

THE STRUCTURE AND REGENERATION PATTERN OF OLD-
GROWTH STANDS IN THE MOIST COLD ENGELMANN
SPRUCE - SUBALPINE FIR SUBZONE OF CENTRAL BRITISH
COLUMBIA

by

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ABSTRACT

The need for sound management practices of high-elevation forests is becoming more and more important in British Columbia; however, there is a lack of information on the dynamics and regeneration pattern of these forests. This pilot study investigates stand dynamics by describing the structure of old-growth stands, and correlating the occurrence of regeneration with site factors. Three study stands, which originated after fire and appeared to be in advanced stages of succession were selected in the Moist Cold Engelmann Spruce - Subalpine Fir subzone, near Smithers, B.C.

All three stands showed the same general stand structure, although the sites were slightly different. The number of seedlings, saplings, alive and standing dead trees of Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) was consistently very low, and, hence, excluded from the analysis. The diameter frequency distributions of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) approximated a balanced distribution, but did not fit with the negative exponential function. The height frequency distributions of fir indicated the presence of at least two canopy strata. The age of the trees at breast height (1.3 m) ranged from 100 to 400 years. The age distributions did not conform to distributions expected in the old-growth stage. The age distribution of saplings indicated that in the past 100 years the number of established saplings has declined. The spatial pattern of firs changed from highly aggregated, to random, to regular, with increasing size (diameter or height). The spatial pattern of the

oldest trees was aggregated possibly indicating remnants of the colonizing cohort.

Since the diameter distributions and the spatial pattern of trees with different sizes are similar to that of a steady state they are not expected to change in the future. Canopy stratification was most pronounced in the oldest study stand, therefore, it is possible the height distribution will never show the inverse-J shape typically expected in old-growth forests. Due to weak size-age relationships the future change in age distribution is difficult to predict.

The fir regeneration showed strong correlations with the presence of decaying wood substrate. There were more than twice as many seedlings on decaying wood than expected from the total cover of the substrate. However, survivorship from seedling to sapling stage was better on the forest floor than on decaying wood. Vegetation cover, light, and humus form showed no correlations with the number and vigour of seedlings. The occurrence of seedlings was also independent of canopy openings. This result implies that gap dynamics was not the driving force for the establishment of fir regeneration. One possible explanation is that snow melts later in canopy openings. The number of seedlings was higher than expected in the intermediate snow melt time zones which roughly corresponds to canopy edge positions.

The future of the spruce component in the study stand was difficult to predict because of the very low number of individuals. The dominant position of spruce trees and presence of recently established seedlings throughout the stands would imply that there was an adequate seed source. However, without

knowledge about survival of seedlings until they reach the canopy it is impossible to say whether the amount of regeneration is adequate for maintaining the spruce population.

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1. INTRODUCTION

1.1. Overview

High-elevation forests in British Columbia (B.C.) are becoming increasingly important not only for timber supply but also as potential areas for conservation. In the interior of the province, logging of high-elevation forests started in the beginning of the century, but only became extensive in the late 1970-s (Coates *et al.* 1994). Most of the management activities take place in naturally developed old-growth stands, yet little research has been done on the structure and dynamics of these stands (Jull 1990, Coates *et al.* 1994, Farnden 1994). Also, there is a need to improve current regeneration methods, because of many cases of regeneration failure (Caza 1991, Coates *et al.* 1994, Farnden 1994).

High-elevation ecosystems of interior B.C. are represented by three biogeoclimatic zones - Spruce-Willow-Birch, Engelmann Spruce-Subalpine Fir, and Montane Spruce, all being influenced by a continental subalpine boreal climate. The Engelmann Spruce-Subalpine Fir zone (ESSF) (Krajina 1960, 1965; Meidinger and Pojar 1991) has the largest area and the widest distribution compared not only to the interior subalpine zones but to all the other 11 biogeoclimatic zones of B.C. The ESSF zone extends from 900 to 1700 m elevation in northern B.C. (57° N) and from 1500 to 2300 m in southern B.C., and occupies the area between the Coastal Mountains and Rocky Mountains. Similar ecosystems dominated by Engelmann spruce and subalpine fir extend

southward to Utah and Colorado where they are identified as the spruce - fir forest type (Alexander 1980, 1986).

The main tree species in the ESSF zone are: Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Doug. ex Loud.). Engelmann spruce is considered to be moderately shade-tolerant (Chen 1996), has a high longevity (Alexander and Shepperd 1990) and is usually a dominant canopy species (Krajina 1969, Alexander 1990, Coates *et al.* 1994). Subalpine fir is considered to be very shade-tolerant (Klinka *et al.* 1992), has a moderately high longevity (Alexander *et al.* 1990), and when growing together with spruce is usually a subcanopy species (Krajina 1969, Shea 1985, Veblen 1986, Aplet *et al.* 1988). In the upper limits of the forested subzone and in the parkland subzone of the ESSF zone, subalpine fir is a dominant canopy species, as the occurrence of spruce decreases with increasing elevation (Meidinger and Pojar 1991). Lodgepole pine is a shade-intolerant (Chen 1996) and short-lived species which dominates forest canopies in mid-seral stages, especially in the driest subalpine climates (Lotan and Critchfield 1990, Meidinger and Pojar 1990).

Oliver (1981) developed a classification that categorizes stand development after major disturbance in temperate forests of North America into several stages. He avoided applying the climax theory of Clements (1916) which has been disputed for some time (Connell and Slatyer 1977, Cook 1996). The classification has gained a wide acceptance and has been used in many studies,

including investigations of the stand dynamics in high-elevation spruce - fir forests (e.g., Aplet *et al.* 1988, Jull 1990).

Oliver (1981) distinguished four stand developmental stages: (1) stand initiation, (2) stem exclusion, (3) understory reinitiation, and (4) old-growth (Oliver 1981, Oliver and Larson 1990). At the *stand initiation stage* any regeneration that survived disturbance is released and newly established seedlings utilize the available growing space. In the *stem exclusion stage* the established trees fill the available growing space by crown expansion thus preventing the establishment of regeneration. With the breaking up of the canopy in time, growing space becomes available for the establishment of seedlings and understory vegetation in the forest understory which characterizes the *understory reinitiation stage* when trees regenerate and grow without the influence of external disturbances. The final stage of stand development is the *old-growth stage* "when the trees regenerate and grow without the influence of external disturbances" (Oliver and Larson 1990 page 153). Old-growth forests are usually characterized by the balanced or inverse-J shaped distribution in size (diameter and height) and age and the presence of advanced regeneration.

Being under the influence of a continental climate, the most prevalent disturbance in the ESSF zone is fire, which creates a landscape mosaic consisting of stands which vary in their tree species composition and seral stages. Fire usually occurs as a stand-destroying crown event (Romme and Knight 1981, Johnson and Fryer 1989, Jull 1990, Coates *et al.* 1994). The mean

fire return interval varies with climate. In wetter subzones the mean fire return interval is about 350 years, and in the drier subzones about 150 years (Coates *et al.* 1994).

After fire disturbance, lodgepole pine, subalpine fir and/or Engelmann spruce in various combinations colonize the site in the stand initiation stage (Whipple and Dix 1979, Aplet *et al.* 1988, Jull 1990). During secondary succession lodgepole pine is gradually replaced in the canopy (except in the driest subzones where it may be a persistent seral species) by shade-tolerant Engelmann spruce and subalpine fir which form the old-growth stands (Meidinger and Pojar 1990, Veblen 1986, Aplet *et al.* 1988, Coates *et al.* 1994), although the tree species composition of the final successional stage is not yet known. Based on the high shade-tolerance of subalpine fir and its abundant regeneration in the understory of the old-growth stands in the ESSF zone, it could be expected that, in the absence of disturbance, fir may eventually outcompete spruce (Veblen 1986, Aplet *et al.* 1988). There are other theories that hypothesize coexistence of the two species. The coexistence is suggested to be possible through (1) regeneration niche differentiation, which means that the two species require different conditions for establishment; (2) different life histories, which means the greater abundance of fir in the understory is compensated by a higher longevity of spruce (Shea 1985); (3) non-equilibrium coexistence, which means that the disturbances are so frequent that they prevent the competitive exclusion of spruce (Peet 1981).

Most studies investigating dynamics of the high-elevation spruce - fir forest were carried out in the Rocky Mountains of Colorado (Whipple and Dix 1979, Shea 1985, Veblen 1986, Aplet *et al.* 1988), while only a few investigations were conducted in the ESSF zone of B.C. (Day 1972, Jull 1990). Considering the large area and environmental variability within both the ESSF zone of B.C. and the spruce - fir forest of the US Rocky Mountains, it is conceivable that different studies may produce different results with a restricted portability (Coates *et al.* 1994). Therefore, there is a need to investigate the old-growth ESSF forests for a better understanding of their composition and structure in relation to stand dynamics. These kind of investigations will help silvicultural management (such as selecting and applying appropriate silvicultural systems or managing for diversity) and conservation (such as selecting and maintaining reserves and parks) (Day 1972, Weetman *et al.* 1990).

The present pilot study aims to improve our understanding of the dynamics of ESSF forests by describing (1) structure of old-growth forests and (2) the occurrence of regeneration based on sampling data. The study questions are: (1) What are the compositional and structural characteristics of the stands considered to be representative of the most advanced stage in stand development in the study area? and (2) What site factors (canopy cover, vegetation, substrate, humus form, light, snow) does the occurrence of regeneration correlate with?

The study subzone, Moist Cold (ESSFmc), represents an intermediate average fire return interval compared to the wet and dry subzones (Coates *et al.* 1994). Stand structure of only one developmental stage was sampled because establishing a reliable chronosequence would require a large sample size; and the old-growth stage was selected because of its importance in the utilization and conservation of forests (Weetman *et al.* 1990, Forest Practices Code of B.C. 1995). The study stands, which were selected using structural, field identifiable old-growth criteria, were considered to represent advanced stages of secondary succession after fire disturbance. For the regeneration pattern part, most of the factors believed to influence establishment of regeneration, with the exception of wildlife, were included. In the case of soil, only the humus layer was examined because the soils are cold (Farnden 1994) and most roots, even the larger ones do not deeply penetrate the mineral soil.

1.2. Stand Structure

Structure is usually defined as size-age distribution of individuals (Mueller-Dombois and Ellenberg 1974, Daniel *et al.* 1979, Kimmins 1987, Thomas *et al.* 1993). In this study, the definition by Oliver and Larson (1990, page 1) will be used: "Stand structure is the physical and temporal distribution of trees in a stand. The distribution can be described by species; by vertical or horizontal spatial patterns; by size of tree parts, including the crown volume, leaf area, stem, stem cross section, and others; by tree ages; or by combinations of the above." The structure of the study stands was described by species composition,

diameter at breast height (dbh), height, and the age distributions and spatial pattern of saplings and trees.

