladina* and *Cladonia*, which were more common in all other stand types (Appendix 3). The only obvious differences between remnants and other stand types was that *Pinus contorta* was present in the shrub layer of 7 out of 10 remnant stands but absent from the remaining 33 stands sampled. *Salix* spp. were identified as a constant for remnant stands. *Alnus tenuifolia* was identified as an important companion for young stands and *Orthilia secunda* and *Peltigera aphthosa* were identified as a constants. *Dicranum polysetum* was identified as a constant for mature stands.

Table 2.11. Similarity coefficients for understory vegetation between young, mature, old and remnant stand types.

Stand Type	Young	Mature	Remnant
Mature	79.8[1] **83.2**[2] ***83.6***[3] 78.6[4]		
Remnant	79.8 **71.8** ***69.9*** 75.8	77.1 **77.2** ***75.5*** 78.9	
Old	78.5 **66.1** ***66.3*** 74.4	79.8 **73.2** ***73.3*** 77.0	80.8 **76.8** ***74.7*** 78.5

[1] SORENSEN's presence community coefficient (SPCC).
[2] MOTYKA's quantitative version of SPCC using percent cover.
[3] MOTYKA's quantitative version of SPCC using prominence (percent cover X sqrt(presence).
[4] MOTYKA's quantitative version of SPCC using Goldstream coefficient (presence X sqrt(cover).

Table 2.12. Diagnostic species as per Pojar *et. al.* (1987) identified for old, remnant, young and mature stand types.

Stand Type	Diagnostic Type	Vegetation Species
Old forest	Differential[1]	*Spiraea pyrimidata, Listera caurina, Smilacina racemosa*
	Constant[2]	*Calamagrostis canadensis, Clintonia uniflora*
	Constant dominant[3]	*Ptilium crista-castrensis*
	Important companion[4]	*Sorbus sitchensis*
Remnant	Constant	*Salix* spp.
Young	Constant	*Orthilia secunda, Peltigera aphthosa*
	Important companion	*Alnus tenuifolia*
Mature	Constant	*Dicranum polysetum*

[1] species presence class is ≥ III and least 2 presence classes greater than in other stand types.
[2] species presence class = V in only 1 stand type and species significance is <5.
[3] species presence class = V in only 1 stand type and species significance is ≥5.
[4] species presence class ≥ II, species significance variable, species absent from other units
Note: presence classes as percent of frequency are I=1-20, II=21-40, III=41-60, IV=61-80, V=81-100 and species significance classes by percent cover are 1=0.4-1.0, 2=1.1-2.2, 3=2.3-5.0, 4=5.1-10.0, 5=10.1-20.0, 6=20.1-33.0, 7=33.1-50.0, 8=50.1-75.0, 9=75.1-100. (Pojar *et. al.* 1987).

Detrended correspondance analysis (DECORANA) did not differentiate well between the assigned stand types. There was a fairly dense concentration in the centre of both axes composed of plots representing all stand types (Figure 2.8). This result is consistent with the floristic similarity previously described among all plots. The first axis did separate young stands from old stands reasonably well. Young stands occurred nearer the origin and old stands nearer the end of axis 1 (Figure 2.8). Remnants were well scattered about the two dimensional space indicating a high diversity of vegetation among stands of this type (Figure 2.8). Remnant stands accounted for a high proportion of the spread of axis 2 with plot 34 occurring near the origin and plot 16 occurring near the end of the axis. Examination of the vegetation differences which appeared to account for this separation indicated higher amounts of subalpine fir and *Alnus crispa* in the plots near the origin of Axis 2 and higher amounts of *Shepherdia canadensis* and lodgepole pine near the axis end.

I detected differences in total percent cover, within different vegetation layers, between stand types. Percent cover of the tree layer was significantly greater for young stands than for old and remnant stands (Table 2.13). Lower tree cover in old and remnant stands corresponded to higher cover in the shrub layer which was significantly greater than in young or mature stands (Table 2.13). The cover of the moss layer within remnant stands was significantly lower than within old stands (Table 2.13).

In summary, the vegetation of remnants did not show distinct differences compared to the other stand types and thus did not support the hypothesis that island remnants are floristically different from the other stand types. However, the presence of lodgepole pine in the shrub layer of some remnants but no other stands indicates differences in vegetation development. Remnants accounted for most of the floristic variation expressed along axis 2 of the ordination.

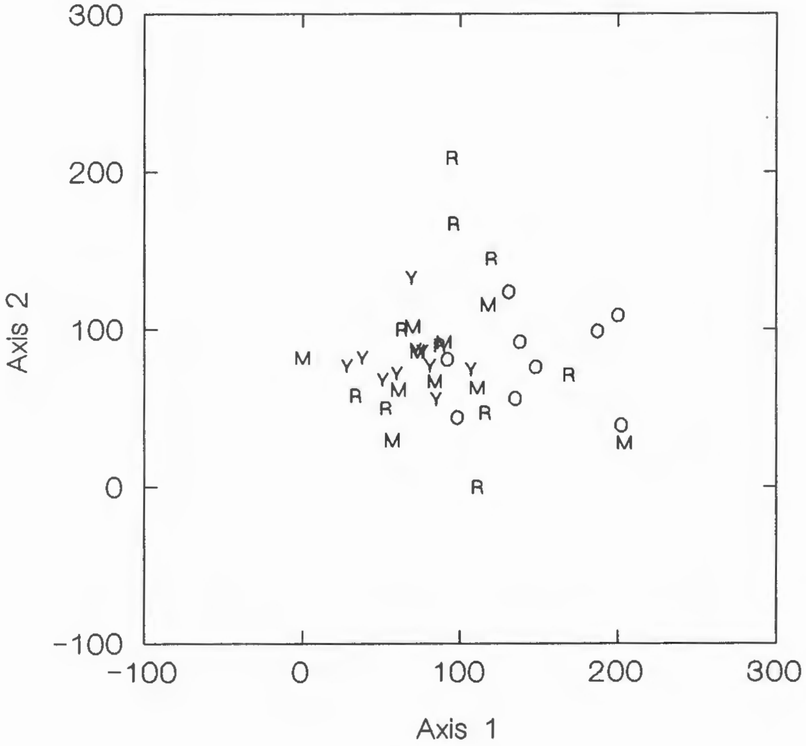

Figure 2.8. DCA stand ordination for young (Y), mature (M), remnant (R), and old (O) stands.

Table 2.13. Mean and range in percent cover within four vegetation layers of the young, mature, remnant and old stand types (Means followed by a different letter are significantly different at $p<0.05$).

Stand Type	Tree Layer	Shrub Layer	Herb Layer	Moss Layer
Young	43.5^{a} (31-60)	26.5^{a} (11-34)	21.4^{a} (8-34)	88.5^{ab} (72-99)
Mature	35.1^{ab} (18-52)	19.9^{a} (3-41)	28.1^{a} (9-58)	92.7^{ab} (78-99)
Remnant	26.2^{b} (17-59)	38.4^{b} (16-71)	29.2^{a} (9-50)	75.7^{a} (10-99)
Old	24.1^{b} (12-41)	39.6^{b} (26-50)	36.5^{a} (11-80)	94.4^{b} (74-99)

2.4 DISCUSSION

Are Island Remnants Distinct?

High variability characterized all measured attributes within the four stand types I examined. However, some forest habitat attributes differed among stand types and remnant stands can be differentiated from other stand types based on these differences. The strongest differences were in overstory and understory tree regeneration; however some differences for CWD and floristics were also significant.

Overstory stand structure

Attributes relating to overstory stand structure were generally successful at differentiating the stands into the 3 different age class matrix stands and remnant stands. Overstory attributes have been previously demonstrated to have high discriminating power for separating age-classes (Spies *et. al.* 1991) but no known studies have demonstrated the distinctiveness of remnant forest patches. The discriminating power of overstory attributes for differentiating matrix forest in different age-classes is not unexpected since the age-classes were based on the age of overstory trees. As observed in the data, the two general processes of stand development and succession lead to decreased density and increased tree size over time. In addition, as the stand opens up the density of late successional smaller-diameter, shade tolerant trees such as subapline fir increase, leading to high variability in tree diameter. The ability to discriminate remnant stands based on overstory stand attributes is more difficult to explain. However, disturbance relating to the wildfire event which initiated some of the remnants may explain the differences. Lower density of larger (>25 cm) trees may relate to stem mortality during the fire and greater total density may relate to the influx of new regeneration, particularly lodgepole pine, after the fire. The weak ability to differentiate between remnants and old stands may underline the high variability in conditions before, during and after the formation of remnant stands and the fact that ages of the remnants are most similar to the old stands. Differences in initial stand age, lack of or variability in intensity of fire within the remnant and variability in post-disturbance factors affecting stand structure such as wind and disease could all lead to high variability in overstory stand structure of remnants. Remnant stands most affected by wildfire are likely to be the most different from old stands.

CWD

CWD volume was highly variable and CWD attributes were not as useful at discriminating between stand types as other stand structure variables. CWD distribution across time and space is complex due to the many factors that influence CWD input. Spatial distribution and timing of mortality due to biotic agents such as insects and disease and abiotic factors such as wind and fire strongly influence CWD distribution precluding a strong relationship of CWD with stand type. In younger stands, CWD distribution relates more to the previous stand occupying the site than to the current stand. CWD input from the new stand is low due to the small size of dead and dying stems but total volumes are often high due to the residual CWD from the previous stand (Spies and Franklin 1988).

A simple model for describing changes in CWD biomass during succession after a stand level disturbance has been proposed by Harmon *et. al.* (1986) and validated for Douglas-fir stands in the Pacific Northwest (Spies *et. al.* 1988; Agee and Huff 1987) and eastern subalpine forests (Lambert *et. al.* 1980). A large initial pulse of CWD from the pre-disturbance stand is followed by a decline due to low input from the small diameter developing stand and finally an increase due to individual tree mortality in older stands. A large initial pulse in CWD production has been substantiated for B.C. coastal western hemlock stands but in this case there was no noticeable increase in older stands (Wells 1996). I also found high average levels of CWD volume in young stands indicating a pulse of CWD from the pre disturbance stands but variability was high. This high variability can be accounted for by the broad range in potential stand conditions present prior to disturbance. An average fire return interval of 80-100 years estimated for these forests by

Andison (1996) and no strong preference for age of burning would mean that stands could burn a number of times in a short period of time (i.e., 40 years) leading to low levels of CWD. Andison (1996) also sampled stands over 200 years of age which if burned would lead to relatively high levels of CWD. This potential difference in stand age at time of disturbance in combination with other factors such as differences in disturbance intensity make for a broad range of CWD in young stands possible. The concentration of CWD in later stages of decay (i.e., decay classes 4 & 5) indicates that most of the material from the pre-disturbance stands had been on the ground long enough to have passed through the initial stages of decay. It also indicates a low level of recruitment subsequent to the initial pulse from the pre-disturbance stand. A similar pattern was evident in the mature stand type but the peak was shifted to decay class 5. By this time a proportion of CWD from the pre-disturbance stands could be undetectable having been incorporated into the humus. A more balanced level of CWD volume in remnant and old stands indicates a more steady input of CWD from factors such as periodic death of individual large trees.

Regeneration and floristics

Lodgepole pine regeneration in the understory of some remnants was a key feature distinguishing them from old stands. In general, higher amounts of early successional species (i.e., lodgepole pine, white spruce and black spruce) could be used to differentiate remnants from old forest. This is an indication of the influence on island remnants of the disturbance which isolated them.

There was a high degree of similarity (> 60%) in vegetation among all stand types sampled. As a general rule, when similarity coefficients between vegetation units are greater then 50%, separation into plant associations is not likely to be ecologically meaningful (Mueller-Dombois and Ellenberg 1974). I expected high similarity because all stand types were primarily sampled from within one site series, the SBSmk1/06 (DeLong *et. al.* 1994). By definition all sites within the same site series will produce the same plant community at climax (Pojar *et. al.* 1987). The stands I sampled had all closed crown and enough time had elapsed in even the youngest stands (i.e., 40 years) for any shorter lived early seral species (e.g., *Epilobium angustifolium*) to have declined.

Of the species which formed a unique diagnostic combination for old stands, only *Smilacina racemosa* has been previously found to be associated with old forests. In a study of succession in sub-boreal forests by Clark (1996) this species was located at the same end of the species ordination as older stands in the stand ordination. For remnant stands, the presence of lodgepole pine in the shrub layer, lower moss cover than old stands, and high variability indicated by the ordination could all be related to variation in disturbance history. In particular it could relate to the presence/absence and relative intensity of disturbance within remnants during the wildfire through which they survived.

Percentage cover of the shrub layer was higher in remnants and old stand types than in mature and young stand types and appeared to correspond to lower cover of the overstory tree canopy. Increases in shrub cover with stand age were previously documented in a study by Clark (1994).

Effects of Wildfire on Island Remnants

The stand structure demonstrated by the age-class sequence of the matrix stands illustrates the typical development of lodgepole pine stands following stand-replacement wildfire in landscapes such as the area being studied (DeLong and Tanner 1996). Lodgepole pine produces most of its seed in serotinous cones which release seed only under intense heat (Lotan 1974). Thus, after wildfire, seed is released and lodgepole pine regenerates readily and rapidly on the burned substrate and the post disturbance stand is dominated by a relatively even-aged cohort of lodgepole pine. Once the initial cohort of lodgepole pine is established, regeneration of lodgepole pine is restricted since most of the seed has been released from the cones and because lodgepole pine is a pioneer species which is poorly adapted to shade (Krajina 1982). Other species which only regenerate from live seed sources and are more shade adapted (e.g., spruce and subalpine fir) tend to dominate the understory. This pattern of stand development has been previously documented in the SBS (Kneewshaw 1991, Clark 1994).

In 7 out of the 10 remnant stands an alternate pattern of stand development was evident as characterized by the presence of a second cohort of lodgepole pine. In 2 of the plots the second cohort was indicated by a second peak in the diameter class distribution of lodgepole pine. In the other plots it was indicated by the presence of lodgepole pine regeneration in the regeneration plots, and/or lodgepole pine presence in the shrub layer according to the vegetation surveys. The evidence is strong (> 100 stems/ha) in 3 of these plots. In these stands the presence of a large second cohort of lodgepole pine is evidence that the fire that replaced the surrounding stand may have disturbed the remnant stand enough to initiate a second lodgepole pine cohort. The presence of more lodgepole pine and hybrid white spruce, both of which prefer mineral soil substrate for regeneration, indicate that mineral soil may have been exposed within some of the remnants during the wildfire which initiated them. Evidence of fire within all these remnants was indicated by the presence of fire scarred trees whose scar age was similar to that of the surrounding young forest. Regeneration plots containing lodgepole pine also had thinner forest floors on average than all other plots (3.5 cm vs 5.1 cm), suggesting forest floor consumption at the time of the disturbance.

The finding that the size distribution of the second cohort of lodgepole pine initiated within the remnants was distinct from those in the surrounding stand was surprising. One might expect the size class distributions to be similar since they were the consequence of the same disturbance.. However, there were distinct differences in timing and duration of lodgepole pine recruitment. There was very little lodgepole pine in the understory of young stands and it was mostly in larger height classes. Thus the structure of the young stands is even-aged with lodgepole pine stems almost completely restricted to the overstory. In contrast, the height class structure of the remnant stands indicated uneven-aged lodgepole pine regeneration with a peak occurring in the lowest height class and a more spread out distribution approximating a negative exponential curve.

Uneven-aged structure and a negative exponential distribution have been reported for lodgepole pine in the Sierra Nevada of California (Parker 1986) and on xeric, nutrient-poor sties in Yellowstone National Park, Wyoming (Despain 1983). These stands experience continuous or intermittent understory lodgepole pine regeneration and are characterized by a lack of crown fires. The uneven-aged stand regeneration is a result of annual seedfall from non-serotinous cones. Lotan (1967) determined that in such stands the ratio of serotinous to non-serotinous cone type trees is lower than in landscapes that experience stand replacement wildfire. In the sub-boreal landscape I studied however, selection would favor serotinous-coned trees due to the frequency of stand replacement wildfire. Assuming that lodgepole pine remnants do not reoccur in the same position in the landscape studied, the two distinct regeneration patterns displayed by the remnants and the surrounding young forest suggest that lodgepole pine may exhibit both serotinous and non-serotinous regeneration strategies regardless of long-term selection pressure for cone serotiny. The likelihood of a remnant displaying the alternative uneven-aged regeneration pattern likely decreases with the size of the remnant since disturbance related to a fire is less likely to penetrate into larger remnants. This was supported by the data since the largest remnants sampled did not display the alternate regeneration strategy. DeLong and Tanner (1996) has indicated that the majority of remnants are < 10 ha in size and thus an uneven-aged regeneration pattern in remnants may be fairly common. Whether this alternate regeneration system is a response which is initiated by disturbance, or is simply a function of the presence of sufficient open-cone bearing trees to facilitate uneven-aged regeneration, requires additional research.

As with the presence of a second cohort of lodgepole pine, the presence of reindeer lichens (*Cladina* spp.) in remnant stands may provide evidence of disturbance of the forest floor by the wildfire which initiated the surrounding stand. None of the similarly aged old stands had reindeer lichens present within them. Previous studies have indicated the displacement of reindeer lichens by moss over succession (Maikawa and Kershaw 1976; Foster 1985). These authors relate this displacement to stand closure which occurs late in successional development (i.e., 130 - 200 years) in the stands they studied. They hypothesize that increased crown closure increases shade and available moisture which favours the mosses. Stand closure does not provide a reasonable explanation for the reduction of lichen in this study. The stands with the greatest crown closure, as estimated by percent cover of the tree layer, are the young and mature stands. Lichens were present in these stands but absent in the more open old stands. It is more likely that Cladina and Cladonia lichens are displaced by mosses over time due to the build-up of the forest floor which appears to favour the mosses.