The structure of high-elevation spruce-fir old-growth forest shows the following characteristics. The studies in Colorado found that generally 20-30% of the stems are Engelmann spruce and 80-70% are subalpine fir. However, in terms of basal area (BA) the ratio is reversed: spruce generally represents about 70% of the total BA and fir 30%, indicating that the large number of firs is due to abundant regeneration (Alexander 1974, Alexander 1985, Roovers and Rebertus 1993). The dbh and height distribution of fir showed the inverse-J shape (Alexander 1985, Roovers and Rebertus 1993). Spruce had a similar dbh distribution in the study by Alexander (1985), but Roovers and Rebertus (1993) found bimodal distributions, with two canopy layer boundaries at 13 and 23 m. These boundaries are indicated by local minimums in the height frequency distribution (Roovers and Rebertus 1993). The age distribution of old-growth forests is expected to show an inverse-J shape like dbh distribution. In the case of fir, this was observed by Roovers and Rebertus (1993) and Aplet *et al.* (1988). Spruce on the other hand showed a bimodal distribution (Roovers and Rebertus, 1993) even at the stand age of 575 years (Aplet *et al.* 1988). The spatial pattern of trees appears to change with size. Leemans (1991) found the spatial pattern in old-growth Norway spruce (*Picea abies*) forests to be random for seedlings, aggregated up to distances of 10 m for saplings, and random again for canopy trees.

The objectives of the structural analysis were to (1) compare dbh and age distributions with steady state functions, (2) evaluate the relationships between dbh, height and age, (3) describe the spatial pattern, and (4) compare the structural attributes between and within stands, when possible. The definition of steady state is that in the absence of major external disturbance the stand structure remains unchanged. The comparison of plots within and between stands can provide a good indication of the variability of structural attributes. Since all of the study stands are considered old-growth based on field identifiable criteria (see Chapter 2), between-stands comparison of structures would indicate the range or variability in structural attributes of old-growth stands.

Reconnaissance indicated that the site factors are relatively homogeneous within the study stands, although there are some differences in sites between stands. Therefore, if site is a major determining factor in stand development, plots within a stand are expected to be more similar than plots in different stands. On the other hand, if there is just as much within-stand as between-stand variation, then the previous disturbance was not homogeneous within the stand, or the initial floristic composition differed, or some other stochastic processes played an important role. It is possible that stands with very different floristic composition and structure could occur on similar sites (Rowe 1961, Lyon and Stickney 1976, Oliver 1981).

As it is not known how well the steady state functions should fit the distributions, several methods were used. Since regression analysis provides the most reliable results, regression analysis was accepted as final. There is also no

standard method for comparing distributions. Again, several methods were used and the results were compared.

1.3. Regeneration Pattern

The structural variability of the tree layer, in conjunction with a variability in surface substrates, should provide ample opportunities for the establishment of seedlings of shade-tolerant species, such as subalpine fir. In fact, the presence of regeneration in the forest understory is one of the characteristics of the old-growth stage. It is important to study the pattern of regeneration, particularly in relation to species and microsites (Hofgaard 1993, Frölich and Quednau 1995), to be able to predict future stand structure.

Canopy openings, or gaps, were shown in many studies to be related to the presence of advanced regeneration in forest understories. For example, gaps were one of the most important factors in predicting the presence of advanced regeneration of balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) in the boreal forests of Quebec (Kneeshaw and Bergeron 1996). In the subalpine forest of Japan, Yamamoto (1993) found that fir (*Abies mariesii*), which was usually present before gap formation, readily released, while spruce (*Picea jezoensis* var. *bondoensis*) usually established after the gap formation. The density of Norway spruce (*Picea abies*) regeneration in forests of east-central Sweden increased with increasing gap size (Qinghong and Hytteborn 1991). In the Engelmann spruce-subalpine fir forest of Colorado, Shea (1985) found that

on wet sites 63% of spruce and 45% of fir seedlings occurred in gaps, while on dry sites the seedling occurrence decreased to 34% for spruce and 1% for fir.

Understory vegetation may create favourable conditions for germination and seedling growth by providing protection from desiccation or frost damage. In other situations, it may create unfavourable conditions by hindering regeneration and decreasing seedling survival (Zasada and Gregory 1969, Noble and Ronco 1978). The cover of woody vegetation overtopping seedlings was identified as the best growth predictor for Douglas-fir (*Pseudotsuga menziesii*) seedlings (Wagner and Radosevich 1991). For Engelmann spruce, a competition index, which is based on the cover and height of competing vegetation, was found to be negatively correlated with the seedling growth (Comeau *et al.* 1993, Kneeshaw and Bergeron 1996). Comeau *et al.* (1993) also demonstrated that the competition index or growth of Engelmann spruce seedlings can be predicted from available light measured as “the fraction of full sunlight penetrating the vegetation canopy” above the seedlings. However, on high-elevation sites in the Rocky Mountains of Colorado where sun angles are low, available light is not a good growth predictor for Engelmann spruce and subalpine fir seedlings (Alexander *et al.* 1990, Alexander and Shepperd 1990).

Snow is probably also an important factor influencing the establishment of regeneration, however little is known about its influence on regeneration. Brooke (1970) has shown that snow can cause mechanical damage by creeping on steep slopes. In the study stands, where slopes were gentle, snow is more

likely to influence the occurrence of regeneration by the melt pattern in early summer. It is known that more snow accumulates in canopy openings than under the canopy (Harestad and Bunnell 1981, Hanley and Rose 1987, Askin and Dragunas 1995) and since the growing season is short (about three months), a difference of only a few weeks in the disappearance of snow might be significant for regeneration (Brooke 1970).

The quality of forest floor or humus form, especially the thickness of litter, is an important edaphic factor determining the regeneration capacity of various microsites. Litter depth greater than about 2.5 cm was found to effectively prevent the establishment of Engelmann spruce seedlings, while subalpine fir seedlings are easily established even on excessively thick forest floors (Knapp and Smith 1982). Downed coarse woody debris (or "nurse logs") and exposed mineral soil are the substrates that support abundant regeneration of Engelmann spruce and subalpine fir (Knapp and Smith 1981, Harmon *et al.* 1986, Geier-Hayes 1987). In humid climates, the survival of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) seedlings increased with increasing thickness of litter even on relatively undecayed logs (Harmon 1987). However, the long-term survival and growth performance of the seedlings established on decaying wood may be poor because of the low nutrient content of wood (Harmon 1987).

The structural analysis would be incomplete and the question about the future stand development could not be fully answered without examining the

pattern of regeneration in the study stands. Therefore, the objectives of this study were: (1) to examine the relationship between the location of seedlings and canopy cover and time of snow melt; (2) to investigate which site factors (vegetation, light, humus form, or substrate) correlate best with the number and vigour of seedlings; and (3) to make inferences about factors affecting the survival of seedlings to the sapling stage, particularly in relation to substrate materials. Since this study is based on sampling, it can only provide descriptions and correlations and cannot answer the question of *why* the regeneration occurs where it does.

2. METHODS

2.1 Study Area

The study area was located in the Moist Cold Engelmann Spruce - Subalpine Fir subzone (ESSFmc) (Krajina 1960, 1965; Meidinger and Pojar 1991) near Smithers, B.C. (54° 47' N 127° 10' W). The ESSF zone is under the influence of the continental subalpine boreal climate. There are no long term climatic data available for the study area, but the ESSFmc subzone's climate can be characterized by cold winters, cool, dry summers, relatively low annual precipitation (450-650 mm), light snowpack (70-150 cm) and a mean annual temperature of -0.7 °C (Banner *et al.* 1993, Farnden 1994). Mean monthly temperatures are below 0 °C for 6 months and above 10 °C for 1 month (Farnden 1994). The zonal soils are Humo-Ferric Podzols with Hemimor humus forms (Agriculture Canada Expert Committee on Soil Survey 1987; Green *et al.* 1993, Banner *et al.* 1993).

Subalpine fir and Engelmann spruce are the major tree species in old-growth stands on zonal sites in the ESSFmc subzone. Lodgepole pine is common in early-seral stands. The most common understory species include: *Vaccinium membranaceum*, *Vaccinium ovalifolium*, *Menziesia ferruginea*, *Cornus canadensis*, *Rubus pedatus*, *Clintonia uniflora*, *Pleurozium schreberi*, and *Barbilophozia floerki*.

2.2. Stand Selection and Plot Layout

Three unmanaged, old-growth stands were selected for the study near Smithers (Table 1). Since the stands had to be identified before sampling, selection was based on the structural definition of old-growth (Hamilton and Pojar 1991, Franklin *et al.* 1981) instead of criteria based on population processes (Hayward 1991). In this context old-growth is defined as those forest stands that have no pioneer species (e.g. lodgepole pine), have advanced regeneration, abundant snags, and coarse woody debris (Franklin *et al.* 1981, Thomas *et al.* 1988, BCMOF 1989). All stands selected (Table 1) had (1) originated after fire, which is confirmed by the presence of charcoal in the forest floor (Lorimer 1985, Jull 1990) and (2) had an intermediate position along the soil moisture - nutrient gradient (Klinka *et al.* 1989).

Table 1. Location and characteristics of the study stands. SNR = soil nutrient regime, SMR = actual soil moisture regime.

	Stand 1	Stand 2	Stand 3
Location	McKendrick Pass	McKendrick Pass	Hudson Bay Mountain
Elevation (m)	1165	1040	1157
Aspect	NE	NW	SE
Slope (%)	10	5	10
SNR	Medium	Poor	Rich
SMR	Fresh	Slightly dry	Moist

The field work was conducted during the summer of 1992. In each stand (1, 2 and 3) three 52 m by 52 m plots (A, B, and C) were established using a right-angle prism and measuring tape (Figure 1a). The accuracy was checked by laying out three sides of the plot and measuring the fourth which should be 52 m. The corners were re-established until the measurement was within 5% (2.6 m) of the expected value. On all plots a 4 m by 4 m grid was established thus providing 169 subplots (Figure 1b). The four meter grid size was selected as a compromise between having a fine resolution for measuring different attributes at the center of the subplots and being able to measure light in all quadrats in a short time. In the centre of the 4 m by 4 m subplots, 1 m by 1 m quadrats were established to evaluate regeneration and site factors. Also, in each A plot a 12 m wide transect was selected so that it would represent the canopy conditions within the plot (Figure 1c).

2.3. Stand Structure

2.3.1. Sampling and Data Collection

Individuals of the tree species were classified into three categories based on dbh and height: trees (≥ 10 cm dbh), saplings (< 10 cm dbh and ≥ 1.3 m height) and seedlings (< 1.3 m height). Dbh was selected as a distinguishing characteristic, because it is the easiest to measure. Measurements on trees and saplings are described below, measurements on seedlings and site factors are presented in section 2.4.1. - Regeneration Pattern Sampling and Data Collection.

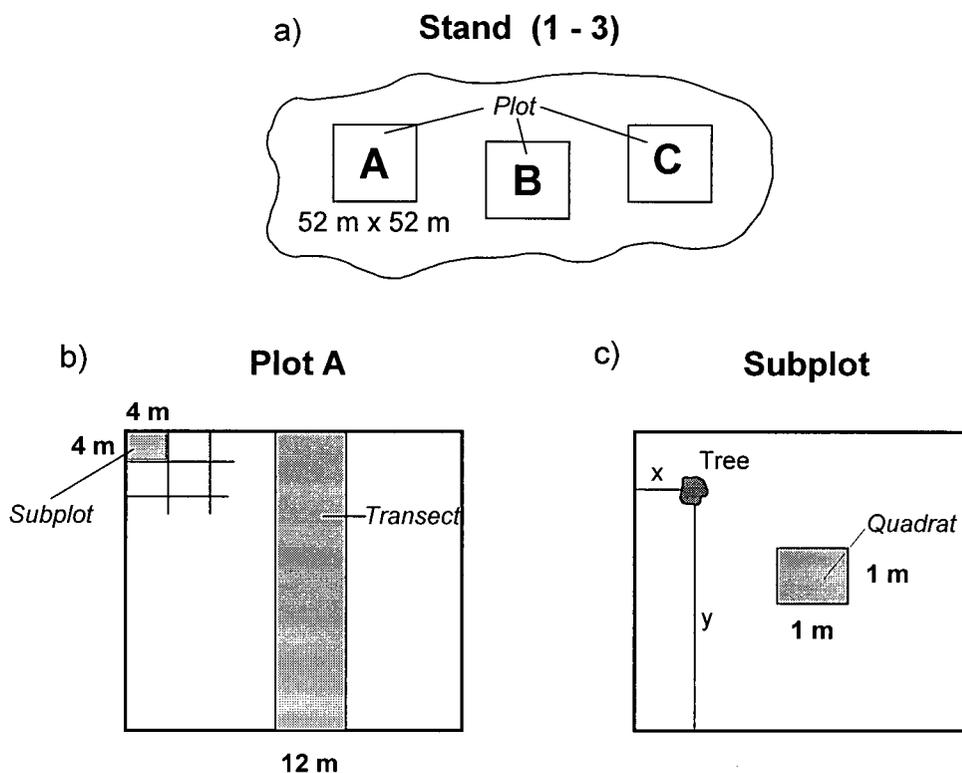


Figure 1. Schematic diagram illustrating the location and size of a) plots; b) subplots; and c) quadrats and the method of mapping locations within subplots.

For all live trees species, dbh, height, crown height, crown diameter, vigour, age and location were recorded on the A plots; species, dbh and height were recorded on the B plots; and only species and dbh on the C plots. In the case of snags (standing dead trees), location was noted on the A plots; species and dbh in all plots.

Dbh was measured outside the bark to the nearest 0.1 cm using a dbh tape. Height and crown height (height of the lowest live branch) was measured to the

nearest 0.1 m using a clinometer; and the measurements were taken from at least tree height distance from the trees. Crown diameter was measured in two perpendicular directions with a measuring tape to the nearest 10 cm and then the two measurements were averaged. Vigour was subjectively estimated based on the following criteria:

- 1 - dead individuals.
- 2 - broken or damaged top, individuals thought to be severely damaged, and probably will not survive for the next growing season.
- 3 - moderately damaged individuals that are likely to survive several growing seasons, but growth is retarded.
- 4 - relatively healthy individuals with some growth.
- 5 - very healthy individuals with excellent growth.

To get an estimate of age, trees were cored at breast height using methods described by Jozsa (1988). The cores were mounted on wooden holders and then sanded. The trees were cored at breast height because (1) during timber cruising the age is measured at breast height, (2) heart rot is less extensive at breast height than closer to the ground.

The locations of trees within the subplots were recorded by measuring X and Y coordinates from the 4 m by 4 m gridlines to the side of trees (Figure 1c). The measurement error is estimated to be about 10 cm. The coordinates were adjusted by half of dbh so the coordinates would represent the center of the trees. If any measurement was greater than 4 m, then all other measurements within the subplot in the same direction were adjusted.

In the case of saplings, species, dbh, height, crown diameter, vigour, location, base age and, for some saplings breast height (bh) age and rooting substrate were recorded on the A plots; species and dbh on the B and C plots. Dbh, crown diameter, vigour and location were measured in the same way as for trees. Height was measured to the nearest 0.1 m using a measuring rod.

To determine the base age of saplings, disks at the base were cut as close to the germination point as was possible. Also, in a systematically selected subsample, disks at breast height were cut as well. Breast height disks were obtained from saplings so that time to reach breast height could be estimated. The disks were sanded and rings were counted using a dissecting microscope with a maximum of 40 x magnification.

The rooting substrate of saplings was determined in the richest and poorest A plots (Table 1) (plot 2A and half of plot 3A because of time constraints). The substrate was categorized as: forest floor (FF), decaying wood (DW), and mineral soil (MS).

2.3.2. Data Analysis

The inverse-J distribution plays an important role in describing balanced diameter as well as steady state age distributions; therefore, its derivation will be shown in some detail. DeLiocourt (*in* Meyer 1952) observed that the ratio (q) of number of trees in neighbouring dbh classes is constant in balanced dbh distributions (balanced meaning that the distribution stays the same over time in the absence of major disturbance) or dbh distributions covering large areas.

The constancy of ratios implies that the dbh frequency distribution follows a negative exponential function (Meyer 1952, Leak 1965). This result can be derived in the following way. If the number of trees in a dbh class (noted by y) is proportional to the number of trees in a neighbouring class, then the difference between the neighbouring classes (noted by Δy) is also proportional to the number of trees in either dbh class. The proportion also depends on the dbh class width (noted by Δx). Therefore, the difference in number of trees between two neighbouring dbh class is:

$$\Delta y = ky\Delta x, \quad \text{where } k \text{ is a constant.}$$

$$\frac{\Delta y}{\Delta x} = ky, \quad \text{if } \Delta x \rightarrow 0, \text{ then}$$

$$y' = ky$$

This simple differential equation can be solved by separation. The solution is:

$$y = Ce^{kx} \quad \text{Equation 1}$$

where C and k are constants, x is dbh and $e = 2.71828\dots$. If $k < 0$ (and $C > 0$) then the curve is inverse-J shaped and is called a negative exponential function (Meyer 1952, Leak 1965). Equation 1 can be rewritten in a more practical form:

$$n_i = ae^{bD_i} \quad \text{Equation 2}$$

where n_i is the number of trees in the i th dbh class, D_i is the midpoint of the i th dbh class, and a and b are parameters.

Although forest stands in steady state have been described with constant quotient value (Meyer 1952), it is uncertain how close the dbh frequency

distribution should match the negative exponential function to be able to say that the dbh structure will stay the same over time.

In the case of age distribution, C is the number of individuals entering the population at age zero and $|k|$ is the mortality rate in Equation 1 (Hett and Loucks 1976). This means that if the mortality rate is the same for all age classes, then the age distribution will also have an inverse-J shape.

For the description of structure a summary table of some simple statistics (mean, standard deviation, extreme values) was compiled for dbh, height, crown diameter, age, basal area and volume of trees and saplings. (Because of low values, basal area and volume were not calculated for saplings). Volume was calculated using the B.C. Forest Service (1976) equations for Forest Inventory Zone J, which is applicable for the study area.

Before proceeding with the comparison of plots it is important to consider the species composition. The number of spruces was consistently very low in all size categories and in all plots (Figure 2, Appendix). Because of the low numbers, spruce was excluded from further analysis.

For each structural attribute, the description and comparison of plots/stands involved the following steps. Box plots were used to visually compare plots, and histograms were used to evaluate the shape of the frequency distribution. If it seemed useful, density trace diagrams were used to further investigate the shape of the frequency distributions or to identify minimum or maximum points. The means were then compared by one-way analysis of

variance. If the distributions appeared to be similar in shape, then contingency tables and the Kolmogorov-Smirnov test were used for within- and between-stand comparisons. Because of the central significance of the inverse-J distribution, graphical and regression analysis was used to evaluate the fit of the structural attribute that appeared to follow the inverse-J shape. Finally, the relationships between the various structural attributes were also evaluated using regression analysis. On some occasions, the selection of the next analysis depended on the results, so it was necessary to refer to some of the results in the methods section.

Although histograms are an excellent way of inspecting data distributions, there is a problems with them: the selection of class width is usually arbitrary, and changes in class width can dramatically change the shape of the histogram (Chambers *et al.* 1983).

One way of determining the optimal class width without changing the shape of the frequency distribution is by using cumulative frequencies and regression analysis (see page 25). Another way to make the class width selection less arbitrary as well as “smoothing” the graph, is to use density trace diagrams (Chambers *et al.* 1983). The density trace diagram is based on calculating the local density over some interval width h according to the formula:

$$\text{local density at } x = \frac{\text{number of observations in } [x - h / 2, x + h / 2]}{h \times \text{total number of observations}}$$

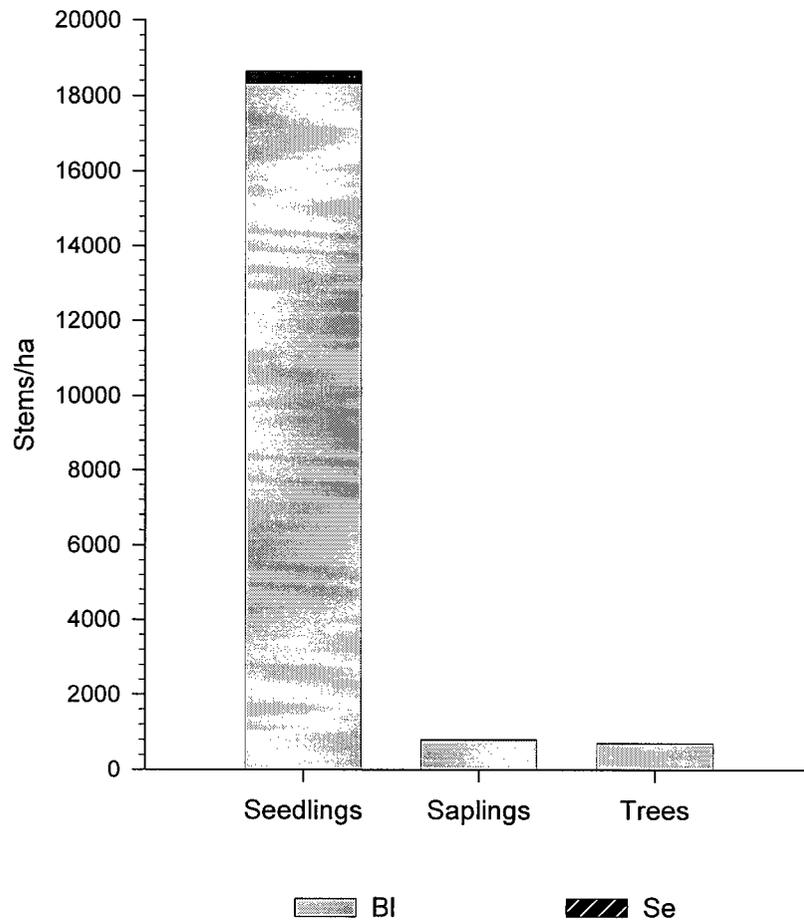


Figure 2. Species composition for live seedlings, saplings and trees. (Bl = subalpine fir, Se= Engelmann spruce). The number of stems was calculated for seedlings by combining the data from three crown transects; for saplings and trees by combining data from all nine plots.