The degree of disturbance experienced by remnants may account for the spread of remnant plots along axis 2 of the vegetation ordination. The association of lodgepole pine and subalpine fir with opposite ends of this axis corresponds to the association, within sub-boreal forests, of lodgepole pine with more recently disturbed sites and subalpine fir with later successional stages.

Management Implications

The finding that remnants could be discriminated from other stand types could be useful given the current direction of ecosystem management initiatives in British Columbia. Wildlife tree patches are being left in current harvest openings in British Columbia under the guidance of Biodiversity Guidelines (B.C. Ministry of Forests, 1996). One of the premises of the guidelines is that the closer harvest disturbances approximate natural disturbances the more likely we are to maintain biological diversity in B.C.'s forests. The discriminant equations developed could be used to test the similarity in overstory stand structure between wildfire tree patches designed within harvest openings and remnants left by wildfire.

Remnants contained higher numbers of large (> 25 cm d.b.h.) live trees and snags than the mature stand type. Since the number of large trees and snags in managed stands are unlikely to exceed those found in the mature stand type, leaving remnants within managed stands should provide an important legacy of larger diameter trees and snags throughout managed stand rotations. This could be very important for species such as the black-backed woodpecker which prefers larger diameter trees for nesting.

The relatively high number of trees within remnants containing evidence of feeding cavities indicates that they may provide important habitat for cavity feeding birds. It was also noted that all the trees with presence of feeding cavities within the young stands were individuals that had survived the stand replacement wildfire. Preferential selection of wildfire remnants by cavity feeding bird species has not been clearly documented. However, Hutto (1995) found certain bird species to be highly associated with stand-replacement wildfire and some species (e.g., the hairy woodpecker) were highly negatively correlated with fire intensity. Lower fire intensities would likely be correlated with higher levels of live tree retention which would approximate the conditions found in remnants.

In the young stands (40-70 yrs old) that would represent mid-rotation managed forests, there is a lack of recently killed CWD (i.e., decay states 1&2), especially in larger diameter classes. With higher utilization standards and a general increase in utilization level from harvested stands, this lack of recently downed CWD would be apparent throughout the rotation. Unmanaged remnants of the natural forest, left within harvested areas, could provide an important source of recently downed larger diameter CWD throughout the rotation of the surrounding managed stand.

One of the major concerns of forest managers with leaving wildlife tree patches and riparian reserves in cutover areas is that there may be a lot of windthrow within them. In the remnant forest patches examined, there was little evidence of recent windthrow beyond what might be expected due to the age of the stands. The distribution of CWD volume by decay class, and density of larger standing trees in remnants were not different from the old forests. This indicates that the remnants are at least as stable as the old forest matrix. Examining wildfire remnants could provide important information about the design of windfirm wildlife tree patches.

The finding that remnants had higher shrub cover than the young stands which initially surround them indicates that remnants could provide important areas of forage for ungulates. This could be especially important during the period of time when forage availability beneath the young stand is limited due to high crown cover.

CONCLUSIONS

In landscapes dominated by stand replacement wildfire, island remnants appear to provide unique habitat conditions that are not present elsewhere in the landscape. They provide the sharpest contrast to the developing young forest which surrounds them and therefore likely provide important habitat for species requiring specific habitat elements such as large diameter trees or large diameter soft snags. Remnants are most similar to old forest (i.e., > 140 years) and thus could provide important old forest habitat in managed landscapes where a high percentage of the forest is being managed on shorter rotations (i.e., 80 - 100 years). High variability among island remnants indicates differences in conditions before, during and after disturbance. Including reserved patches in managed stands should be an important technique to provide similar habitat variability to that present in natural forests.

The evidence from this study suggests that the interior of most remnants is affected by the disturbance which has isolated them and this leads to a pattern of lodgepole pine regeneration that is rare in the remainder of the landscape. This pattern of lodgepole pine regeneration illustrates the complex nature of stand dynamics at smaller spatial scales. To typify the natural stand dynamics of lodgepole pine as even-aged in the landscape studied would be to ignore the uneven-aged regeneration dynamics illustrated by some island remnants. Further examination of these natural examples of uneven-aged lodgepole pine regeneration in the sub-boreal landscape could provide managers with an optional silvicultural system for the management of lodgepole pine. This is important given the demands of the public and the direction of the Forest Practices Code of B.C. to make greater use of silvicultural systems other than clearcutting.

Since the history of high rates of industrial logging in sub-boreal and boreal forests is both recent and localized in areas of older forest, the potential still remains for fundamental changes in resource management philosophy. The implications of modeling forest harvest on the spatial patterns of wildfire needs to be tested at a variety of spatial scales. The arguments for altering forest harvest pattern at the landscape level have been well documented (DeLong and Tanner 1996; Bunnell 1995; Wallin *et. al.* 1994; Hunter 1993) and the arguments for retaining legacies of the previous stand are numerous (Franklin 1993; Hansen *et. al.* 1991; Maser 1988). It is important that we now determine fundamental differences between natural disturbance and harvesting designed to approximate natural disturbance. Wildfire tree patches and riparian reserves are currently being left in openings in British Columbia according to direction from the Forest Practices Code and Biodiversity Guidelines. Results of this study will enable habitat comparisons between these reserves and island remnants. These comparisons may indicate the need for alterations to the management of reserves based on differences between them and island remnants deemed to be functionally important.

This study illustrates the potential importance of smaller elements in the landscape that may be missed or discounted in coarser scale studies. Island remnants provide habitat diversity at intermediate scales and may play functionally important roles in maintaining biological diversity. Managing reserves within harvested areas to approximate the habitat characteristics of island remnants should be an important consideration in sub-boreal landscapes where frequent large wildfires were historically common.

CHAPTER 3 - ISLAND REMNANTS AND NATURAL REGENERATION

3.1 INTRODUCTION

Within northern forests, planting has become the preferred method of regeneration after clearcutting for the more difficult species to regenerate such as Douglas-fir and white spruce. Recently however, a shift towards greater reliance on natural regeneration within northern forests has been suggested based on both economic and ecological arguments (Booth *et. al.* 1993). Successful natural regeneration requires that seed be dispersed relatively evenly over the harvested area. Serotinous species such as lodgepole pine can regenerate from seed released from cones during fire or other disturbance. In contrast, white spruce and Douglas-fir require live standing trees as a seed source. Eberhart and Woodward (1987) have hypothesized that, following wildfire, island remnants played an important role as live seed sources for re-establishment of the surrounding forest.

Seedling establishment at any single location within a disturbance is influenced by a variety of factors including: quality of substrate for regeneration; amount and quality of seed provided by the seed source; and microenvironmental conditions before and after seed dispersal. Distance to seed source has been determined to be important in establishment of non-serotinous conifer species. Agee and Smith (1984), working in mixed species subalpine forests in the Olympic peninsula, reported very low regeneration of all species at distances greater than 200 m from the seed source. Douglas-fir regeneration occurred only in close proximity to the seed source. Ryker (1975) reports that most seed from Douglas-fir falls within about 1 chain (approx. 20 m) of a stand edge.

My study area represents the northern limits of the range of Douglas-fir. Within the study area Douglas-fir is most abundant on drier sites, primarily on coarser-textured ridges and hills. Even on sites where it is abundant in the overstory, it is generally absent in the understory which is typically dominated by subalpine fir (DeLong et. al. 1993). Given Douglas-fir's limited distribution and poor regeneration under its own canopy in northern ecosystems, it is possible that remnant survivors of wildfire are critical in maintaining the species' distribution within these forests. Remnants often represent the only live Douglas-fir seed source in large burned over areas. It is thus important to determine the role of remnant Douglas-fir as a seed source for regenerating the surrounding forest. Understanding this relationship is needed to support development of ecologically-based management prescriptions in northern forests. This is especially critical now that harvesting has replaced wildfire as the dominant disturbance shaping this landscape (DeLong and Tanner 1996).

I hypothesize that there is a significant negative relationship between Douglas-fir recruitment and distance from remnant Douglas-fir patches. If my hypothesis is supported, I will interpret this finding relative to Douglas-fir regeneration after wildfire.

3.2 METHODS

Using a combination of forest cover maps and aerial photos I selected three patches of Douglas-fir remnants within 40-60 year old forests. Remnant patches were considered to be patches containing a minimum of 4 Douglas-fir stems that had survived wildfire. I only considered remnant patches that were at least 500m from the edge of wildfire boundaries and/or 500m from other remnant patches of Douglas-fir stems.

I established four line transects (NE, NW, SE, SW) that radiated out from the approximate centre of the remnant (Figure 3.1). Along each transect I established circular 7.99 m radius (200 m^2) sample plots at 20 m intervals, and within each recorded height and d.b.h. for all Douglas-fir's $\geq$ 1.3 m in height. Heights were measured using a Criterion Laser and diameter using a diameter tape. Within one randomly located plot per transect I measured all tree species in the same manner as Douglas-fir in order to determine proportional contribution of Douglas-fir to total stand volume. At each plot I measured humus depth (cm) at 5 randomly located positions and recorded the average. I also evaluated and recorded relative soil moisture regime through assessment of a variety of site

Figure 3.1. Schematic of Douglas-fir remnant spoke plots showing layout of transects and measurement plots.

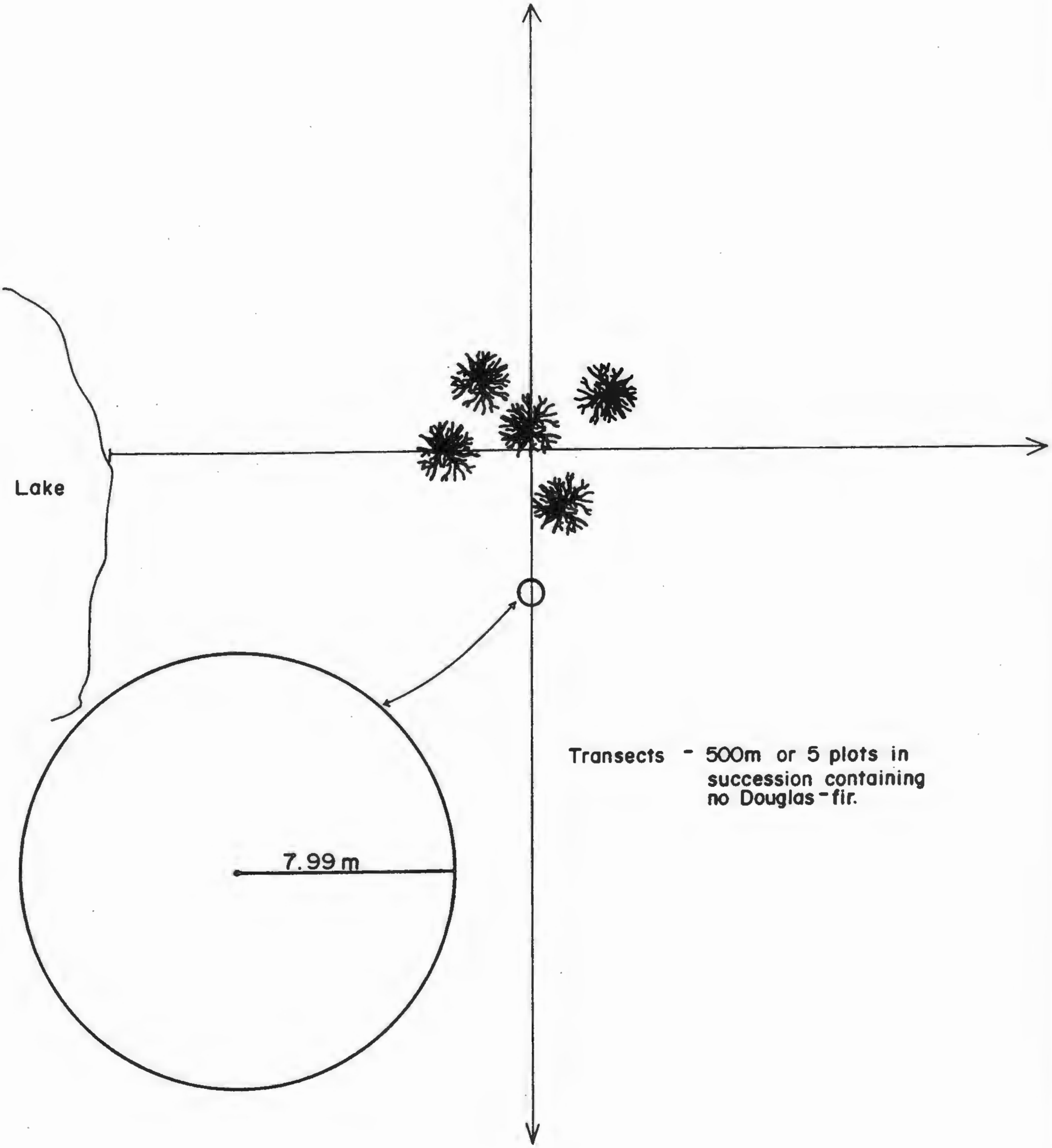

Figure 3.1. Schematic of Douglas-fir remnant spoke plots showing layout of transects and measurement plots.

and soil factors (Pojar *et. al.* 1991). Any individual remnant Douglas-fir stems within sight of the transect were noted. Sampling along each transect was continued until one of the following occurred: 5 plots in succession contained no Douglas-fir; 500 m had been reached; or a physical barrier (e.g., lake) was reached.

3.3 ANALYSIS

I calculated tree density and volume by species for each sample plot. Volume was calculated using B.C. Ministry of Forest Inventory equations for whole stem volume. For each remnant, I computed summary statistics for density and volume by distance, pooled by direction.

I used multiple regression to examine the relationship between Douglas-fir density and independent variables including: distance from the remnant patch (DI); distance from a individual Douglas-fir remnant stem (DIS); humus depth (HD); and relative soil moisture regime (MR). After viewing two-dimensional scatterplots of each independent variable and Douglas-fir density I used a log transformation of DI and DIS to achieve a linear fit. I did not transform HD and MR since they showed no apparent relationship with Douglas-fir density. I analyzed each of the three remnants separately and I initially included all independent variables in the regressions. However, after I viewed the results of this analysis I removed any non-significant variables (i.e., $p< 0.05$) and repeated the regression with the remaining variables. Following the final regression I examined a plot of the residuals against predicted variables in order to assess homogeneity of variance of the residuals (Wilkinson *et. al.* 1996). Initially I only examined total Douglas-fir density but a thorough examination of the data revealed that small diameter stems had a large influence on the regression. Therefore I completed a second set of regressions where smaller diameter stems (<7.5 cm d.b.h.) were removed.

I computed the relative contribution of Douglas-fir volume to total volume by dividing Douglas-fir volume for each plot by the average total volume of plots where all species were measured.

3.4 RESULTS

Douglas-fir recruits initiated after the disturbance, were present surrounding all of the Douglas-fir remnants sampled. Douglas-fir recruits were present in all plots within 100m of a remnant and in 22 of 39 of plots 100-300m from a remnant. Nine of 20 plots that were further than 300m from the closest remnant contained recruits. Recruits were present in 76 of 89 plots within 100m of any known remnant Douglas-fir stem.

There was a general trend of decreasing Douglas-fir stem density as distance from the remnant increased (Figure 3.2). Of the variation in total Douglas-fir density (TD) 29-68% was explained by distance from the remnant (DI) (Table 3.1). Humus depth and moisture regime were not significant ($p>0.05$) for any of the multiple regressions which included them, so these variables were removed and simple linear regression analysis was conducted using distance only. For 2 of 3 remnants, models including distance from the closest remnant stem (DIS) violated the assumption of homogeneity of variance of residuals. For the remaining remnant, DIS accounted for a greater portion of the variation in TD then DI. For the remnant with the strongest distance/density relationship, 75% of the variation in TD was explained by DI for distances up to 100 m (Figure 3.3). As well, ANOVA followed by Tukey's multiple comparisons indicated significant differences in total density between 20 m and 60, 80, and 100 m and between 40 m and 100 m (Table 3.2). Smaller stems (< 7.5 m in height) were primarily responsible for the general pattern of decrease in stems as distance from the remnant increased (Table 3.3). When these stems were removed from the data the amount of variability in stem density (MD) explained by distance (i.e., r^2 of the regression) decreased (Table 3.1). The distribution of larger Douglas-fir stems, especially those > 17.5 m in height, appeared to be unrelated to distance from the remnant (Table 3.3). This pattern was observed in all 3 remnants sampled.