Usually the local density is calculated at s , $2s$, $3s$, *etc.* values (where $s \leq h/2$) so two parameters, s and h would define the density trace diagram for a given set of data. Generally the higher the s and h values are, the smoother the graph becomes. The s and h values were determined by using several

combinations and selecting the one which provides relatively smooth curves without too much loss of detail. To further smooth the graph, a cosine weight function was used to calculate the density trace (Chambers *et al.* 1983).

The mean values of the structural attributes were compared using one-way analysis of variance and Tukey's multiple range test (Neter *et al.* 1990). Only those means were compared which showed differences greater than the minimum significant difference. The minimum significant difference was set based on expected measurement errors. Homoscedasticity was checked using Bartlett's test with $\alpha = 0.01$ (Walpole 1982). To statistically compare distributions, contingency table analysis (Walpole 1982) and the Kolmogorov-Smirnov test (Neave and Worthington 1988, Shea 1985, Veblen 1986) were used. Since the Kolmogorov-Smirnov test is sensitive to *any* kind of differences between two distributions (Neave and Worthington 1988), not just differences in shape, standardized distributions were compared to eliminate possible differences in mean or variance. Both the contingency table analysis and the Kolmogorov-Smirnov test require several comparisons to hold at the same time; therefore, the α value was adjusted using Bonferoni's adjustment to ensure an $\alpha = 0.05$ overall error rate (Neter *et al.* 1990). For both comparisons, plots within stands were compared to see whether there were any significant within-stand differences. Then, using the results from the graphical comparison, plots which appeared to be similar but were from different stands were also compared. The SYSTAT package (Wilkinson 1990) was used for the Kolmogorov-Smirnov

test, all other statistical analyses were done using SAS release 6.08 (SAS Institute Inc. 1989).

2.3.2.1. Diameter Structure

Since dbh was intensively sampled, it was possible to compare distributions within- and between-stands. In the box plot graph, the plots were ordered according to visual similarity. A class width of 1 cm was used in the histograms, as the minimum significant difference was set to 1 cm. The dbh distributions were non-normal and the Bartlett's test indicated heterocedasticity; therefore, logarithmically transformed means were compared. Since the dbh distributions appeared to be quite similar, they were further compared using contingency tables and Kolmogorov-Smirnov tests.

In all plots, the dbh distributions conformed closely to an inverse-J shape. The fit of the negative exponential function on the dbh frequency distributions was evaluated graphically. Plots were created using the ratios (q) of neighbouring dbh classes and logarithmically transformed frequency values, and the dbh class midpoints. The q -values were calculated using a dbh class width of 5 cm — a smaller width would result in many 0 and non-defined values and a larger class width in too few points. If the distribution is close to the negative exponential, the q -values should be the same, and frequency values should show a linear trend on logarithmic scale.

The regression analysis followed the methods described in Varga and Klinka (1996). Instead of the frequency distribution, the cumulative frequency

distribution was used to avoid problems with selecting class width and classifying dbh values equal to class boundaries. The following equation was fit (which is the indefinite integral of Equation 1):

$$cf = \alpha e^{\beta dbh} + \gamma \quad \text{Equation 3}$$

where cf is cumulative frequency, α , β and γ are parameters. To evaluate the fit, residuals were plotted and an approximate lack of fit test was used (Varga and Klinka 1996).

As a comparison, the regression analysis and the lack of fit test were carried out on frequency distributions with a class width of 1 cm using the same procedure as in the case of cumulative frequencies. The q -values were also calculated using the b values from the fit of Equation 2 on frequency distributions: $q = e^{-2b}$ (Meyer 1952). To check whether the results depend on the sample size, the analysis was also carried out on plots combined within stands and then on all plots combined. The class width was selected so that it was the closest to the reconstructed negative exponential function, which best fitted the cumulative frequency distribution. The cumulative frequency distribution of plot 3C had the best fit with the negative exponential function, therefore, this plot was used to select the dbh class width. First, Equation 1 was reconstructed from the regression coefficients α and β resulting in $a = 89.56$ and $b = -0.05110$. Then, the class width was selected which provided the minimal mean squared error (MSE),

$$MSE = \frac{\sum_{i=1}^k (89.56e^{-0.05110D_i} - n_i)^2}{k-2}$$

where n_i is the number of trees in the i th dbh class, D_i is the midpoint of the i th dbh class and k is the number of classes.

2.3.2.2. Height Structure

The analysis was carried out for combined sapling and tree heights on the A plots. The class width of 1 m, representing the minimum significant difference, was chosen for histograms. The height distributions were non-normal and the Bartlett's test indicated significant heterocedasticity, therefore, logarithmically transformed means were compared. Because of the low number of distributions (three) and the apparent differences in the shape of distributions, no statistical comparison was applied. Also, regression analysis was not used because the shape of height distributions did not approximate the inverse-J distribution.

However, the occurrence of bi- and trimodal height distributions, indicating a stratified canopy, warranted further investigation. The canopy strata were compared with crown heights and with the dbh distributions using the dbh - height regression results.

The selection criteria for the dbh - height regression model were (1) good fit with the data; (2) as few variables as possible; and (3) as simple form as possible. Since a regression model will be used within the data range, the curve behaviour for dbh values >80 cm was not a consideration. Using the

Tablecurve® software package by Jandel Scientific the following model was selected:

$$height = b_0 + b_1 dbh^2 + b_2 dbh^{2.5} + b_3 dbh^3$$

The fit of the regression model was evaluated with an approximate lack of fit test. Since the intercept should be at 1.3 m (breast height), the intercepts were tested to see whether they were significantly different from 1.3. Using the developed regression models, the canopy boundary values were projected to the dbh distributions to compare the location of minimum/maximum values on dbh and height frequency distributions. (Since the developed dbh - height regressions had a good fit these regressions were used to predict dbh values from height, although the equations may not be the least square solution for height - dbh relationship.)

2.3.2.3. Age Structure

Separate analyses were used for saplings and trees, since saplings were aged at base and trees at breast height. As trees were distinguished from saplings by dbh, the minimum age for trees varied from plot to plot. A relatively high number of cores (24% of all cores for plot 1A, 16% for plot 2A and 23% for plot 3A) could only provide minimum age (number of recognizable rings) due to heart rot. No age correction was applied considering the very weak relationships between age and dbh or height. The minimum significant difference was set to 10 years resulting in a 10 year class width in the histograms. In the case of trees with heart rot the minimum age was plotted. The Bartlett's test indicated

significant heterocedasticity, therefore, logarithmically transformed means were compared. No statistical comparison was applied because of the low number of distributions and apparent differences in the shape of distributions. In addition, regression analysis was not used, as the shape of the age distributions did not approximate the inverse-J distribution.

Since the trees were cored at breast height (bh), the time required to reach bh was also calculated using the saplings which were aged at both base and bh. The correlation between time to reach bh and base age, base diameter and dbh was calculated to determine whether the time to reach bh is independent from these variables.

For the dbh - age and height - age regressions, simple linear models were used, as transformations or more complicated models only marginally improved the fit and made interpretations much more difficult.

2.3.2.4. *Spatial Pattern*

To evaluate the spatial pattern, Morisita's I_δ index was used (Morisita 1959). This index is not sensitive to density (Morisita 1962) but does depend on quadrat size. The calculation of I_δ :

$$I_\delta = q \frac{\sum_{i=1}^q n_i (n_i - 1)}{N(N - 1)}$$

where q = number of quadrats, n_i = number of trees in the i^{th} quadrat and

$$N = \sum_{i=1}^q n_i \quad \text{or } N = \text{total number of trees in all quadrats.}$$

If the spatial pattern is random, (*i.e.* the quadrat counts follow the Poisson distribution (Thompson 1956, Pielou 1977)) the expected value of I_δ , $E(I_\delta) = 1$. For aggregated patterns, the expected value of I_δ is between 1 and q , and for regular patterns, less than 1 (but greater than 0). The I_δ value can be tested with a χ^2 test, since $I_\delta (N-1) + q - N$ has a χ^2 distribution with $q-1$ degrees of freedom.

Contiguous quadrat sampling was used (Greig-Smith 1983) because the Morisita's index provides more reliable information with systematic sampling than random sampling (Hairston *et al.* 1971). Since the trees and saplings were mapped, it was possible to re-sample them using any kind of sampling technique. To aid the calculations, a spatial analysis program (SPA) was developed using Borland C++ language. The program makes it possible to restrict the calculations to certain subsets of trees (e.g. trees with dbh 10-20 cm) or to certain parts of the plot.

The randomness of sapling and tree spatial patterns was tested for each 10 cm dbh class, upper and lower canopy height classes and 50-year age classes at $\alpha = 0.05$ level. For each size/age class, quadrats with side length of 1 to 26 m at 1 m increments were used. The starting point for the contiguous quadrat was set so the analysis was carried out at the central portion of the plot.

2.4. Regeneration Pattern

2.4.1. Sampling and Data Collection

Seedlings were measured along the crown transects and in the quadrats. In the case of crown transects, the species, location, and rooting substrate of seedlings were recorded. Also the crown projection of trees and saplings were mapped and on plot 3A snow was measured within the transect. Location and rooting substrate were recorded as for the saplings. The crowns were mapped by measuring crown radius in four directions parallel with the plot boundaries. Since the crowns were often distorted, this provided a more accurate representation of crowns, than the average crown diameter.

Snow depth, water equivalent and melting pattern were determined from December 23, 1992 to May 20, 1993. Snow depth and the water equivalent (determined by weighting) were measured using a snow tube once a month around 28 poles. (The poles were arranged so that 13 were in the middle of canopy openings, 7 were under the canopy edge, and 8 were under the canopy.) Water equivalent, which is the vertical depth of water that the melting of snowcover would produce, was measured by weighing the snow tube; and snow density was calculated by dividing the water equivalent by the snow depth (Gray and Male 1981). In shallow snow, (less than 50 cm deep) snow depth was measured with a ruler because the snow tube becomes relatively inaccurate (Gray and Male 1981). When the snow started to melt (April 15, 1993), areas

without snow were mapped once a week until the snow disappeared (May 20, 1993).

In the quadrats, the following attributes were recorded or measured: species, vigour, and rooting substrate of seedlings; and understory vegetation cover, substrate, light level, and humus form. Vigour and rooting substrate were recorded as for the saplings.