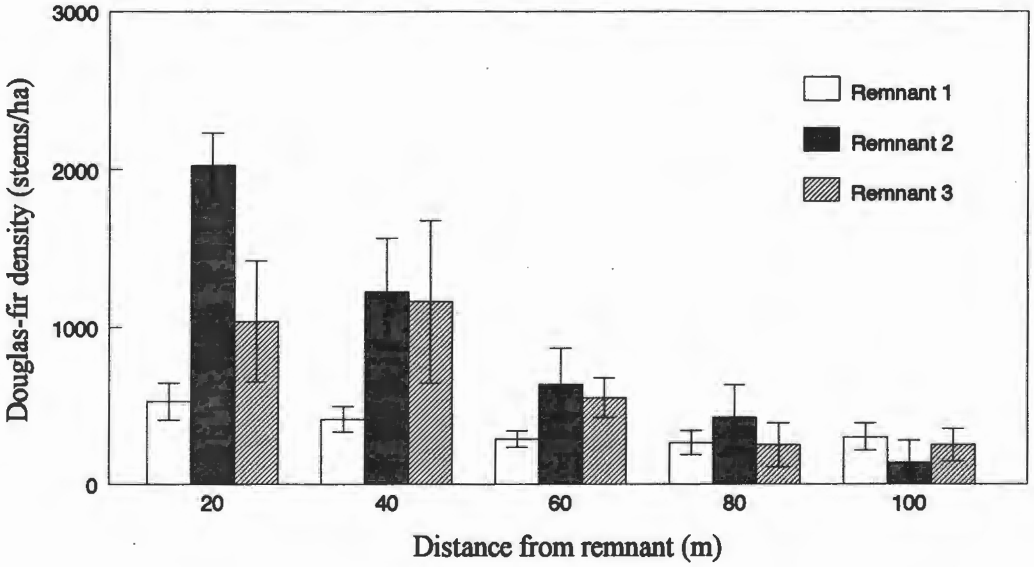

Figure 3.2 Douglas-fir density as a function of distance from Douglas-fir remnants.

Table 3.1. Linear regression equations predicting density of Douglas-fir stems >1.3 m (TD) and >7.5m (MD) in height based on distance from Douglas-fir remnant patches (DI) and stems (DIS).

Remnant	Equation	*n*	r^2	*F*
Remnant 1	TD = 582.1 - 118.2 (DI)	37	0.29	15.60**
	TD = 749.9 - 119.7 (DIS)	37	0.40	24.49**
	MD = 487.9 - 72.5 (DI)	37	0.24	12.31**
	MD = 397.2 - 64.9 (DIS)	37	0.38	21.35**
Remnant 2	TD = 3633.5 - 677.6 (DI)	35	0.68	74.07**
	MD = 926.0 - 162.9 (DI)	35	0.41	24.36**
Remnant 3	TD = 1879.9 - 303.9 (DI)	42	0.27	15.93**
	MD = 549.5 - 88.4 (DI)	42	0.17	9.54**

**Significant at $p < 0.01$

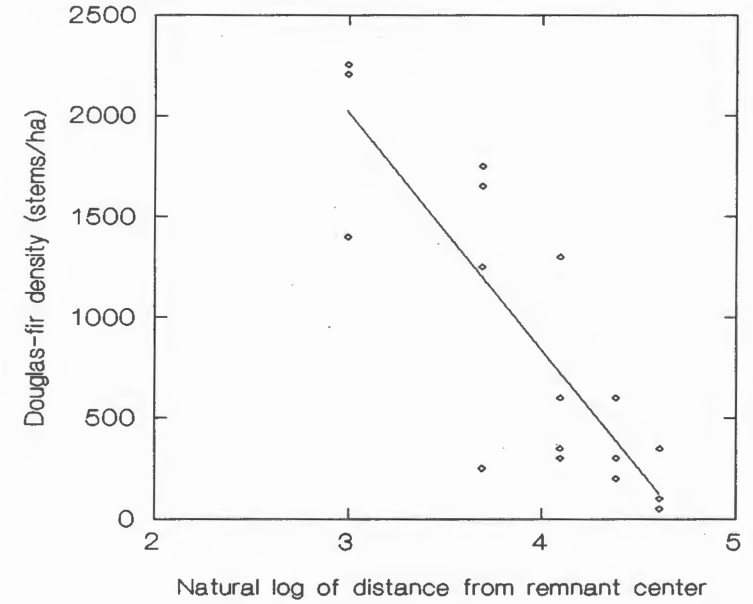

Figure 3.3 Douglas-fir density as a function of natural log of distance from center of remnant 2 for distances up to 100 m ($y = 5541.7 - 1176.7\,x$, $n = 20$, $r^2 = 0.75$).

Table 3.2. Mean number of stems per hectare of Douglas-fir stems >1.3m in height at different distances from Douglas-fir remnants (means followed by a different letter are significantly different at $p < 0.05$, $n=20$) .

Remnant	Distance from remnant (m)				
	20	40	60	80	100
1	525^{a}	412^{a}	287^{a}	263^{a}	300^{a}
2	2025^{a}	1225^{ab}	638^{bc}	425^{bc}	138^{c}
3	1038^{a}	1162^{a}	550^{a}	250^{a}	250^{a}

The change in density with distance is much more pronounced in remnant 2 than the others and is almost absent for remnant 1. This large difference in distribution with distance between the remnants is largely explained by the large differences in the density of stems < 12.4m in height (Figure 3.2 & Table 3.3). When these shorter stems are not considered the differences between remnants is reduced and no consistent pattern with distance is evident.

Within the 3 sites studied, Douglas-fir volume contributed up to 22% of the total volume within a single plot while the average for plots within a 100 metres of the remnant was 10%.

Since a strong relationship between Douglas-fir recruitment and distance was found for only 1 of the 3 remnants examined I rejected the hypothesis of a significant negative relationship between Douglas-fir recruitment and distance from remnant Douglas-fir patches. However, the presence of Douglas-fir recruits surrounding all the remnants sampled indicates that they may be an important source of recruitment.

Table 3.3. Average Douglas-fir density (s.p.h.) for different height classes at different distances from remnant 1 (bold), 2 (normal), and 3 (italic) (pooled by direction).

Distance (m)	Height class limits (m)			
	< 7.5	7.5 - 12.4	12.5-17.4	>17.4
20	**250** 1662 *625*	**175** 312 *288*	**63** 50 *125*	**38** 0 *0*
40	**288** 812 *525*	**50** 250 *400*	**63** 125 *175*	**12** 38 *62*
60	**75** 225 *263*	**163** 288 *150*	**38** 75 *125*	**12** 50 *12*
80	**100** 225 *212*	**50** 150 *12*	**88** 25 *12*	**25** 25 *12*
100	**100** 62 *138*	**88** 38 *112*	**100** 12 *0*	**12** 25 *0*

3.5 DISCUSSION

The results of this study indicate that 27-75% of the variability in Douglas-fir recruitment after wildfire can be accounted for by distance from remnant Douglas-fir patches depending on which remnant and what distances were considered. Previous information available on the importance of distance to seed source is not consistent. Ryker (1975) suggests that in moist habitat types distance from a seed source is not important for establishment of Douglas-fir. Boe (1953) determined that Douglas-fir seeds are cast in nearly equal numbers between distances of 4-12 chains (approx. 80-250 m). However, Agee and Smith (1984) found that Douglas-fir recruits were only present within a short distance of the seed source. Due to the variability in results, the present study could not support any of the previous findings.

Recruits that were established immediately following the wildfire appeared to be less affected by distance than more recent recruits. Taller stems which more likely represented early recruits were not strongly related to distance from the remnants. However, for one of the remnants studied, shorter recruits were strongly correlated to distance from the remnant. These differences in recruitment could be related to a number of factors which are altered over the course of succession. One such factor which could explain the differences is wind dispersal on hard snow. This phenomenon remains unstudied but a number of people working in northern forests suggest it as an explanation for occurrences of natural regeneration kilometres away from the nearest seed source in large clearcuts. The likelihood of wind dispersal on snow likely changes significantly over the course of succession. Immediately following wildfire wind velocity at the ground surface would be high and greater wind and solar action on the snow surface would make hard snow crusts more likely. However, once a relatively dense new canopy has formed wind velocity at the ground surface is reduced and snow crusting is less likely. Thus early in succession, recruitment would be less spatially restricted due to the increased likelihood of wind dispersal on snow. This suggests that models of spatial recruitment of tree seedlings should be developed separately for early post-disturbance conditions and later successional stages. This point is made in a recent paper by Ribbens *et. al.* (1994) on modeling seedling recruitment. The authors acknowledge that their model developed using data from 90 - 130 year old stands was not directly applicable to clearcuts which are subject to different weather and wind dynamics.

The presence of a higher number of recent recruits in plots adjacent to the remnant patches than in plots further away indicates that the remnant trees still form the most important seed source even though 40 - 60 year old Douglas-fir trees were present throughout the sampled areas. Although the average contribution of Douglas-fir to total volume in plots within 100 metres of the remnants was not high (i.e., 10%), it is still significant considering that as few as 6 trees made up the remnant patch and Douglas-fir is at the limits of its ecological range.

One factor which could explain the differences in pattern of recruitment with distance observed for the 3 remnants is seedbed conditions. However, two factors measured that relate to seedbed condition, relative soil moisture regime and humus depth, did not appear to influence recruitment over the range measured. Other factors that might explain the differences such as the amount of current seedfall, quality of the seed, and amount of current seed predation were not measured.

The fact that Douglas-fir recruits were present in the stands sampled provides evidence that wildfire remnants provide an important source of Douglas-fir recruitment in the landscape. The average fire return for the study area has been estimated at 90 years and there is evidence of fires having returned to an area in as little as 20 years (Andison 1996). Given this short fire return interval, the fact that seeds for Douglas-fir recruitment can only be provided by a live seed source and that cone production increases with the age emphasizes the relative importance of Douglas-fir that has survived fires for providing recruitment in the landscape.

3.5 CONCLUSIONS

Douglas-fir remnants left by wildfire provide a source of seed for Douglas-fir recruitment in the post fire regenerating forest. Recruitment immediately following the wildfire appeared to be more randomly distributed than expected but this may be due to exceptional dispersal conditions during this time period. Recruitment later in succession decreased exponentially as distance increased from the remnant. Patches of Douglas-fir left in managed cutovers could provide an important source of recruitment for the surrounding stand which will augment planted or natural lodgepole pine and white spruce.

CHAPTER 4 - CONCLUSIONS

4.1 CONCLUSIONS

This research on island remnants has examined elements of the landscape which, although representing a small proportion of the total landscape, appear to be ecologically distinct and provide important ecological services to the surrounding forest. My findings suggest a need to examine natural disturbance at multiple scales and not ignore rarer landscape elements. Previous research on natural systems has tended to focus either on examining pattern and process at large spatial scales or in modal stands at smaller spatial scales. The finding of unexpected patterns of lodgepole pine regeneration in remnants demonstrates that detailed examinations of less common elements in the landscape can lead to important insights about the variability and adaptability of natural systems.

This research provides information to improve forest management based on the premise that forest harvesting designed to approximate natural disturbances or regimes will lead to more ecologically sustainable forest management practices. For example, the findings suggest how wildlife tree patches left in the managed forest may be monitored with respect to their ecological attributes relative to their counterparts in the natural forest. Alternate silvicultural systems to clearcutting are receiving greater attention in northern forests. This research provides the basis for investigating uneven aged regeneration systems for lodgepole pine stands in sub-boreal forests. An alternate uneven-aged lodgepole pine regeneration system could be useful for maintaining mature forest characteristics where this is desired to meet other management objectives (e.g., visual quality). The ecological role of Douglas-fir in northern forests has been the focus of a recent conference and management plan entitled "Management of Douglas-fir at its Northern Limits" (Oniel *et. al.* in prep.). The findings of this study regarding Douglas-fir recruitment provide useful data to assist in predicting the potential recruitment from patches of Douglas-fir left in managed cutovers.

The high variability in ecological attributes of all stand types indicates that conventional statistical approaches which focus on means may be inappropriate for future comparisons between natural and managed stands. Examining aspects of the pattern of variability may provide more insight into ecological meaningful difference.

There are many limitations to our ability to incorporate characteristics of natural disturbance into managed forests. For instance, removal of the trees to make wood products and regulations designed to protect workers restricts our ability to leave large numbers of standing snags. However, leaving patches of trees behind which emulate the ecological characteristics of island remnants is achievable and can bring us closer to our objective of achieving ecological sustainability.

4.2 RECOMMENDATIONS

1) **Retain existing wildfire remnants in areas of younger forest (i.e., <100 yrs old) and create new ones in managed forest by leaving wildlife tree patches that represent equivalent landscape positions and have similar ecological characteristics to the remnants described in this study.** The combination of rarity and uniqueness may make existing remnants a target for protection. However, given that remnants are a product of disturbance and do not get unusually old, protection may not be the most appropriate strategy. Rather, new remnants which emulate those left in the natural forest should be created in the managed forest. Harvesting of existing natural remnants occurring in younger (i.e., 0-70 years) forests should be avoided since this is where remnants likely provide the greatest ecological services to the surrounding forest.

2) **Conduct more research on remnant forest patches and other similar legacies of natural disturbance.** This study has taken the first step in understanding the historic role of island remnants in the natural forest. More study is needed in order to make linkages between the distinctiveness of remnant forest patches and their role in providing habitat for biota, and

provide the necessary information to manage for equivalent habitats in managed stands. In this respect, the support received for FRBC projects “Ecological Significance of Remnant Forest Patches within SBS Plateau Landscapes: Diversity, Abundance, and Habitat Relationships of Forest Birds (FR-95/96-57) and “Investigation of the Positional, Dimensional, Structural, and Ecological Attributes Which Determine the Relative Windfirmness of Riparian Reserves and Wildlife Tree Patches” (FR-96/97-073) is encouraging.

3) Include more flexibility within forest management guidelines in order to manage for similar variability in ecological characteristics to that of the natural forest. Managing for variability may be one of the more difficult challenges facing forest managers. Historically, forest managers have applied relatively simple silvicultural systems over large areas and have built up a set of standards which measure "success" based on targets such as a certain number of well-spaced trees. Greater overall flexibility in silvicultural prescriptions and targets based on attaining some level of variability is necessary if the goal of sustaining forest ecosystems is to be met.

4) Encourage more field tours which demonstrate research findings. This study reemphasizes the importance of field demonstrations of research findings. Although certain measurable differences between island remnants and the young stands surrounding them appeared to be ecologically significant and could be expressed in statistical terms, many intangible differences may be as or more important. It is not until one has trudged through a maze of dense juvenile trees and deadfall to break out into an open brighter remnant to the sound of singing birds that one realizes the limits of our ability to measure and express ecological findings.

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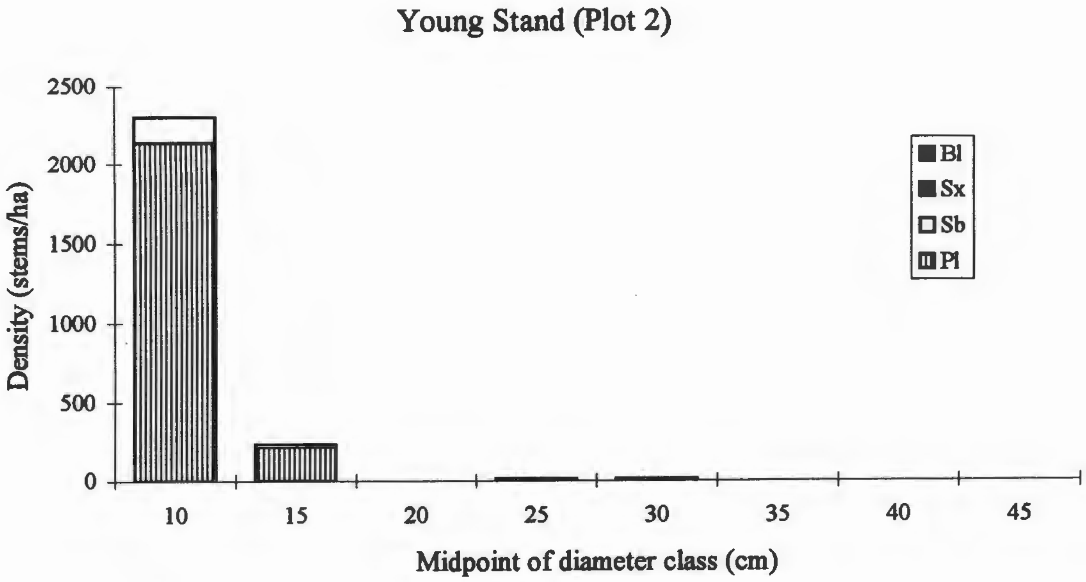
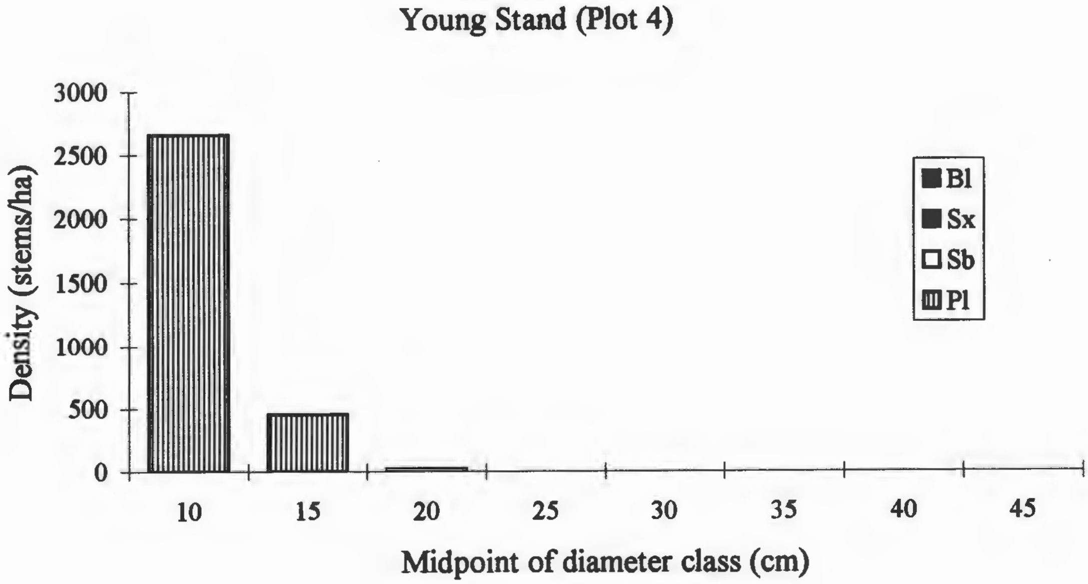
APPENDIX 1. SUMMARY OF SOME STAND, SITE AND SOIL FEATURES OF SAMPLE STANDS.