The percent vegetation cover was estimated according to life form (shrubs, herbs, ferns, mosses and lichens) to speed up sampling. Substrate was estimated as the percent cover of forest floor (FF), decaying wood (DW), and mineral soil (MS) within the quadrat. To characterize available light percent above canopy light (PACL) was used. Above the quadrats photosynthetically active radiation (PAR) was measured in the morning and afternoon under clear sky conditions using a 'Sunfleck Ceptometer' (Model SF-80; Decagon Devices Inc. 1987). The measurements were taken in two perpendicular directions and averaged (Klinka and Carter 1992). At the same time open sky PAR was continuously measured using Li-Cor LI-190SA quantum sensor and LI-1000 datalogger (Li-Cor Inc. 1988). PACL was calculated as the ratio of PAR measured above the quadrat and the open sky PAR at the corresponding time and expressed as a percent. For the humus layer, the thickness of the L, F, and H layers were recorded (Green *et al.* 1993).

2.4.2. Data Analysis

Considering the very low number of Engelmann spruce seedlings observed, this species was excluded from the analysis (Table 13); thus, only the data for subalpine fir were analyzed. Using the crown transect data, each subalpine fir seedling was evaluated as to whether it was located beneath forest canopy cover or a canopy opening. The canopy of each individual tree was represented by a quarter-ellipse (Koop 1989). If there were only two diameter measures for the crown, then the crown was represented by a circle with diameter of the average crown diameter. This situation happened for all saplings in plot 2A and for some saplings and trees in plots 1A and 2A.

The total canopy cover within the crown transects was estimated by generating a 5 cm by 5 cm grid in the computer. Using the coordinates of trees and saplings and the four crown radii values, the centre of each grid cell was marked as being either beneath the canopy (a canopy cell) or not (a canopy opening cell). The ratio of canopy cells to the total number of cells was used to determine the total canopy cover. Although the small cell size increased the computing time, it did not contribute to the measurement and representational errors (crown shapes were approximated by quarter ellipses) already present. The percent of seedlings beneath the canopy was compared to the canopy cover by a z - test (Walpole 1982). It was assumed that the cover of DW and FF are independent of canopy cover.

Snow depth, density, and water equivalent values were plotted against time to check whether the general trend of snow accumulation in openings applies to

the study stands. To assign a snow melt time to the location of each seedling within the canopy transect in plot 3A, the snow melt map was manually digitized by overlaying a 0.25 m by 0.25 m grid on the map and assigning a snow melt time for each cell and eventually to each seedling. The percent of seedlings within snow melt time zones were then compared to the total area of the snow melt time zone using a z - test (Walpole 1982).

The analysis, examining relationships between site factors and the pattern of advance regeneration of subalpine fir, used regeneration and environmental variables. The number of seedlings per quadrat (noBl) and the mean of vigour values of seedlings within the quadrat (mVig) were used as regeneration variables. The mean vigour was set to zero if the quadrat did not contain any seedlings. The following environmental variables were used to describe surface substrates: the cover (%) of forest floor (FF), decaying wood (DW), and mineral soil (MS); thickness of the L, F, and H horizons in the humus form (Green *et al.* 1993); the cover (%) of shrubs, herbs, ferns, mosses, and lichens, and the mean percent of above-canopy light (PACL) (Carter and Klinka 1992). The percent cover of MS was omitted for plot 1A because it was always zero.

As an exploratory step, Pearson correlation coefficients were calculated between all variables to detect the presence of strong correlations among pairs of variables which might cause multicollinearity in further analysis. A *single* high correlation between the regeneration and environmental variables could inflate the canonical correlation values (Dillon and Goldstein 1984). Multiple

correlation analysis with backward elimination was used to detect correlation between individual regeneration and environmental variables (Neter *et al.* 1990). Residual plots were inspected for trends which would indicate the inadequacy of the model. The advantage of multiple correlation is that it is relatively simple and the results are easy to interpret. The disadvantage of this method is that relationships between regeneration variables are not taken into account in the analysis (Manly 1986). To overcome this limitation, canonical correlation analysis was carried out using the correlation matrix of the variables (Grittins 1985). Multiple correlation analysis selects a linear combination of independent variables which correlates best with a dependent variable, while canonical correlation analysis provides a linear combination of one set of variables that correlates best with a linear combination of another set of variables (Dillon and Goldstein 1984). As canonical correlation analysis was used as an exploratory method, no attempt was made to conform the variables to multivariate normality and homoscedasticity.

Since the results indicated that the surface substrate is more important than the cover of understory vegetation and PACL, the success of seedling establishment on DW versus FF was investigated further. The total cover of MS was very low on plots 2A and 3A so it was not included in the analysis. To quantify the success of seedling establishment, a regeneration efficiency coefficient (Geier-Hayes 1987) was used:

$$\text{regeneration efficiency coefficient} = \frac{\% \text{ of all seedlings growing on a given substrate}}{\% \text{ cover of the substrate in the area}}$$

When the given substrate is not present in an area, the regeneration efficiency coefficient is not defined. If the coefficient is greater than one then it indicates that the given substrate provides more favourable conditions for germination and early establishment than other kinds of substrates. A value of less than one indicates less favourable regeneration conditions.

Prior to calculating the regeneration efficiency coefficient, the % cover of FF and DW in different plots was compared. First, the frequency of FF and DW substrate cover within quadrats was plotted. Second, the mean cover was calculated for each plot by averaging the cover values of the individual quadrats. The minimum significant difference between the means was set to 10%. As the difference between the means was greater than 10% only for plots 1A and 3A, these two plots were compared with a one-way analysis of variance at $\alpha=0.05$. Both variables had homogeneous variances at the $\alpha=0.05$ level as indicated by a Bartlett's test.

Third, the regeneration efficiency coefficient was calculated for each quadrat which (1) contained seedlings, and (2) had both FF and DW because the regeneration efficiency is based on a between-substrates comparison. The mean regeneration coefficient values were calculated for both FF and DW for each plot and were compared with a one-way analysis of variance.

The preferred way to determine seedling survival would be to monitor seedlings for a certain growth period. However, such a monitoring could not be

done in this study because it might take decades for a suppressed seedling to reach breast height. One way to resolve this problem is to assume that the saplings present in the study stands represent the seedlings which have survived. Assumptions involved in this approach include: (1) constancy of seed source, (2) constancy of appropriate seedbed (in this case the constancy of the FF and DW cover), and (3) constancy in rates of survivorship. The two substrates types (FF and DW) were used to evaluate seedling survival because they were highly correlated with regeneration variables. Also, the between-plot comparison provided some evidence for constancy of the FF and DW cover. The cover of FF and DW was very similar in plots 2A and 3A, but the difference in the maximum ages of trees was at least 100 years. Therefore, only those saplings which were <100 year-old at the base were used in the survival analysis. For those saplings the regeneration efficiency coefficient was calculated in the same way as shown earlier and compared to the results for seedlings.

3. RESULTS

3.1. Stand Structure

Most structural attributes showed considerable variation (Appendix). The maximum dbh (84 cm), height (49 m) and volume (794 m³/ha) values for fir were high, considering the growth-constraining climatic conditions of the ESSF zone. Stand 3, which was the most productive stand, had the largest maximum sizes (dbh, height). However, the oldest fir trees (about 400 years old) were in plot 2A. The age of these trees approaches the expected life span of fir (Oosting and Reed 1952).

3.1.1. Diameter Structure

The ordering of plots using the box plots indicates that most plots are more similar to the plots from other stands than to the plots from the same stand (Figure 3). Stand 1 showed the most variation and stand 2 the least. Plot 1B represents one of the extremes because of the very high number of saplings (Appendix). The box plots showed that the dbh distributions are skewed for all plots: the median is consistently lower than the mean and the 5th and 25th percentiles are much closer than the 75th and 95th percentiles. The histograms confirmed this observation, all plots were positively skewed (Figure 4). The general trend of the frequency distribution closely approximated an inverse-J shape, although the individual class frequencies varied considerably around the general trend.

The ranking of the mean dbh values for the plots was similar to the order in the box plot (Table 2). The mean values for plots 1C, 2C and 3B were similar and the means in plots 3A and 1B were the extreme values. Comparing the means for plots within stands in the case of stand 2 and 3 there were no significant differences. Also means for plots in stand 1 and 2 were not significantly different from each other with the exception of plot 1B.

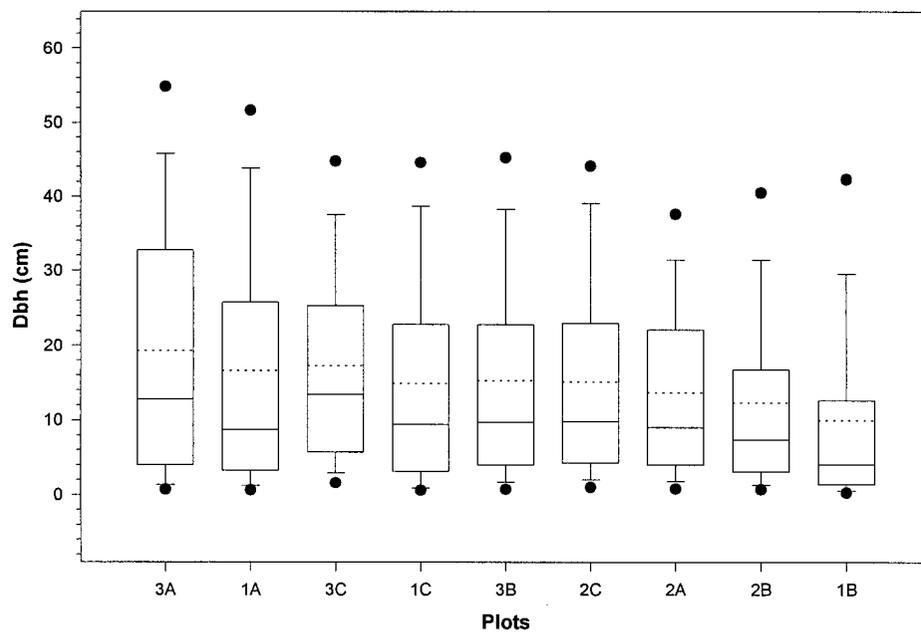
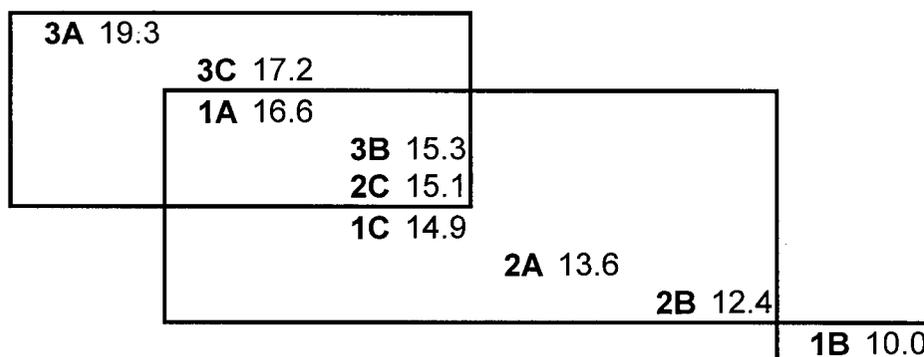


Figure 3. Box plot of dbh of fir for all study plots. The extent of the box indicates the 25th and 75th percentiles of the data. Inside the box the solid line indicates the median, the dashed line shows the mean. Circles denote 5th and 95th percentiles.

Table 2. Summary of comparisons of the mean dbh of fir. The plots and mean dbh values in cm are shown. Values within a column are not significantly different, since the difference between means is less than 1 cm. The boxes indicate the groups within which all means are not significantly different at $\alpha=0.05$ (based on logarithmically transformed data).



The contingency table analysis showed that there were significant differences within stands except in the case of stand 2 (Table 3). The results were consistent with the previous results for stand 2 (plots within stand were similar) and for plot 1B (different from plots 1A and 1C).

Plots 1C, 2C and 3B appeared to be similar based on box plots and means, therefore, these three plots were also compared using the contingency tables and Kolmogorov-Smirnov test in addition to within-stand comparisons. According to the contingency table analysis the three selected plots (1C, 2C, and 3B) were not significantly different indicating that there can be more within-stand than between stand variation.

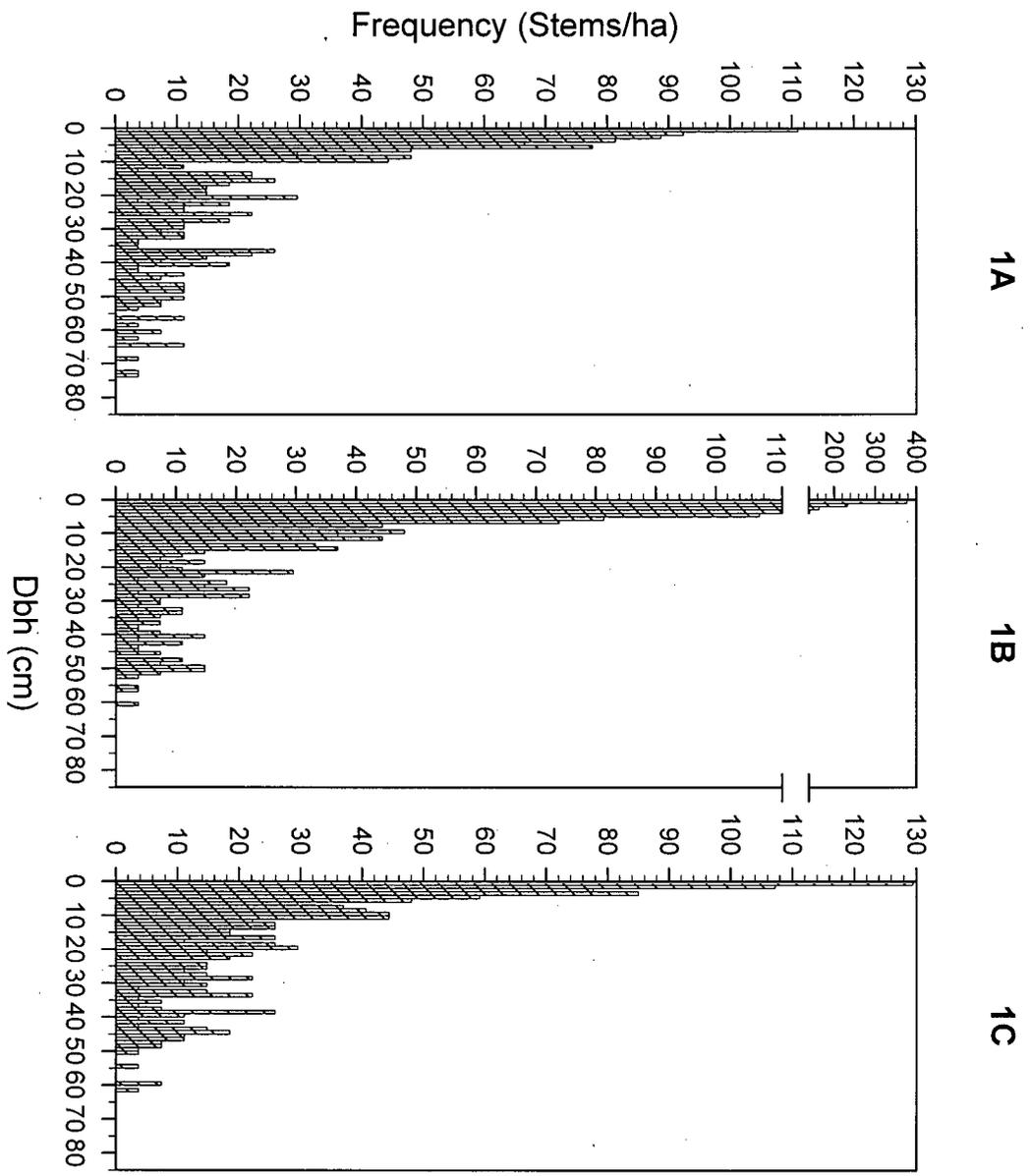


Figure 4. Dbh frequency distributions of fir for all plots using class width of 1 cm.

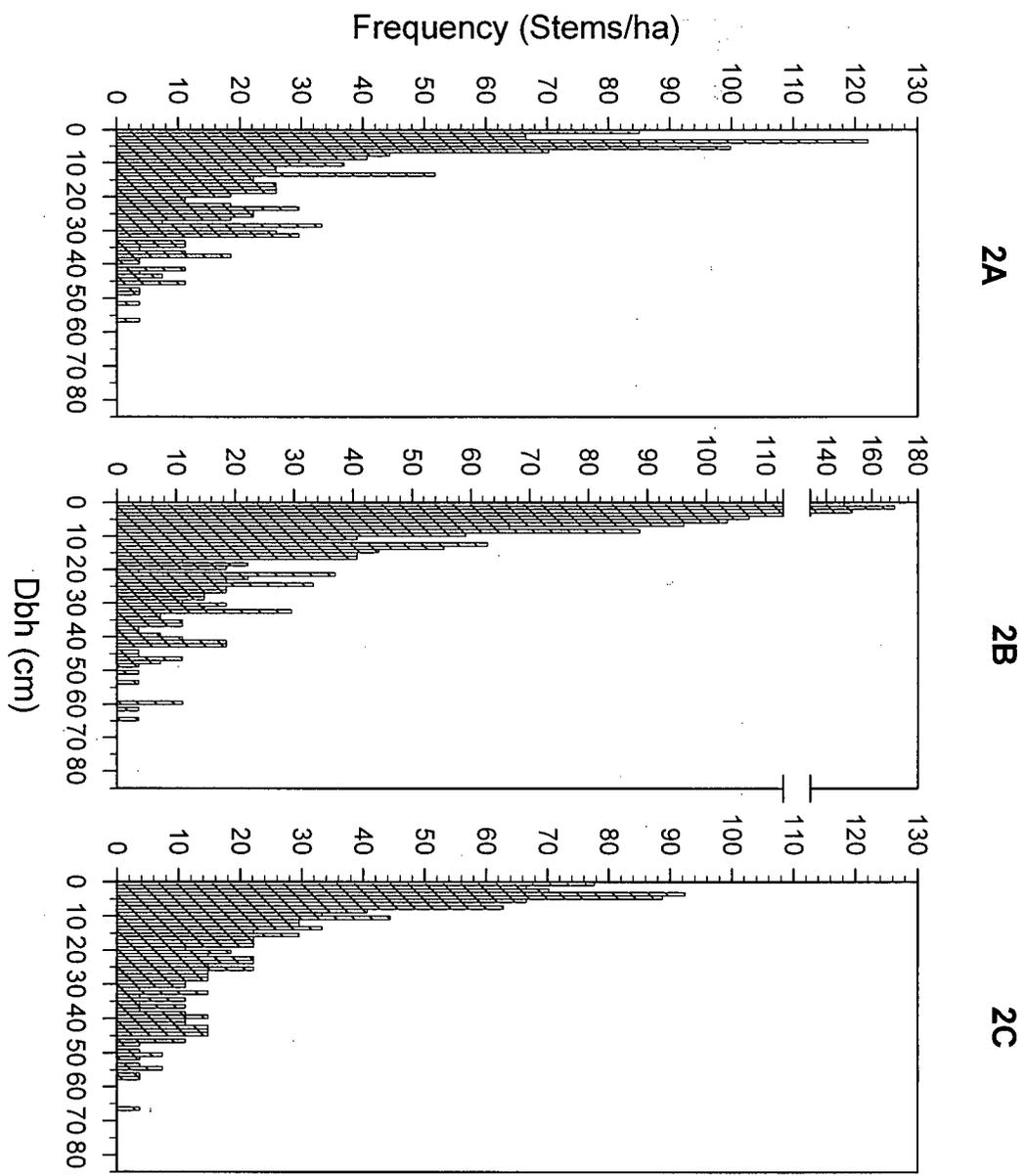


Figure 4. Continued.