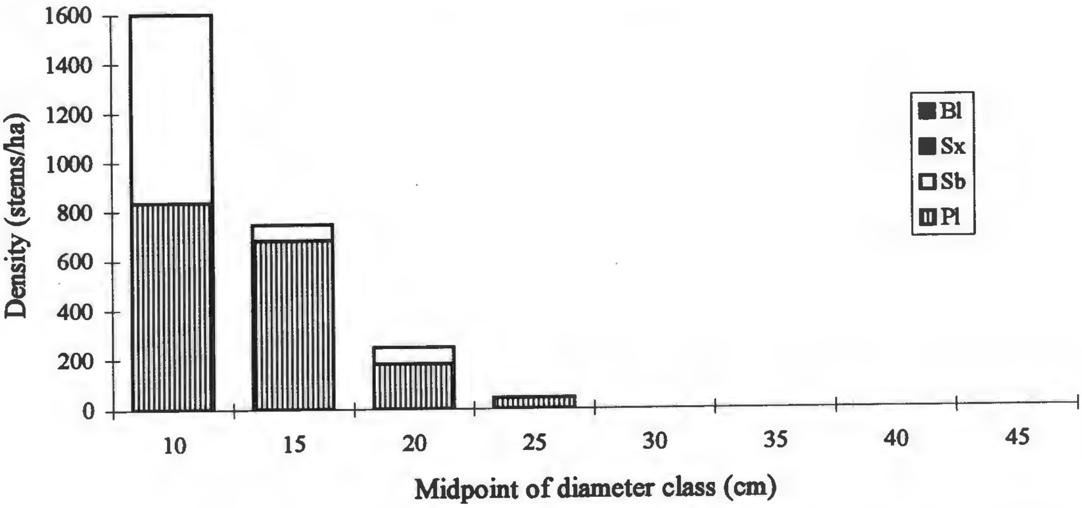
Plot	Type	Age range (yrs)	Density (sph)	Slope position	Soil Texture[1]
1	Remnant	101 - 144	711	level	SiL
2	Young	46 - 56	2544	level	L/SL
3	Remnant	112 - 147	1044	mid slope (15%)	LS
4	Young	47 - 55	3133	level	LS
5	Mature	121 - 132	1478	level	SiL/SiCL
6	Old	162 - 186	911	level	L/SiCL
7	Old	134 - 146	655	level	SiL
8	Old	136 - 165	844	level	SL
9	Old	109 - 147	1389	level	SiCL
10	Mature	84 - 109	1489	mid slope (15%)	SiCL/SiC
11	Old	108 - 196	678	level	SiL/SiCL
12	Mature	99 - 112	1544	level	SL
13	Remnant	67 - 125	1133	level	SL
14	Young	49 - 55	2678	level	LS
15	Remnant	169 - 177	567	level	SL
16	Remnant	72 - 97	1311	level	SL/SiCL
17	Old	161 - 193	1400	level	SL/L
18	Young	58 - 70	2144	level	L
19	Remnant	106 - 124	1744	level	SL
20	Young	47 - 50	3089	level	SL/L
21	Mature	104 - 124	1589	level	SL/LS
22	Old	178 - 196	967	level	CL
23	Mature	98 - 114	1133	level	CL/SiCL
24	Old	164 - 177	1156	level	SiCL
25	Mature	113 - 129	1344	mid slope (5%)	LS
26	Mature	109 - 111	3311	level	SL/CL
27	Remnant	206 - 227	1355	mid slope (10%)	LS/SL
28	Remnant	151 - 223	1622	crest (3%)	SiL/SiCL
29	Mature	76-82	3178	level	SiCL
30	Young	56 - 61	2244	mid slope (3%)	SiL
31	Mature	88 - 99	2444	mid slope (2%)	SL/SiL
33	Young	61 - 69	2644	mid slope (12%)	L/CL
34	Remnant	110 - 131	1400	lower slope (5%)	SL
35	Old	128 - 155	1000	mid slope (8%)	L
36	Mature	62 - 74	1578	level	L/SL
37	Old	212-238	1022	level	L
9317	Young	60 - 62	2800	level	LS
9319	Remnant	142 - 165	767	level	SL
9322	Young	65-66	2544	level	SiL/Si
9324	Young	65 - 66	3089	level	SiL/Si

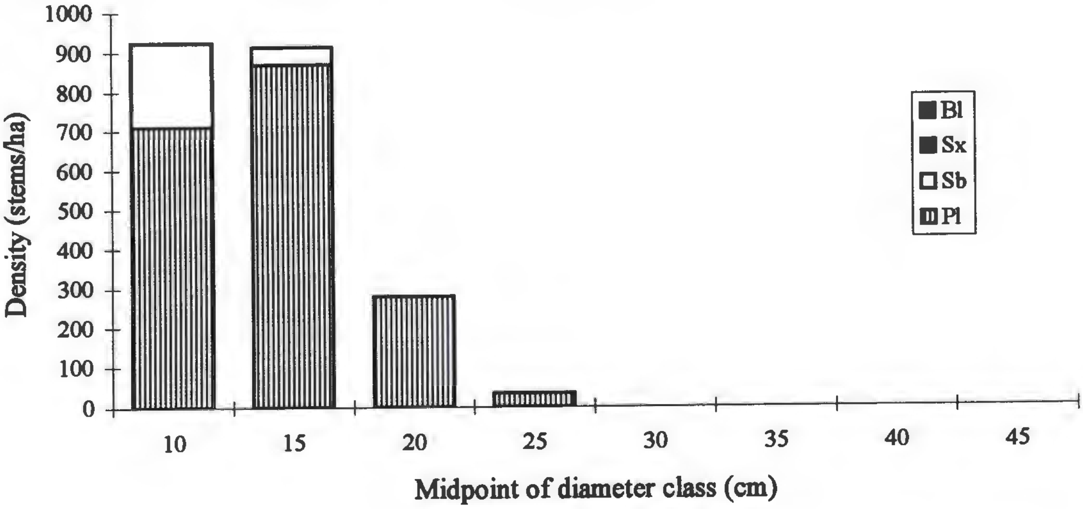
[1] Soil textural classes according to soil textural triangle as follows: CL - clay loam, L - loam, LS - loamy sand, Si - silt, SiL - silty loam, SiCL - silty clay loam, SL - sandy loam.

APPENDIX 2. DENSITY HISTOGRAMS FOR ALL SAMPLE STANDS.

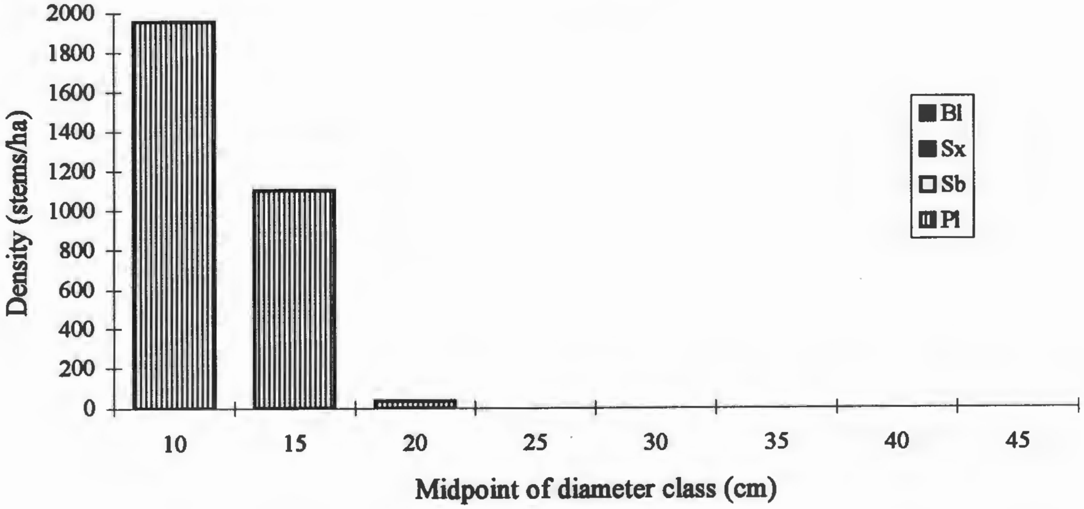

Young Stand (Plot 2)
Density (stems/ha)
2500
2000
1500
1000
500
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
■ Bl
■ Sx
☐ Sb
▥ Pl


Young Stand (Plot 4)
Density (stems/ha)
3000
2500
2000
1500
1000
500
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
■ Bl
■ Sx
☐ Sb
▥ Pl

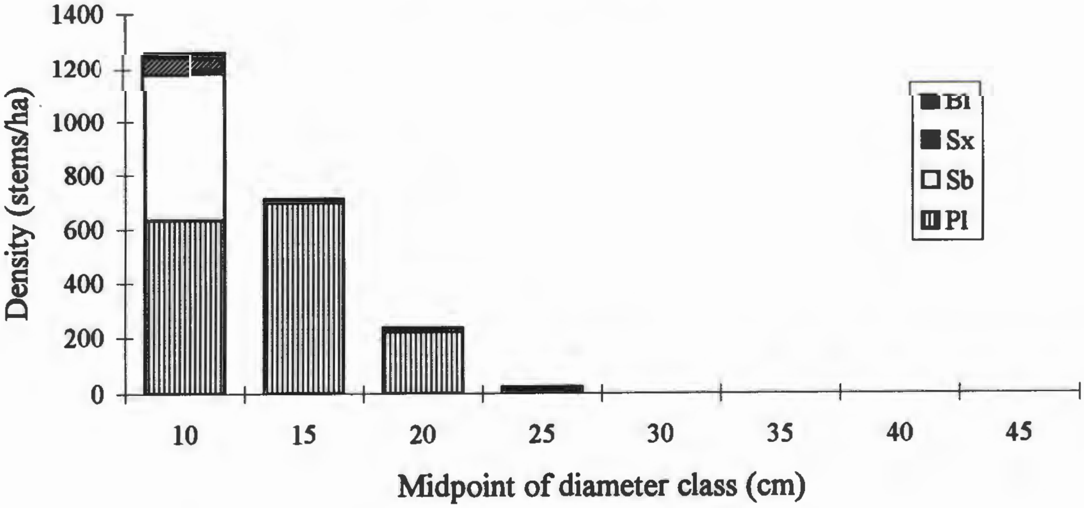

Young Stand (Plot 14)

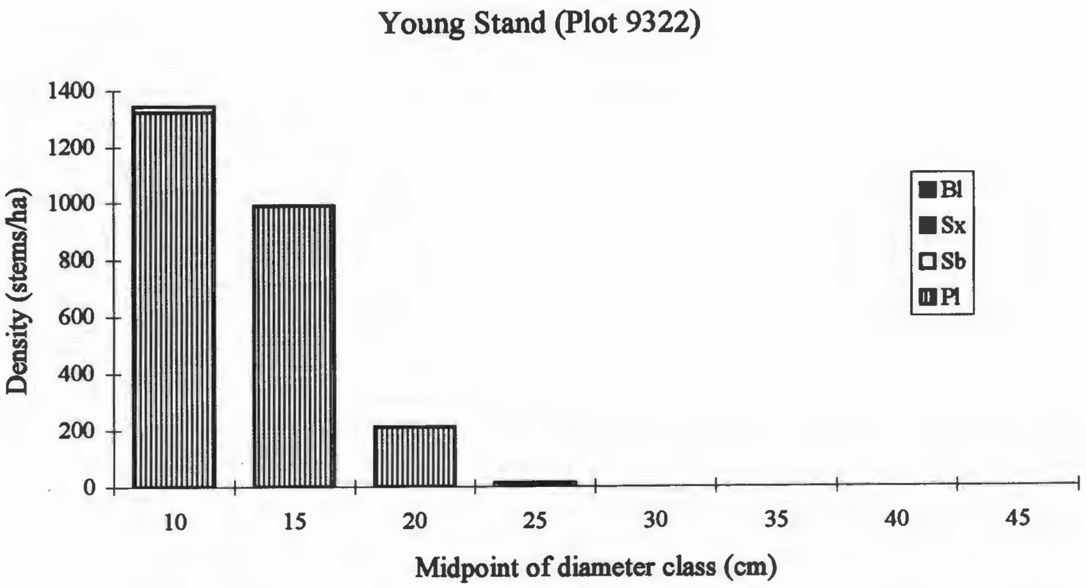

Young Stand (Plot 18)

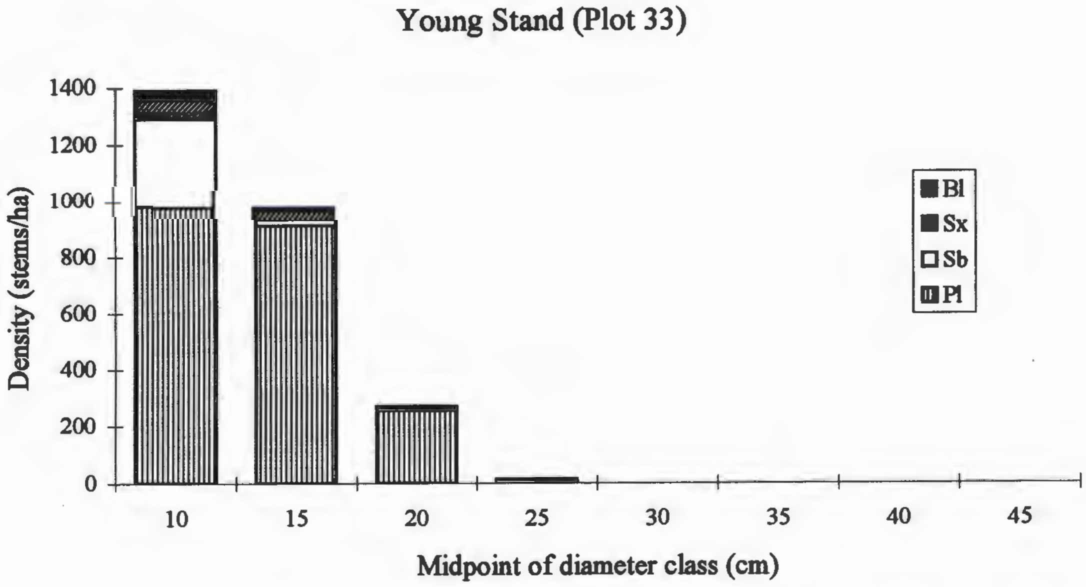
Young Stand (Plot 20)

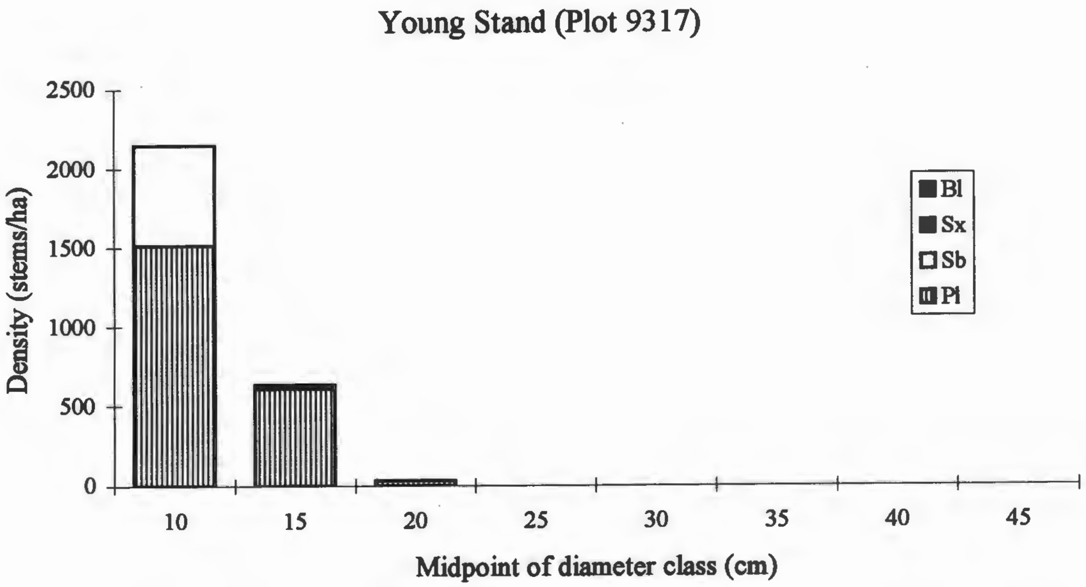


Young Stand (Plot 30)