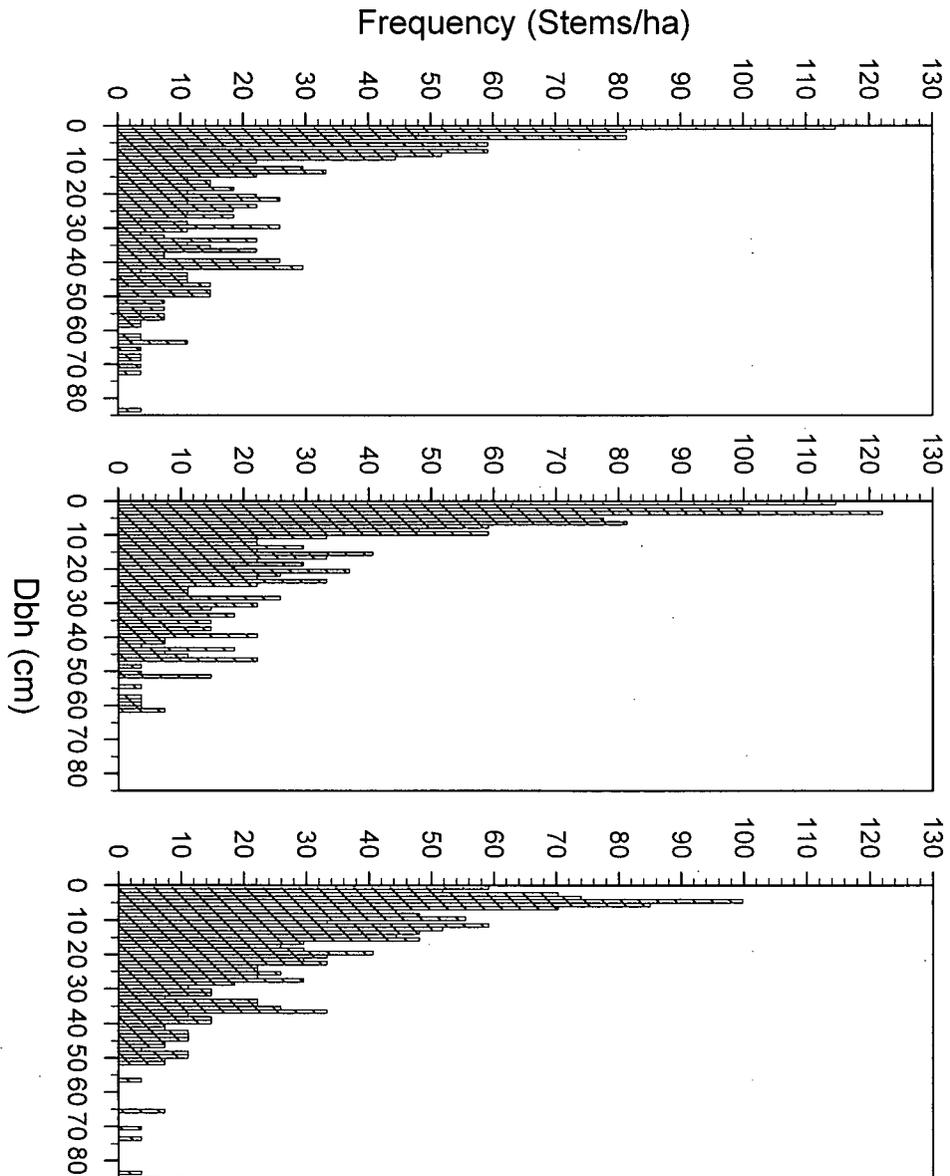


Figure 4. Continued.

The Kolmogorov-Smirnov test gave similar results to the contingency table analysis but in some cases it appeared to be more sensitive (Table 4). The Kolmogorov-Smirnov test indicated significant differences for plot 2B and plots 2A and 2C; and plot 3A became significantly different from plot 3B. From the three similar plots identified before (1C, 2C, and 3B), the 1C-3B comparison was significantly different and the 2C-3B comparison was close to significant ($P < 0.041$).

The graphical evaluation of the fit of the negative exponential function on the dbh distributions provided contrasting results. The ratio of neighbouring dbh classes (q) showed large variation around the mean value, whereas for the negative exponential function the q value is constant (Figure 5). On the other hand, the dbh frequency values generally showed a strong linear trend on a logarithmic scale, and in some cases, the fit appeared to be close to that expected for the negative exponential function (Figure 6).

The regression analysis showed that the negative exponential function did not provide an adequate fit for the cumulative frequency and most of the frequency distributions. The coefficient of determination was high and the standard error of estimate was low (Table 5). However, in the case of the cumulative frequency distributions, all plots showed lack of fit, as indicated by the residual plots (Figures 7 and 8), and the lack of fit test (Table 7). These results may seem contradictory, but, because of the high total variation in cumulative frequencies, the regression could explain a much higher percent of the total variation than the

mean. Cumulative frequencies were consistently overestimated for medium dbh values and underestimated for large dbh values with the exception of plot 3C. Plot 3C showed the best fit, therefore this plot was used to identify the optimal class width which was 1 cm.

The regression coefficients for the frequency distributions were quite close to the reconstructed values (Table 6). In the case of frequency distributions, only plots 3A and 3B did not show significant lack of fit (Table 7). The dbh distribution of plot 3C, which had the best fit using cumulative frequencies, showed significant lack of fit for the frequency distribution. The combined plots also showed significant lack of fit which indicated that the results do not change with increasing sample size.

The q - plots showed more consistent results with the regression analyses (Figure 5) than the other plot types. Plot 3C, did not show closer fit on the q - plots than the other plots in the graphical analysis even though it had the closest fit using regression on cumulative frequencies. Both plot 3A and 3B had good fit using regression on frequencies, but only plot 3B had a good fit based on q values.

Table 3. Results from the contingency table analysis comparing the dbh distributions of plots. NS = non-significant, S = significant at the overall error rate of $\alpha = 0.05$.

Stand 1	1A	1B	1C
1A	-		
1B	S	-	
1C	NS	S	-
Stand 2	2A	2B	2C
2A	-		
2B	NS	-	
2C	NS	NS	-
Stand 3	3A	3B	3C
3A	-		
3B	NS	-	
3C	S	NS	-

Table 4. Results from the Kolmogorov-Smirnov test comparing the dbh distributions of plots. NS = non-significant, S = significant at the overall error rate of $\alpha = 0.05$. The shading indicates results that differ from Table 3.

Stand 1	1A	1B	1C
1A	-		
1B	S	-	
1C	NS	S	-
Stand 2	2A	2B	2C
2A	-		
2B	S	-	
2C	NS	S	-
Stand 3	3A	3B	3C
3A	-		
3B	S	-	
3C	S	NS	-

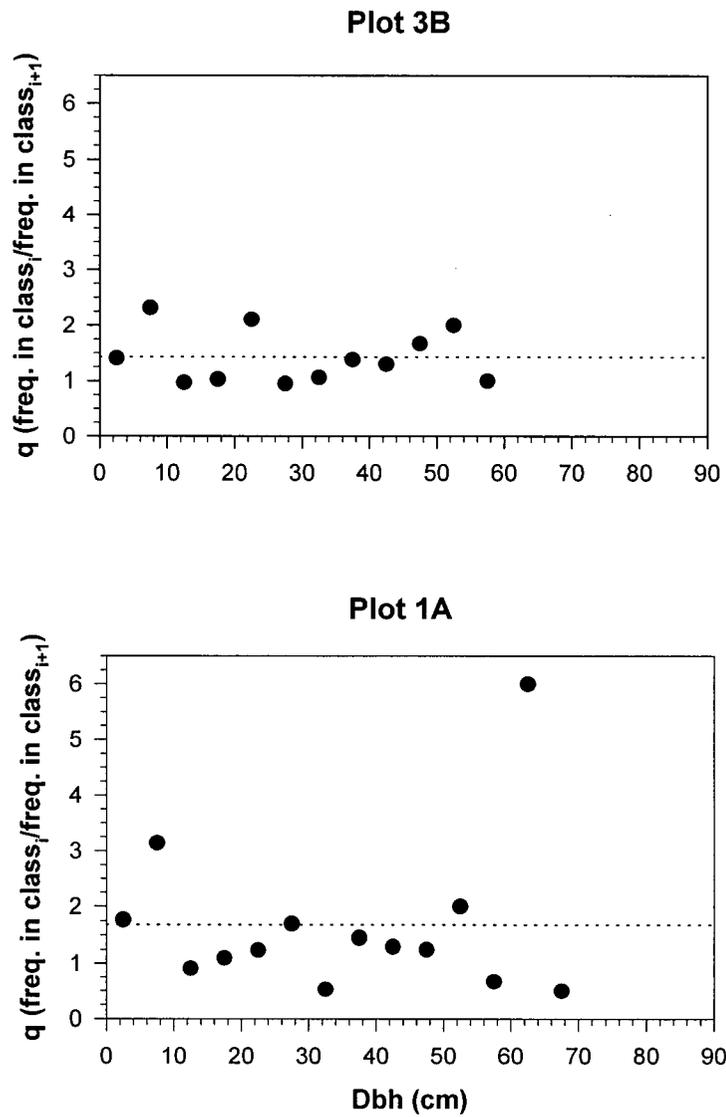


Figure 5. Ratio (q) of number of individuals in neighbouring dbh classes as a function of class midpoint. The ratios were calculated using class width of 5 cm. The two graphs present the plots with lowest (3B) and highest (1A) variation in q values. The dashed line indicates the average q value.

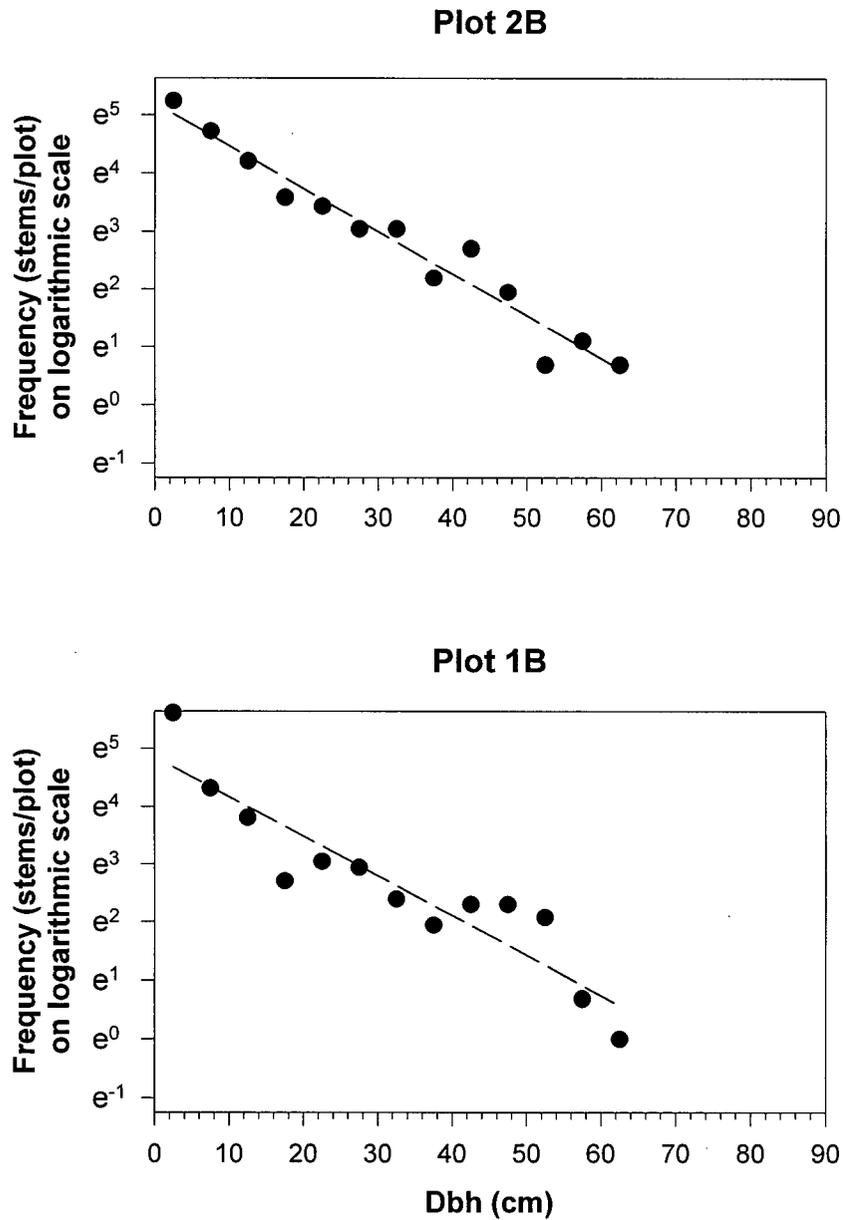


Figure 6. Dbh frequency distributions on a logarithmic scale. The class width was 5 cm. The two graphs present the plots with the best (2B) and worst (1B) linear trend. The dashed line indicates the linear trend expected for a negative exponential function.