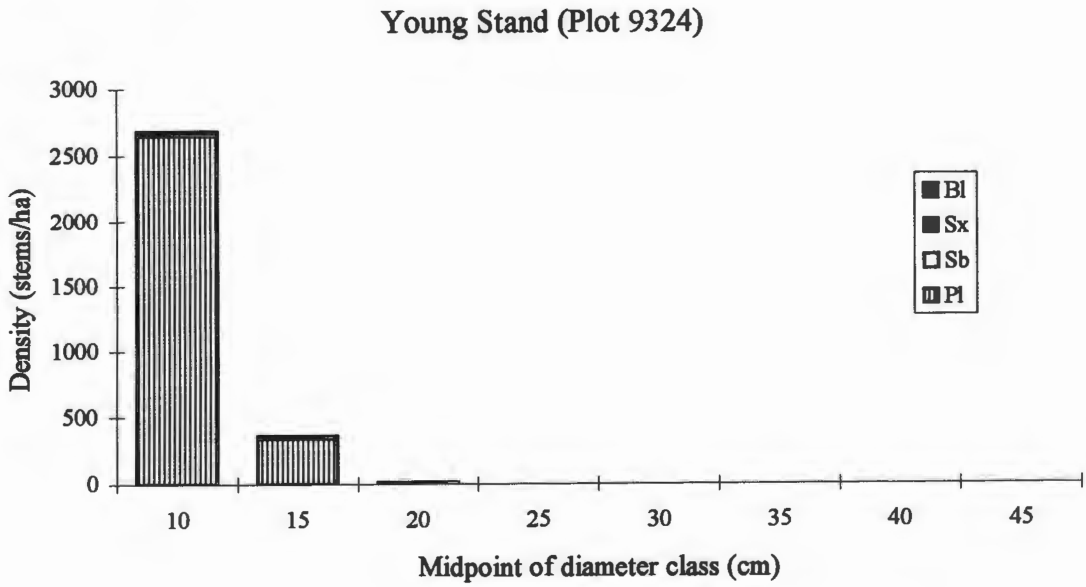



Young Stand (Plot 9322)
Density (stems/ha)
1400
1200
1000
800
600
400
200
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
■ Bl
■ Sx
□ Sb
▥ Pl

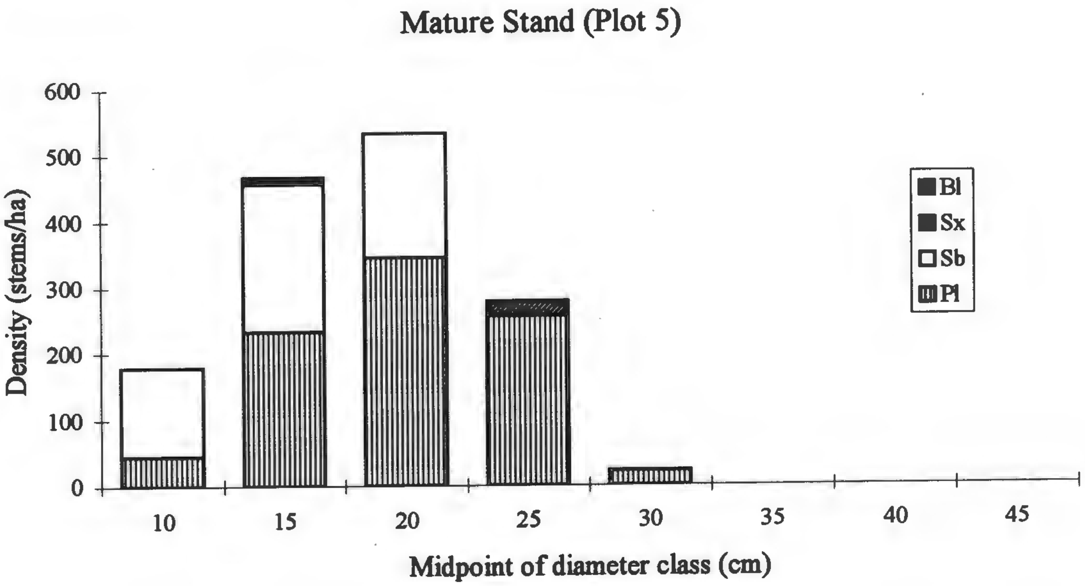

Young Stand (Plot 33)
Density (stems/ha)
1400
1200
1000
800
600
400
200
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
■ Bl
■ Sx
□ Sb
▥ Pl

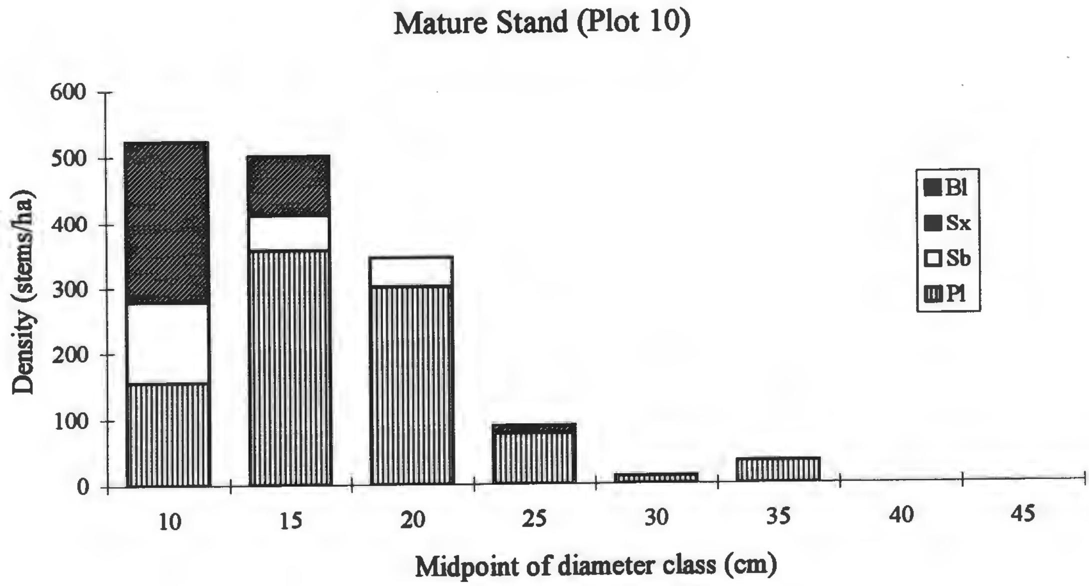


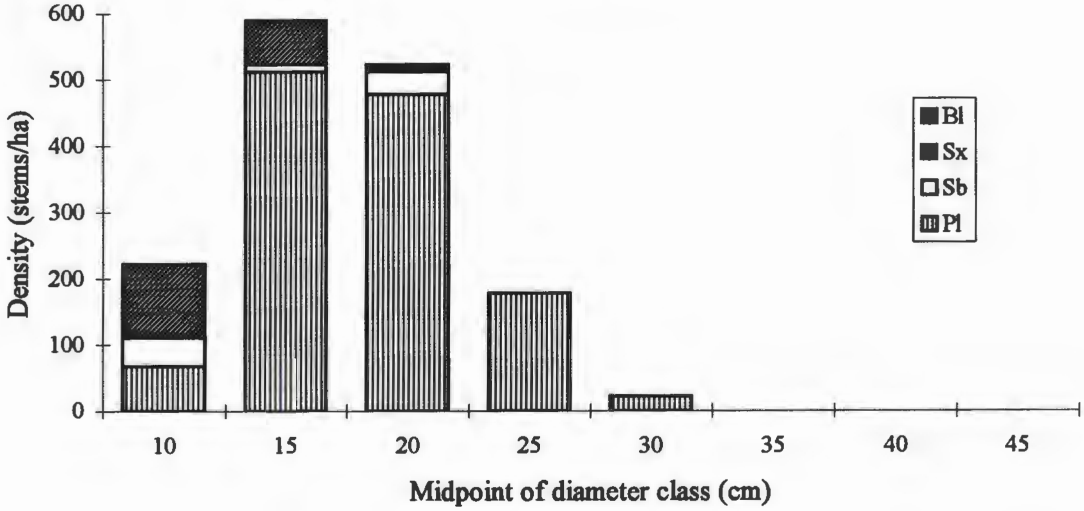
Young Stand (Plot 9317)



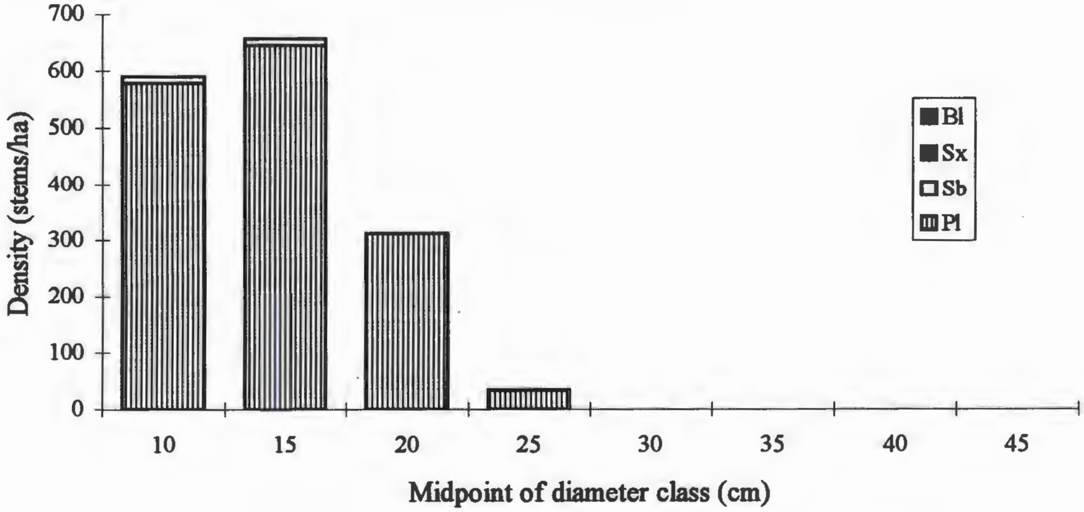
Young Stand (Plot 9324)


Mature Stand (Plot 5)


Mature Stand (Plot 10)

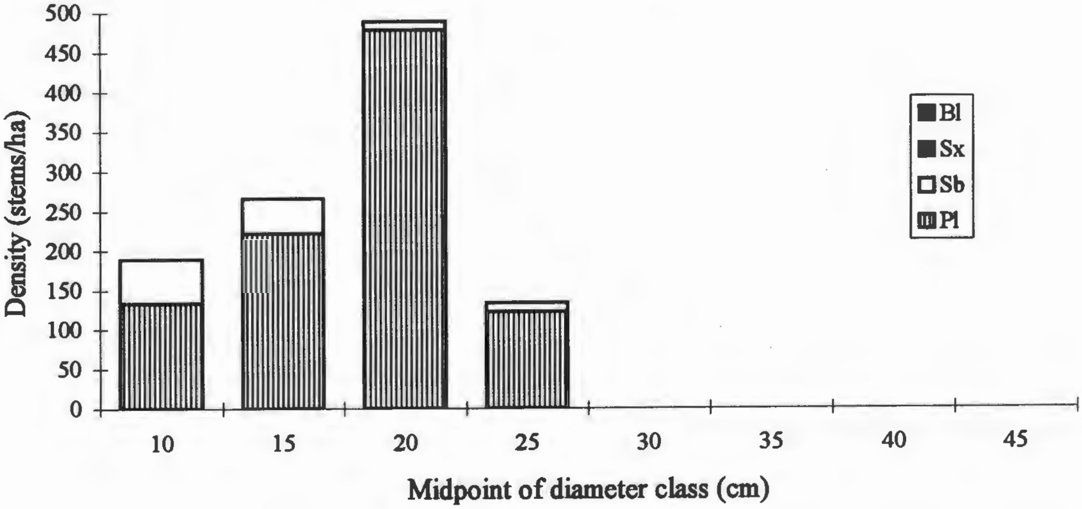


Mature Stand (Plot 12)

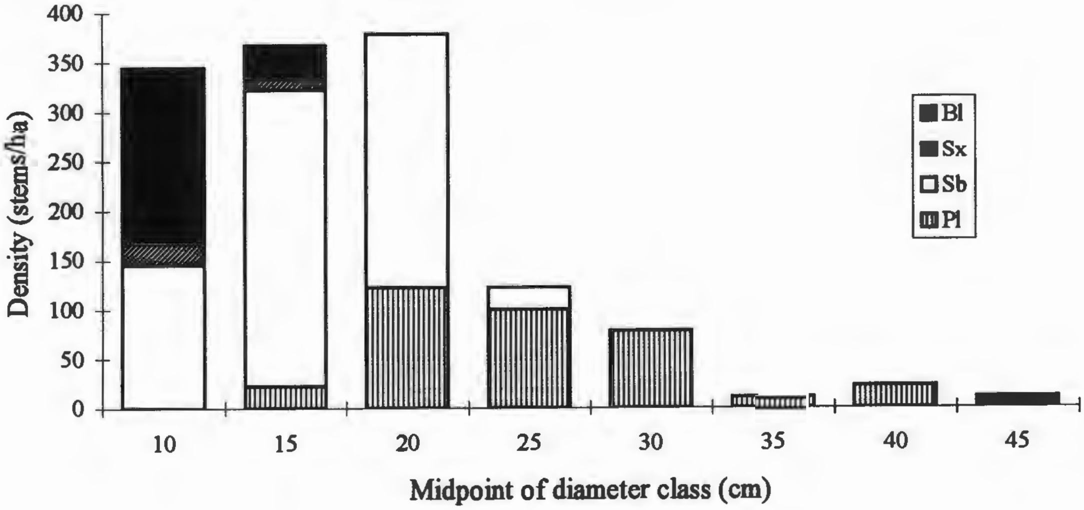


Mature Stand (Plot 21)

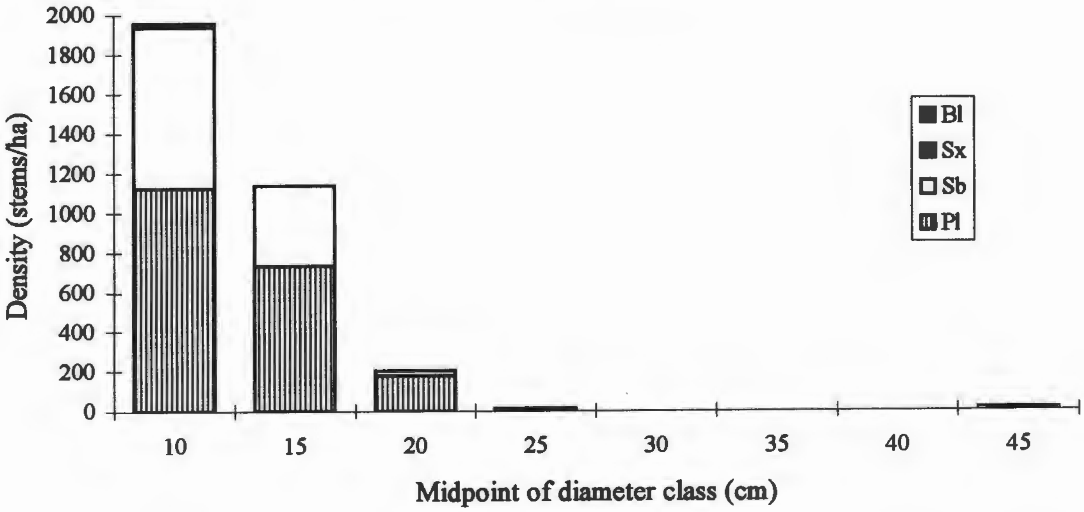
Mature Stand (Plot 23)



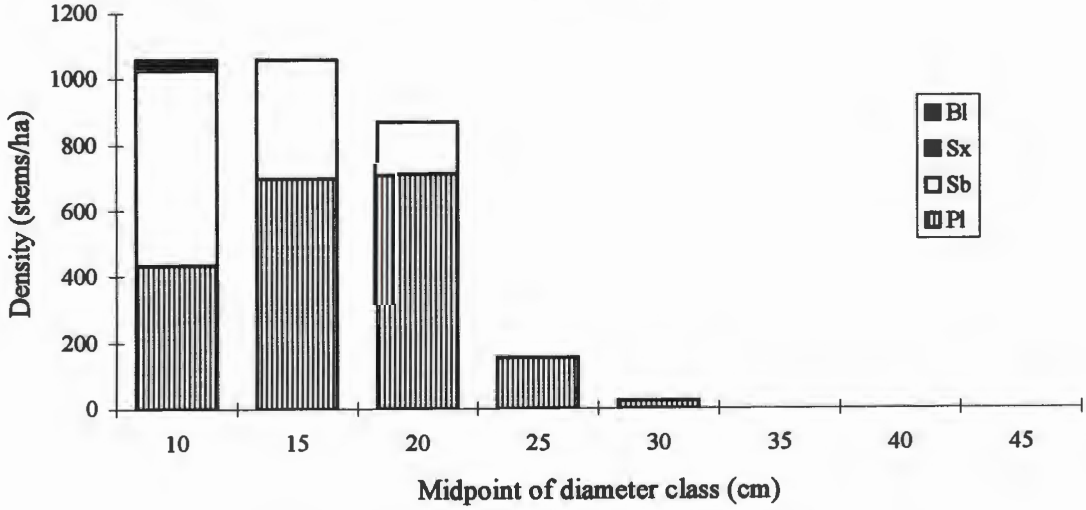
Mature Stand (Plot 25)

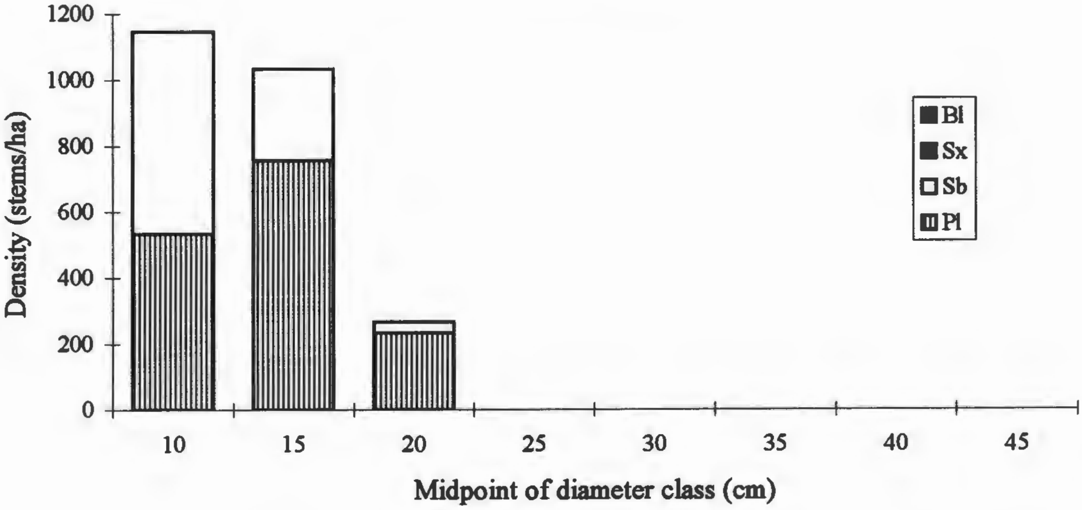


Mature Stand (Plot 26)

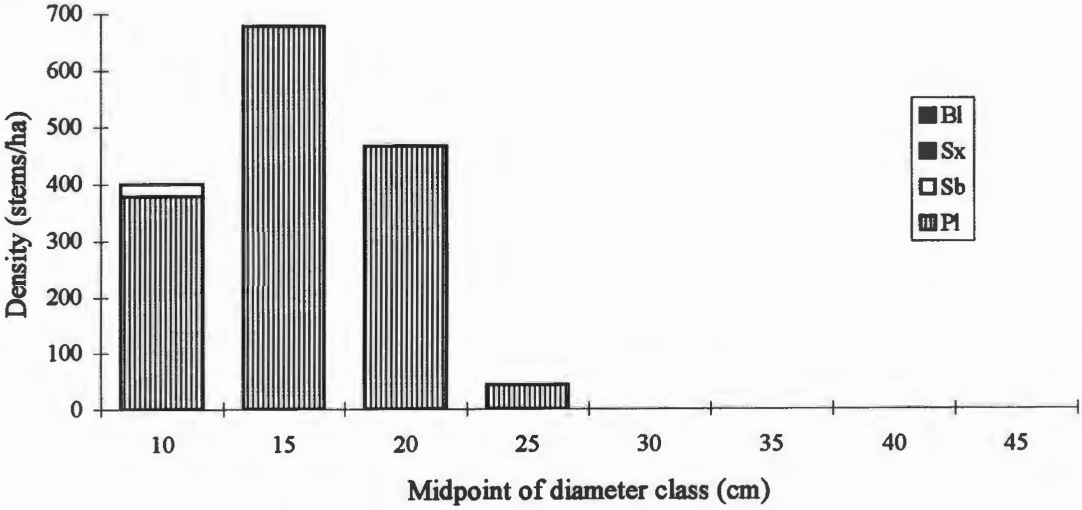


Mature Stand (Plot 29)

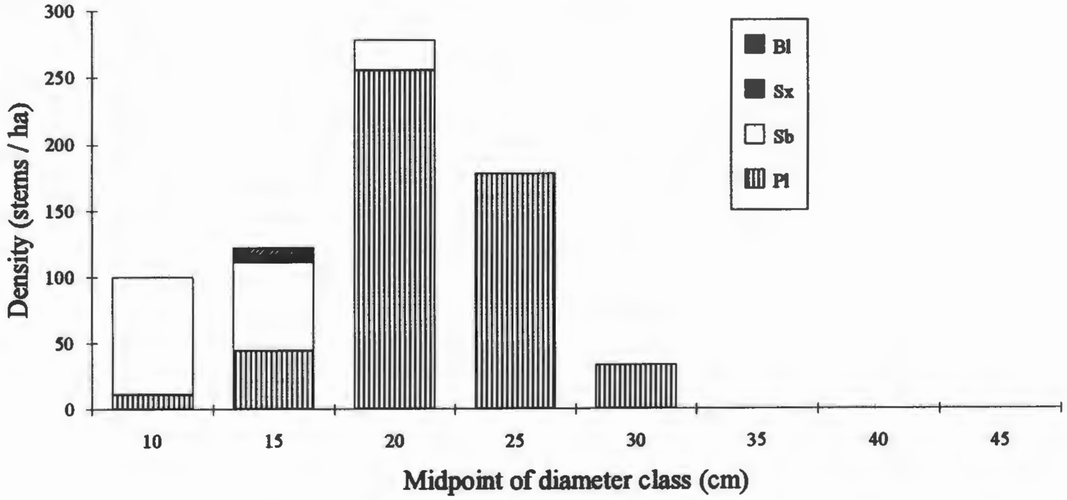




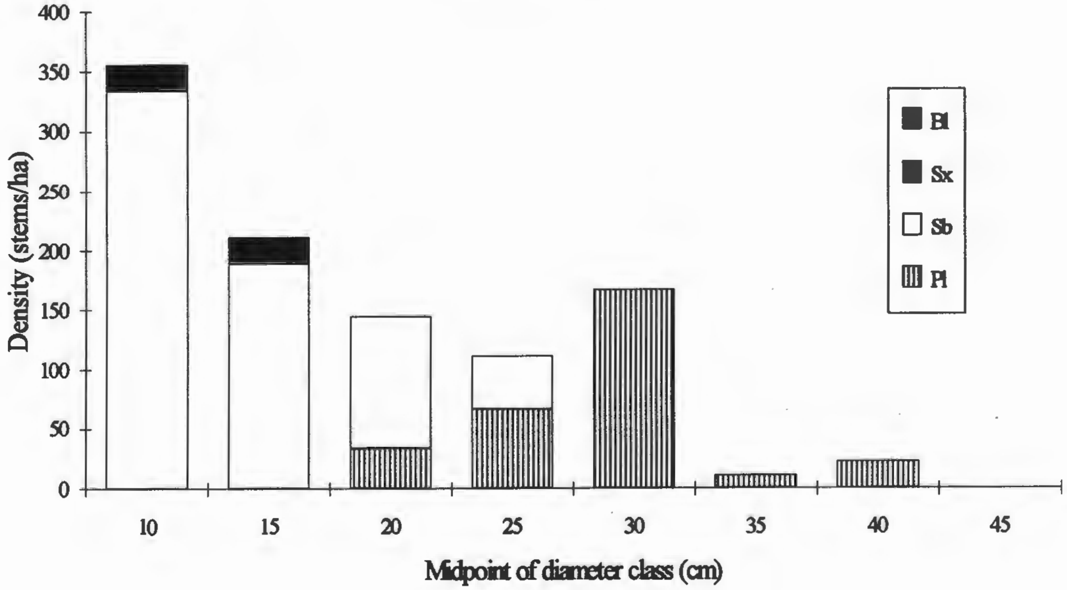
Mature Stand (Plot 31)



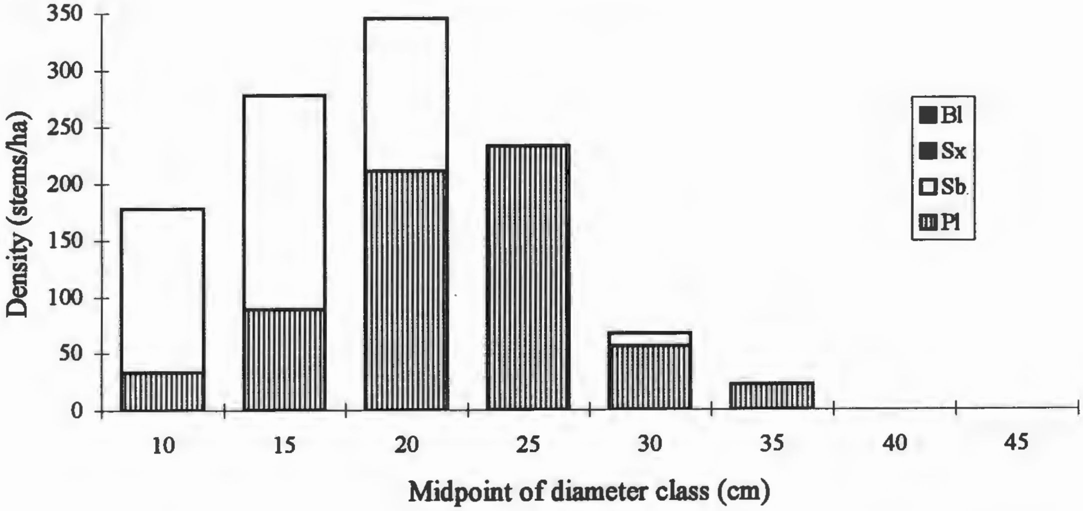
Mature Stand (Plot 36)

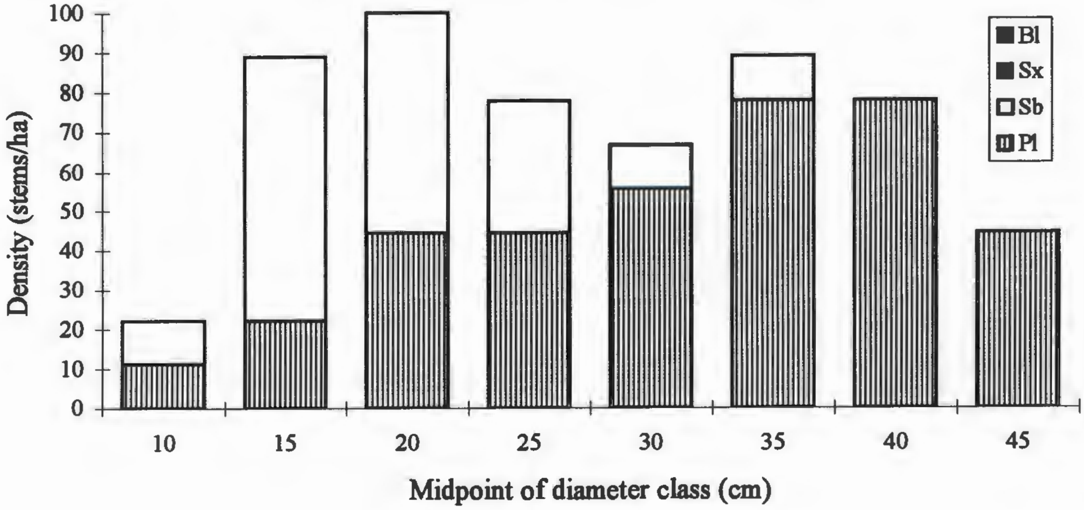


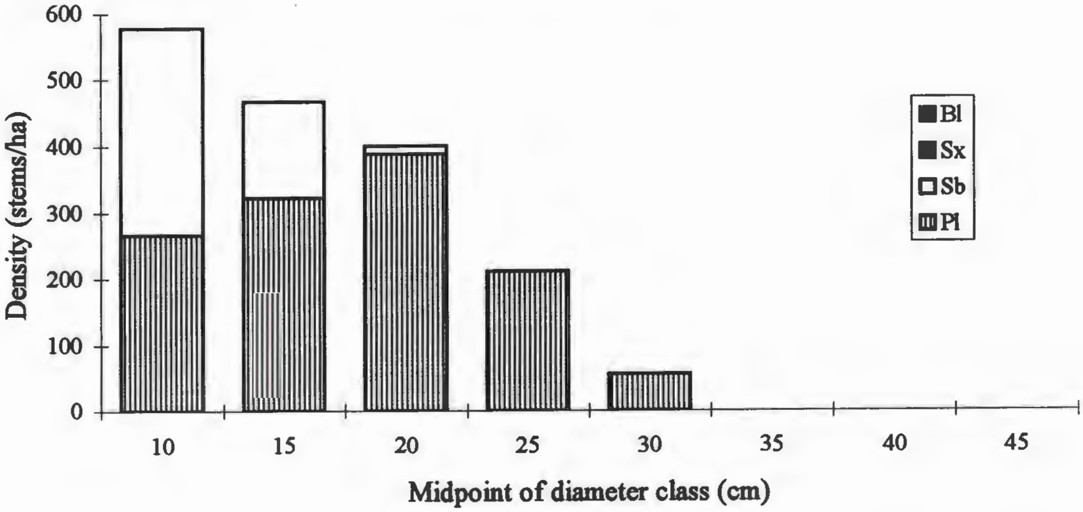
Remnant (plot 1)

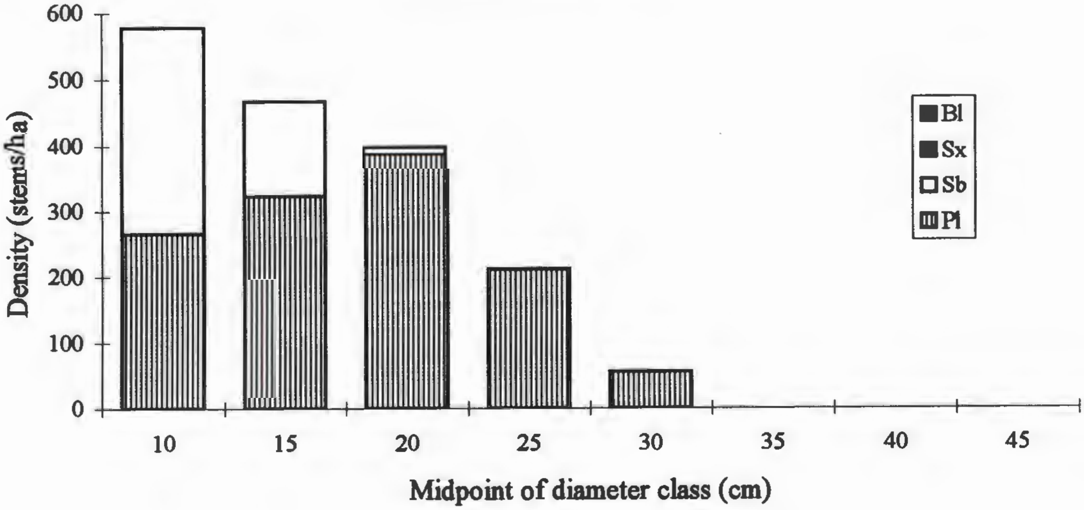


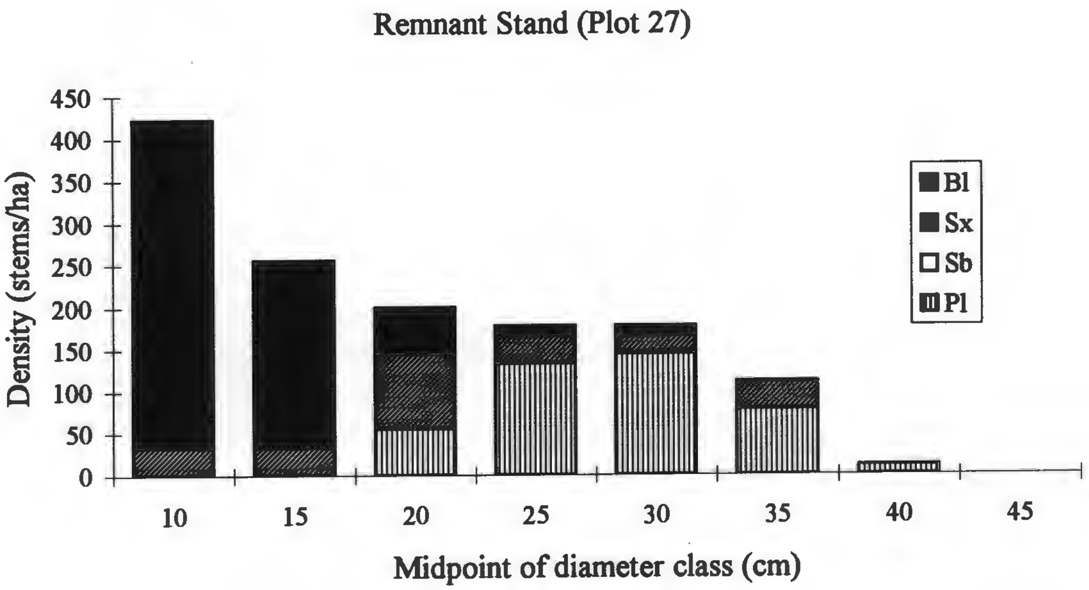
Remnant (Plot 3)

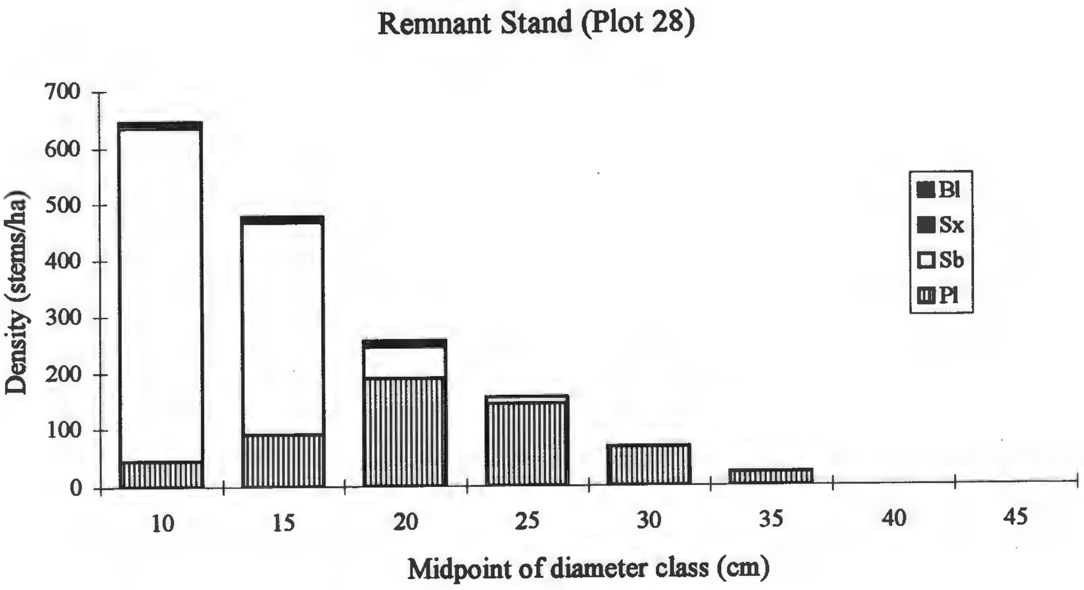

Remnant Stand (Plot 13)

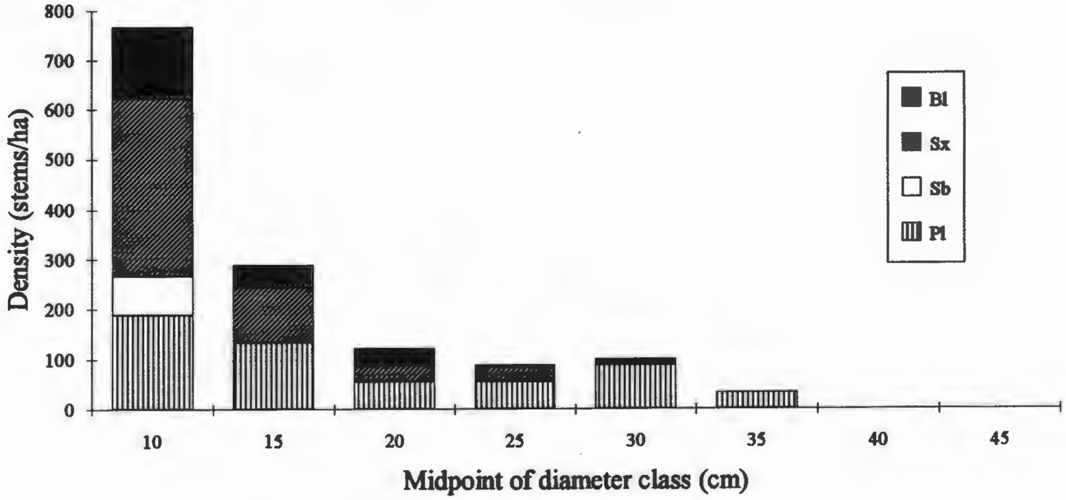

Remnant Stand (Plot 15)


Remnant Stand (Plot 16)

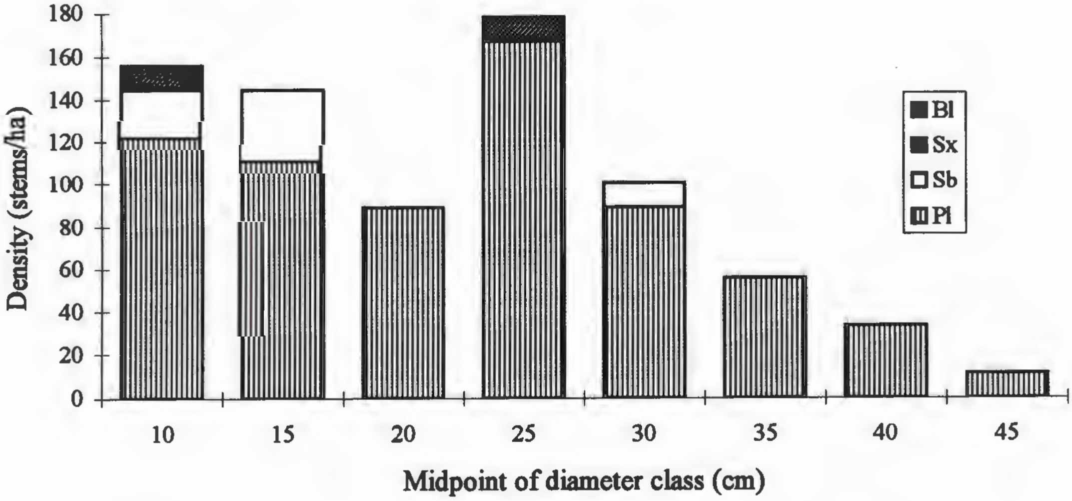

Remnant Stand (Plot 19)


Remnant Stand (Plot 27)
Density (stems/ha)
450
400
350
300
250
200
150
100
50
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
Bl
Sx
Sb
Pl


Remnant Stand (Plot 28)
Density (stems/ha)
700
600
500
400
300
200
100
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
Bl
Sx
Sb
Pl

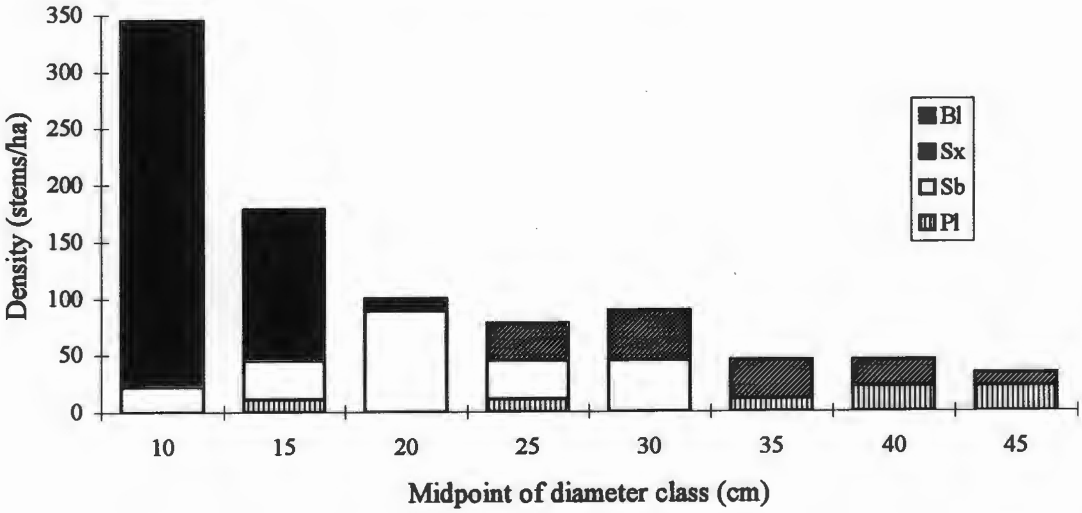


Remnant (Plot 34)

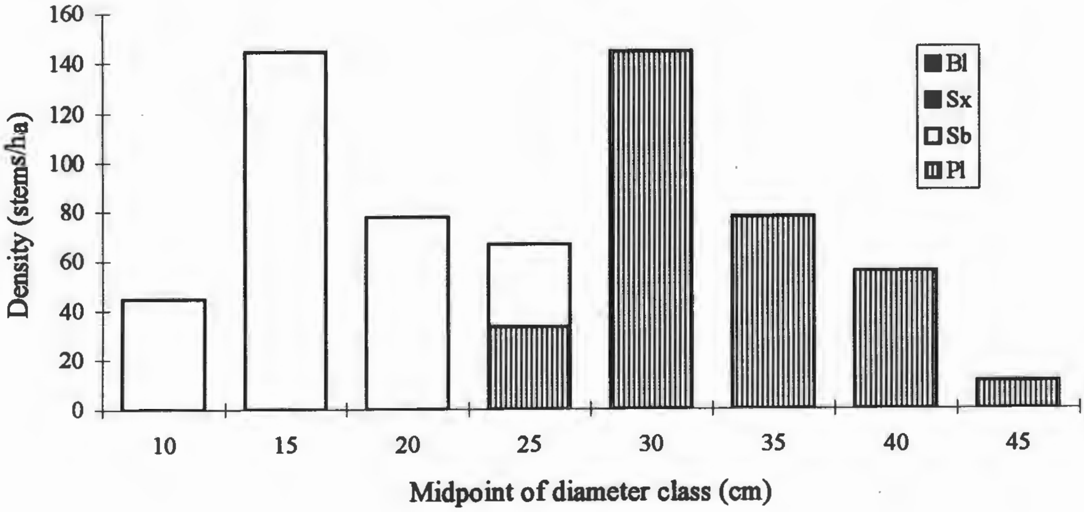


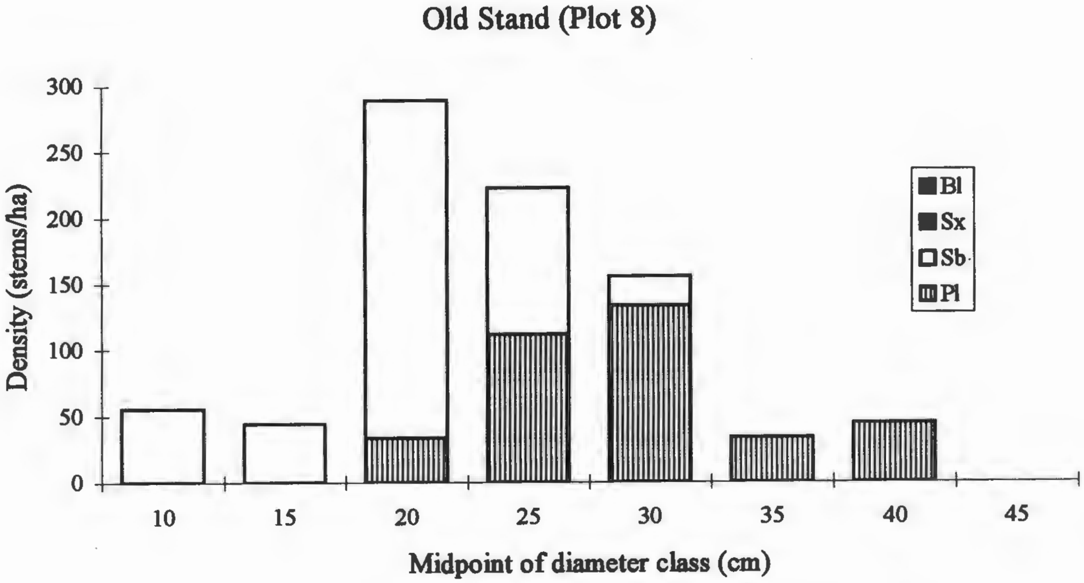
Remnant (Plot 9319)

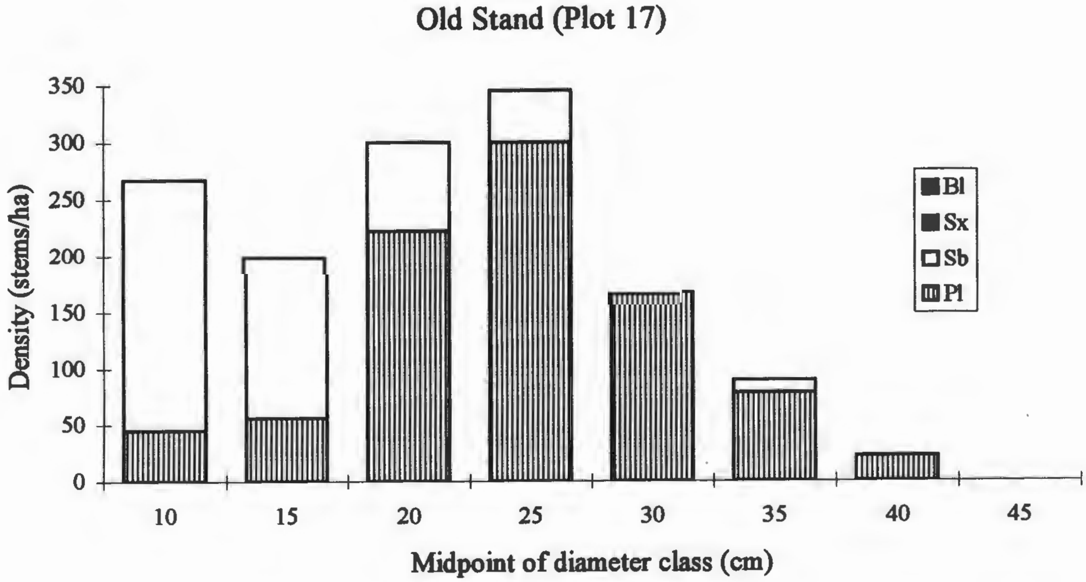
Old Stand (Plot 6)

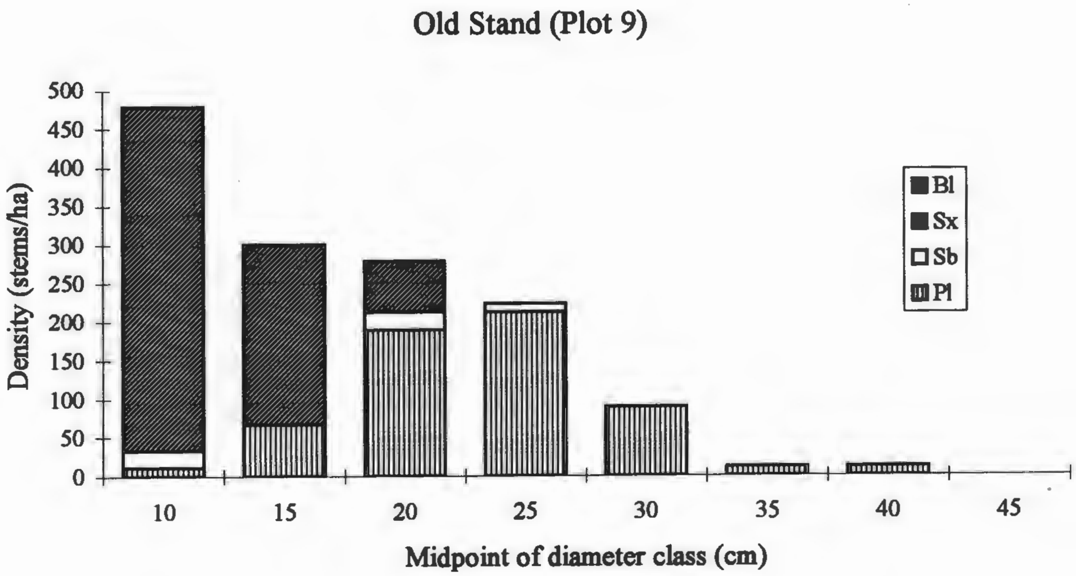


Old Stand (Plot 7)

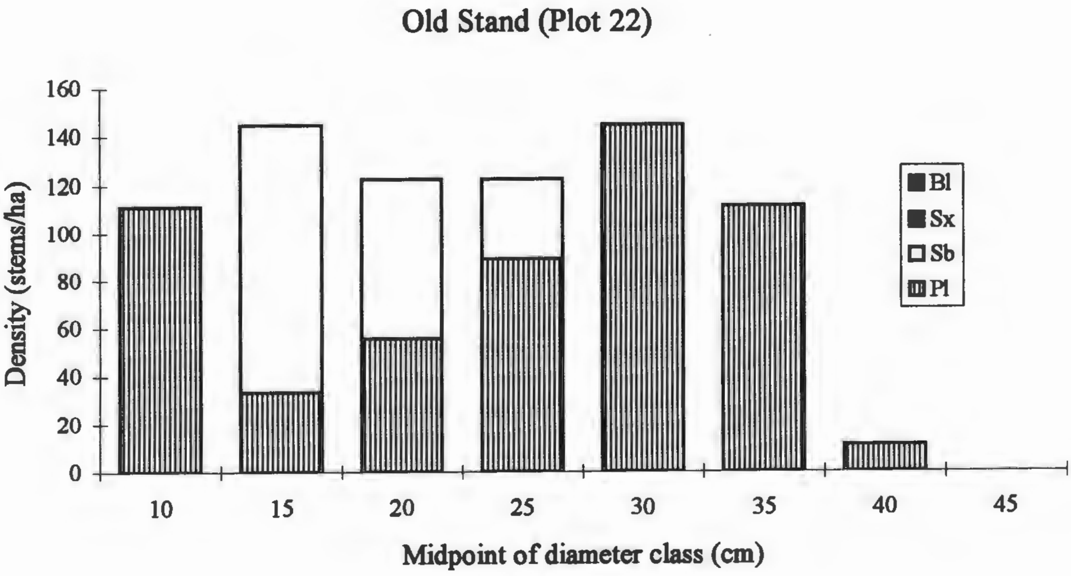



Old Stand (Plot 8)
Density (stems/ha)
300
250
200
150
100
50
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
■ Bl
■ Sx
□ Sb
▥ Pl


Old Stand (Plot 17)
Density (stems/ha)
350
300
250
200
150
100
50
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
■ Bl
■ Sx
□ Sb
▥ Pl

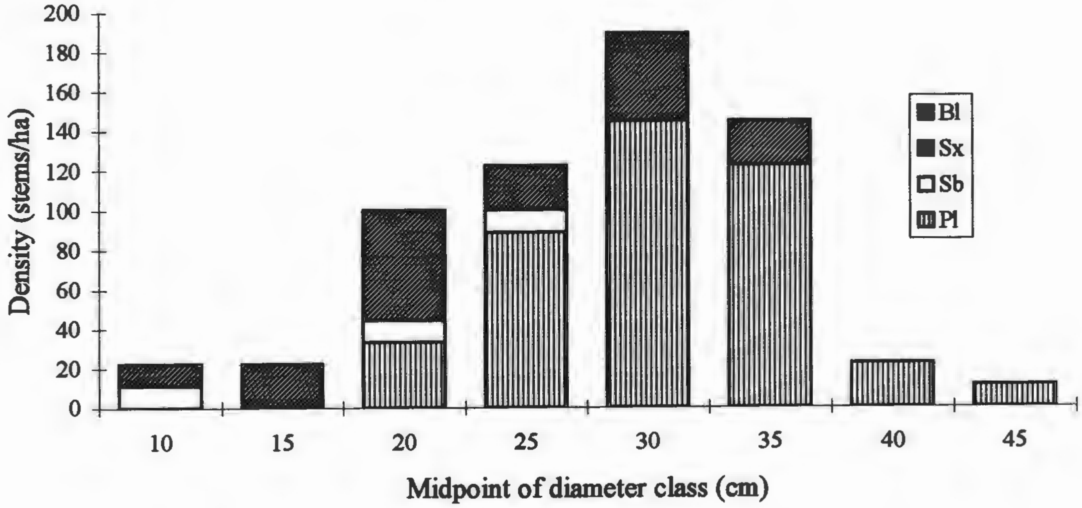


Old Stand (Plot 9)

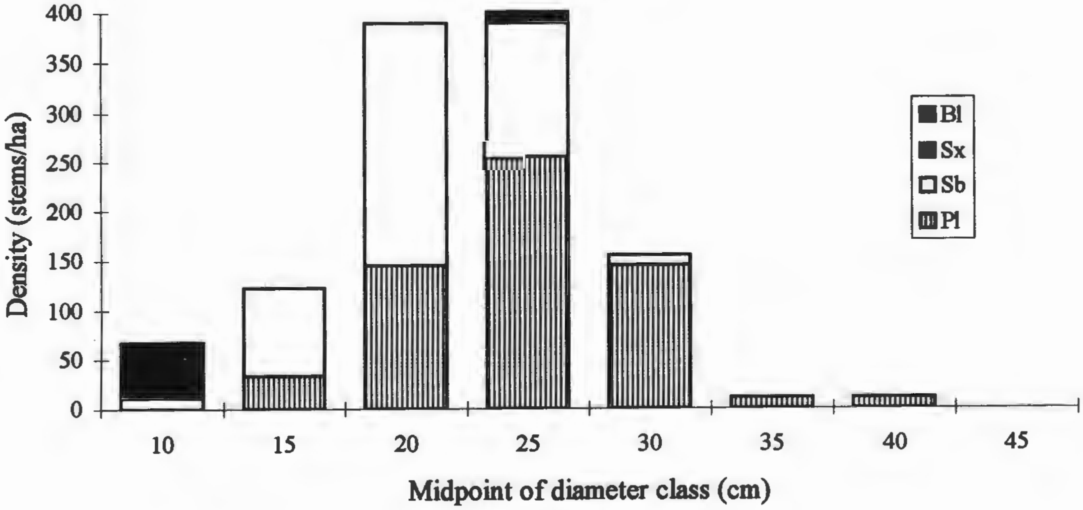


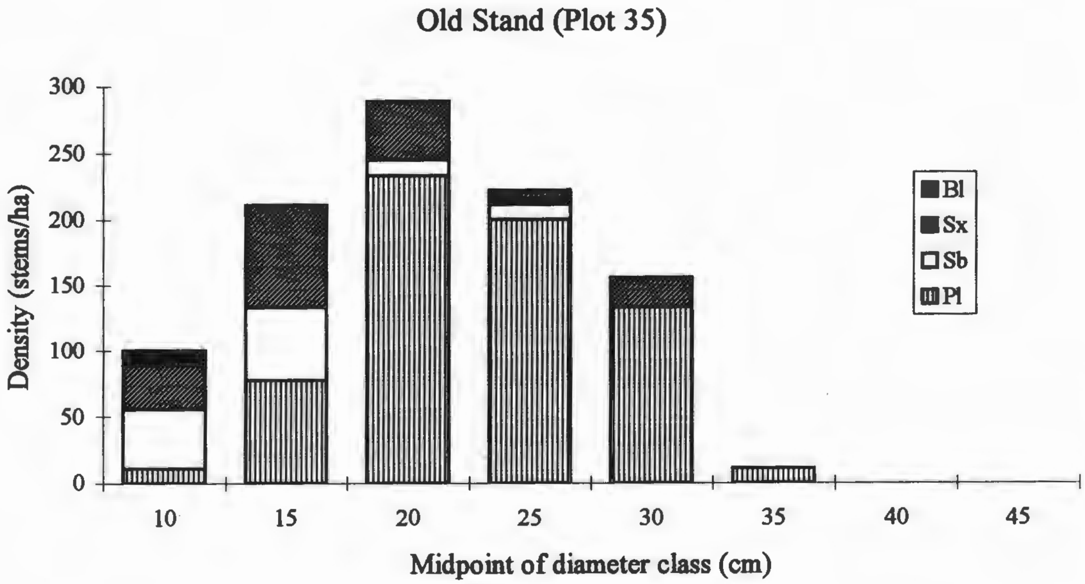
Old Stand (Plot 22)

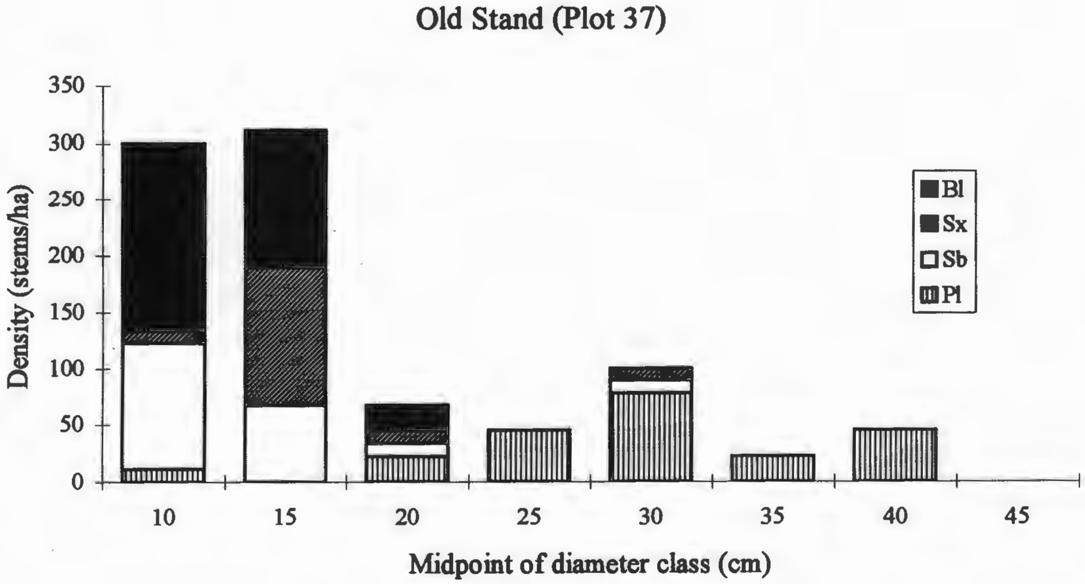
Old Stand (Plot 11)



Old Stand (Plot 24)




Old Stand (Plot 35)
Density (stems/ha)
300
250
200
150
100
50
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
Bl
Sx
Sb
Pl


Old Stand (Plot 37)
Density (stems/ha)
350
300
250
200
150
100
50
0
10
15
20
25
30
35
40
45
Midpoint of diameter class (cm)
Bl
Sx
Sb
Pl

APPENDIX 3. VEGETATION SUMMARY TABLES BY STAND TYPE.

Vegetation unit		Young Stands		Mature Stands		Remnant Stands		Old Stands	
Number of plots		10		10		10		10	
	diag	Presence and Percent cover							
		DCS							
Alnus tenuifolia	(ic)	II	.4						
Orthilia secunda	(c)	V	.1	III	.1	IV	.5	III	.1
Peltigera aphthosa	(c)	V	.9	IV	2.2	IV	1.9	IV	.6
				DCS					
Dicranum polysetum	(c)	III	1.0	V	1.4	IV	1.2	IV	1.0
						DCS			
Salix sp.	(c)	IV	.3	II	.1	V	.3	II	.1
Cladina rangiferina		II	.1	I	.7	III	.1		
Cladina mitis		III	.2	IV	1.7	III	.1	I	.1
Cladonia spp.		II	.2	II	.1	III	.1	I	.1
								DCS	
Listera caurina	(d,c)	I	.1	II	.1	I	.1	V	.2
Smilacina racemosa	(d)	II	.1	II	.1	II	.1	IV	.2
Spiraea pyrimidata	(d)	II	.3	II	.9	II	.5	IV	2.4
Calamagrostis canadensis	(c)	IV	.2	IV	.1	IV	.3	V	.3
Clintonia uniflora	(c)	IV	.8	IV	1.2	III	1.8	V	1.9
Ptilium crista-castrensis	(cd)	III	5.7	IV	13.2	IV	7.3	V	33.5
Sorbus sitchensis	(ic)							II	.1
Rubus pedatus		I	.1	I	.1	II	.8	III	.3
Abies lasiocarpa		III	1.3	IV	4.2	V	5.0	V	6.9
Arnica cordifolia		IV	.2	IV	.4	IV	.2	IV	.6
Cornus canadensis		V	5.5	V	9.0	V	7.7	V	15.3
Epilobium angustifolium		V	.3	IV	.2	V	.1	IV	.2
Festuca occidentalis		III	.1	IV	.1	IV	.1	III	.1
Geocaulon lividum		V	1.2	V	3.6	V	3.5	V	2.9
Goodyera oblongifolia		V	.1	V	.2	III	.1	IV	.2
Hylocomium splendens		III	.6	IV	1.8	III	.7	IV	6.0
Linnaea borealis		V	3.2	V	2.6	V	5.0	V	2.7
Lonicera involucrata		V	1.3	V	.2	V	.5	V	.6
Melampyrum lineare		III	.2	III	1.0	III	.6	IV	.4
Oryzopsis asperifolia		III	.2	IV	.7	IV	.4	IV	.5
Petasites palmatus		V	1.2	III	.4	IV	.3	V	.7
Picea engelmannii xglauca		V	1.7	IV	2.1	V	5.6	V	4.1
Picea mariana		IV	6.9	V	8.5	V	8.3	V	5.2
Pinus contorta		V	32.0	V	24.3	V	17.3	V	18.0
Pleurozium schreberi		V	77.1	V	70.5	IV	49.8	V	53.5
Rosa acicularis		V	3.8	V	3.0	V	1.8	V	2.2
Shepherdia canadensis		IV	3.7	III	2.6	IV	10.0	IV	4.9
Spiraea betulifolia		V	2.5	V	2.1	V	1.8	V	2.4
Vaccinium caespitosum		V	2.7	V	3.9	V	2.9	V	2.4
Vaccinium membranaceum		III	.7	V	2.4	V	4.0	V	6.0
Fragaria virginiana		III	.1	III	.1	III	.3	II	.1
Aster ciliolatus		IV	.3	IV	.4	II	.1	IV	.2
Galium boreale		III	.2	III	.1	II	.1	III	.1
Peltigera sp.		IV	.6	III	.3	I	.4	II	.2
Alnus crispa		IV	2.4	I	.3	III	4.4	IV	3.5
Aster conspicuus		III	.5	II	.7	III	.4	IV	.9
Lycopodium annotinum		IV	.8	II	.1	IV	.4	III	.8
Rubus pubescens		III	.2	II	.3	III	.1	III	.3
Viburnum edule		III	.3	II	.1	III	.1	III	.2
Viola sp.		III	.1	II	.1	IV	.1	III	.1
Achillea millefolium		III	.1	II	.1	II	.1	III	.1
Hieracium albiflorum		III	.1	II	.1	II	.1	I	.1
Pyrola asarifolia		III	.1	I	.1	II	.1	I	.1
Rubus parviflorus		III	.4			I	.2	II	.4
Amelanchier alnifolia		II	.1	III	.5	II	.1	IV	.2
Platanthera orbiculata		II	.1	III	.1	II	.1	IV	.1
Lycopodium complanatum		II	.1	II	.4	IV	.9	III	1.8
Vaccinium myrtilloides		II	.3	II	1.1	III	.4	III	3.7

Vegetation unit		Young Stands		Mature Stands		Remnant Stands		Old Stands	
Number of plots		10		10		10		10	
	diag	Presence and Percent cover							
Equisetum sylvaticum		II	.1	I	.1			III	.1
Agropyron trachycaulon		I	.1			I	.1		
Anaphalis margaritacea				I	.1				
Antennaria microphylla		I	.1	I	.1	I	.1	I	.1
Aquilegia formosa		I	.1						
Aralia nudicaulis		I	.7	I	.5	I	.1	I	.1
Arctostaphylos uva-ursi				I	.1	I	.2	I	.1
Athyrium filix-femina						I	.1		
Aulacomnium palustre		I	.5	II	.1	I	.1		
Barbilophozia lycopodioides				I	.1	I	.1	I	.3
Betula papyrifera		I	.1			I	.1		
Bromus vulgaris		I	.1	I	.1	I	.1		
Calamagrostis rubescens				I	.1				
Calypso bulbosa				I	.1				
Carex sp.				I	.1				
Castilleja miniata				I	.1	I	.1		
Chimaphila umbellata		II	.1	I	.1	I	.1	II	.1
Cladina arbuscula		I	.1			I	.1		
Coeloglossum viride		I	.1						
Corallorhiza trifida		I	.1						
Cornus stolonifera				I	.1			I	.1
Cryptogramma acrostichoides						I	.1		
Dicranum sp.		II	.6	II	.2			I	.1
Dicranum pallidisetum				I	.1				
Disporum hookeri		I	.1	I	.1			I	.2
Dryopteris expansa						I	.1		
Elymus glaucus		II	.1	I	.1	I	.1		
Empetrum nigrum						I	.1	I	.1
Equisetum arvense		I	.1	I	.1	I	.1	I	.1
Equisetum scirpoides						I	.1		
Erigeron sp.		I	.1	I	.1			I	.2
Galium triflorum		I	.1	I	.1	I	.1		
Gaultheria hispidula				I	.1	II	.1	II	.4
Goodyera repens						I	.1		
Gymnocarpium dryopteris						I	.1	II	.3
Hieracium albiflorum				I	.1			I	.1
Hypopitys monotropa						I	.1		
Lathyrus ochroleucus		I	.1	I	.1	II	.1	II	.1
Ledum groenlandicum		I	.1			I	.1	I	.1
Listera cordata		I	.1	II	.1	I	.1	II	.1
Lupinus arcticus		I	.1	II	.1	II	.1	I	.1
Lycopodium obscurum		I	.1			II	.1	I	.1
Lycopodium selago						I	.1		
Maianthemum canadense				I	.1				
Mitella nuda		I	.1	I	.1	I	.1		
Nephroma arcticum		I	.1	I	.2	II	.4	I	.1
Oplopanax horridus								I	.1
Oryzopsis pungens				I	.1	II	.1	I	.1
Osmorhiza chilensis		II	.1	I	.1			I	.1
Peltigera aphthosa				I	.2				
Peltigera canina						I	.1	I	.1
Peltigera malacea		I	.1	I	.1				
Platanthera obtusata		I	.1	I	.1				
Platanthera unalaschcensis						I	.1		
Polytrichum commune		I	1.0			I	.3	I	.1
Polytrichum juniperinum				I	.1	I	.1		
Polytrichum sp.		I	.1	I	.1	I	.1	I	.1
Populus balsamifera		I	.1			I	.1		
Populus tremuloides		II	.1	II	.2	II	.4	I	.5
Pseudotsuga menziesii		I	.1						
Pyrola chlorantha		II	.1	I	.1	II	.1	II	.1
Ranunculus acris		I	.1						

Vegetation unit		Young Stands		Mature Stands		Remnant Stands		Old Stands	
Number of plots		10		10		10		10	
	diag	Presence and Percent cover							
Rhytidiadelphus triquetrus		I	.1	II	.2				
Ribes lacustre		I	.1	I	.1	I	.1	II	.1
Ribes laxiflorum								I	.1
Ribes triste						I	.1		
Salix scouleriana				I	.2			I	.1
Senecio pauperculus						I	.1		
Solidago spp.		I	.1						
Sorbus scopulina		I	.1	II	.1	II	.1	I	.1
Sphagnum capillifolium				I	.1				
Spiraea douglasii		I	.1	I	.4	I	.1		
Stereocaulon sp.				I	.1				
Stereocaulon paschale		I	.1	I	.1	I	.1		
Streptopus amplexifolius		I	.1			I	.1	II	.1
Streptopus roseus						I	.1	I	.1
Thalictrum occidentale		I	.3	I	.1				
Tiarella trifoliata				I	.1	I	.1	I	.1
Tiarella unifoliata				I	.1	I	.1	I	.2
Trisetum cernuum								I	.1
Trisetum spicatum				I	.1				
Vaccinium ovalifolium						I	.1		
Vicia americana				I	.1				
Viola spp.								I	.1