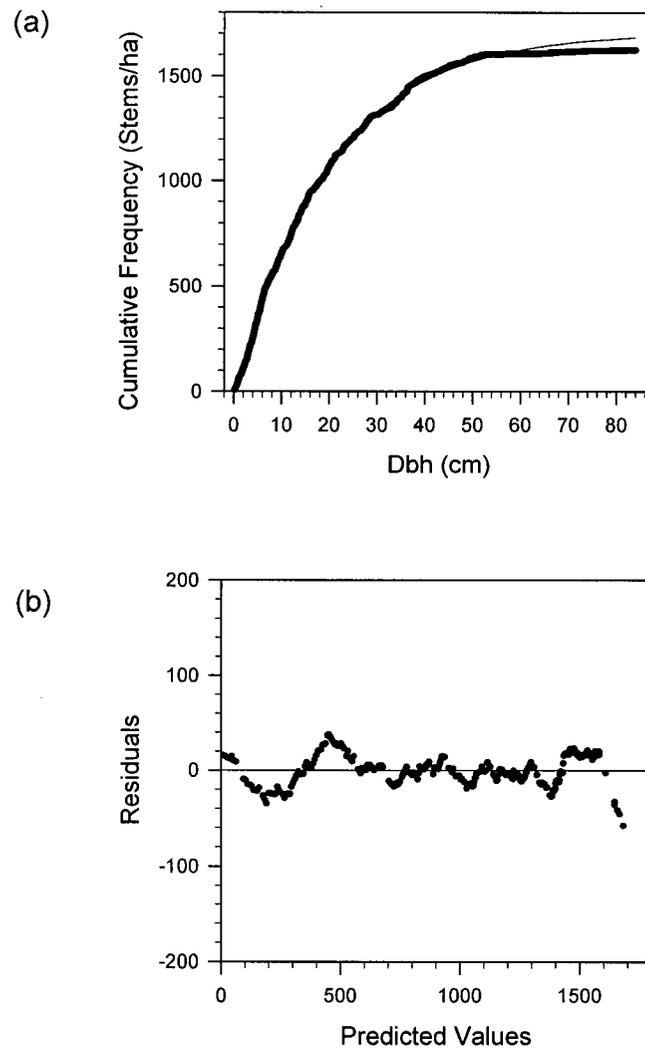


Figure 7. Plots of the best fit of the cumulative dbh frequency distribution with the negative exponential function. (a) Cumulative frequency distribution for plot 3C (thick line) and fitted negative exponential curve (thin line). (b) Residual plot.

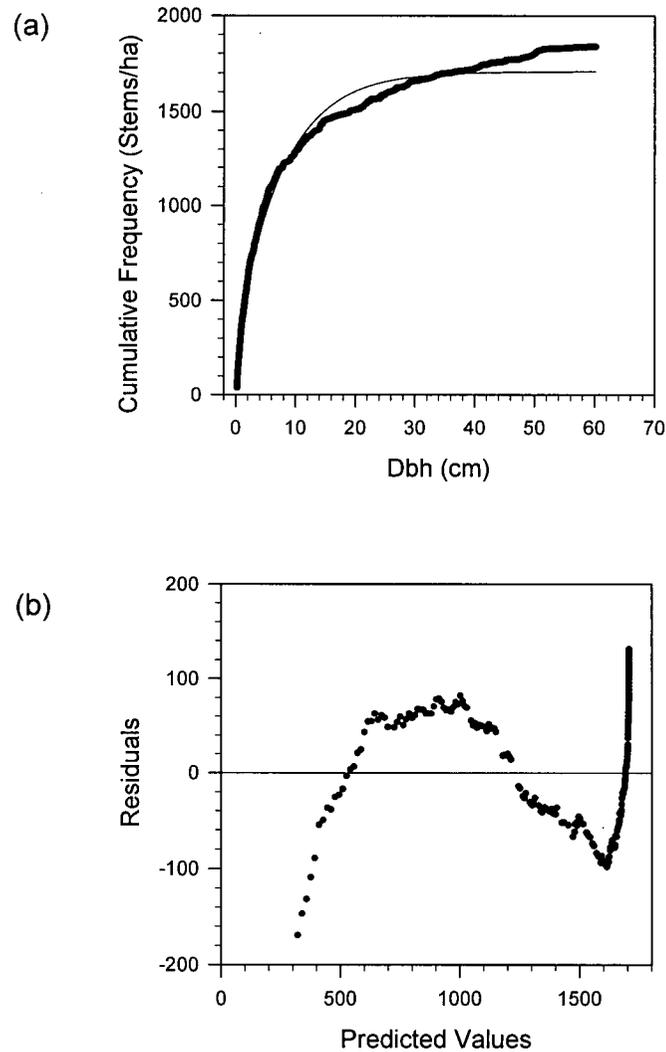


Figure 8. Plots of the worst fit of the cumulative dbh frequency distribution with the negative exponential function. (a) Cumulative frequency distribution for plot 1B (thick line) and fitted negative exponential curve (thin line). (b) Residual plot.

Table 5. Summary of regression analysis of the negative exponential function on the dbh distributions. R² is coefficient of determination and SEE is the standard error of estimate (in stems/ha unit).

Plot	Cumulative frequency distribution		Frequency distribution	
	R ²	SEE	R ²	SEE
1A	0.984	46	0.854	9
1B	0.984	67	0.954	12
1C	0.992	34	0.875	8
2A	0.994	31	0.842	10
2B	0.997	29	0.950	9
2C	0.996	24	0.920	6
3A	0.991	36	0.741	11
3B	0.995	32	0.875	9
3C	0.999	16	0.881	8

Table 6. Summary of regression coefficients for the analyses shown in Table 5. For the meaning of symbols refer to Equations 1 and 3; $\alpha' = -\beta \gamma$; and $q = e^{-2b}$

Plot	Cumulative frequency distribution			Reconstructed frequency distribution			Frequency distribution		
	α	β	γ	a	b	a'	a	b	q
1A	-1089.82	-0.07502	1148.38	81.76	-0.07502	86.15	111.12	-0.11071	1.25
1B	-1558.25	-0.17697	1642.39	275.76	-0.17697	290.66	396.61	-0.28622	1.77
1C	-1152.22	-0.06882	1225.54	79.30	-0.06882	84.35	110.62	-0.10223	1.23
2A	-1337.25	-0.07411	1331.59	99.10	-0.07411	98.68	96.60	-0.07151	1.15
2B	-1816.66	-0.09383	1819.21	170.46	-0.09383	170.70	174.29	-0.09690	1.21
2C	-1263.78	-0.07188	1258.45	90.84	-0.07188	90.46	88.70	-0.06975	1.15
3A	-1205.95	-0.04772	1283.95	57.55	-0.04772	61.28	80.09	-0.07016	1.15
3B	-1474.28	-0.06822	1497.59	100.57	-0.06822	102.16	107.23	-0.07264	1.16
3C	-1752.70	-0.05110	1705.24	89.56	-0.05110	87.13	81.96	-0.04776	1.10

Table 7. Summary of the lack of fit test results of the negative exponential function on dbh distributions showing degrees of freedom (df), sum of squares (SS), F values and the probability of the F value (Prob. F) with the null hypothesis of no lack of fit.

Plot	Source	Cumulative frequency distribution				Frequency distribution			
		df	SS	F value	Prob. F	df	SS	F value	Prob. F
1A	Lack of fit	114	692246.41	327.79	0.000	25	3762.41	3.25	0.000
	Pure error	220	4075.56			56	2596.25		
1B	Lack of fit	123	2207196.75	250.99	0.000	25	5857.68	2.46	0.003
	Pure error	370	26453.05			56	5335.63		
1C	Lack of fit	112	390000.19	231.29	0.000	25	3214.71	2.81	0.001
	Pure error	229	3447.61			56	2564.26		
2A	Lack of fit	121	349047.96	175.25	0.000	25	5189.37	3.94	0.000
	Pure error	241	3966.99			56	2951.55		
2B	Lack of fit	153	417586.04	94.98	0.000	25	3058.98	2.34	0.004
	Pure error	358	10287.62			56	2929.40		
2C	Lack of fit	121	198311.60	103.44	0.000	25	2115.95	4.52	0.000
	Pure error	227	3596.69			56	1049.00		
3A	Lack of fit	121	438964.48	307.05	0.000	25	3260.91	1.29	0.214
	Pure error	226	2670.18			56	5674.60		
3B	Lack of fit	138	415632.31	171.79	0.000	25	2512.32	1.19	0.286
	Pure error	275	4821.19			56	4714.25		
3C	Lack of fit	159	105558.25	45.96	0.000	25	2888.59	2.74	0.001
	Pure error	276	3986.46			56	2358.98		

3.1.2. Height Structure

The mean height values (including trees and saplings) for plots 1A, 2A and 3A were 11.0, 9.5 and 13.3 m respectively. The logarithmically transformed means were not significantly different for plots 1A and 2A, but the mean for plot 3A was significantly different from both of them. The box plot of heights indicated positively skewed distributions similar to the dbh distributions (Figure 9). The histogram of height frequencies confirmed this observation (Figure 10). However, the shape of the frequency distributions did not approximate an inverse-J; rather, it showed modes. Since modal height distribution is consistent with a stratified canopy, it was assumed that the modes represent canopy strata and the minimum values represent the boundaries of the canopy strata.

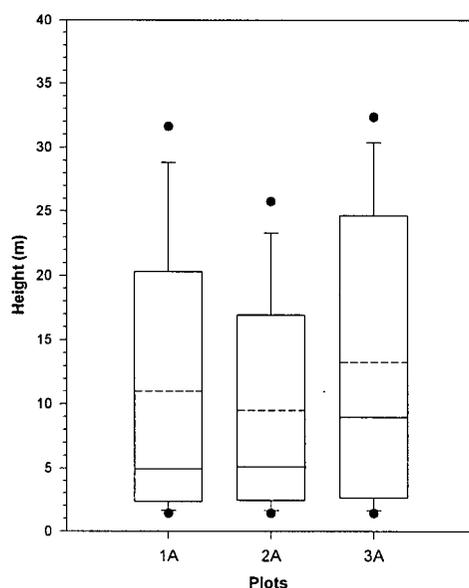


Figure 9. Box plot of tree heights. The extent of the box indicates the 25th and 75th percentiles of the data. Inside the box the solid line indicates the median, the dashed line shows the mean. Circles note 5th and 95th percentiles.

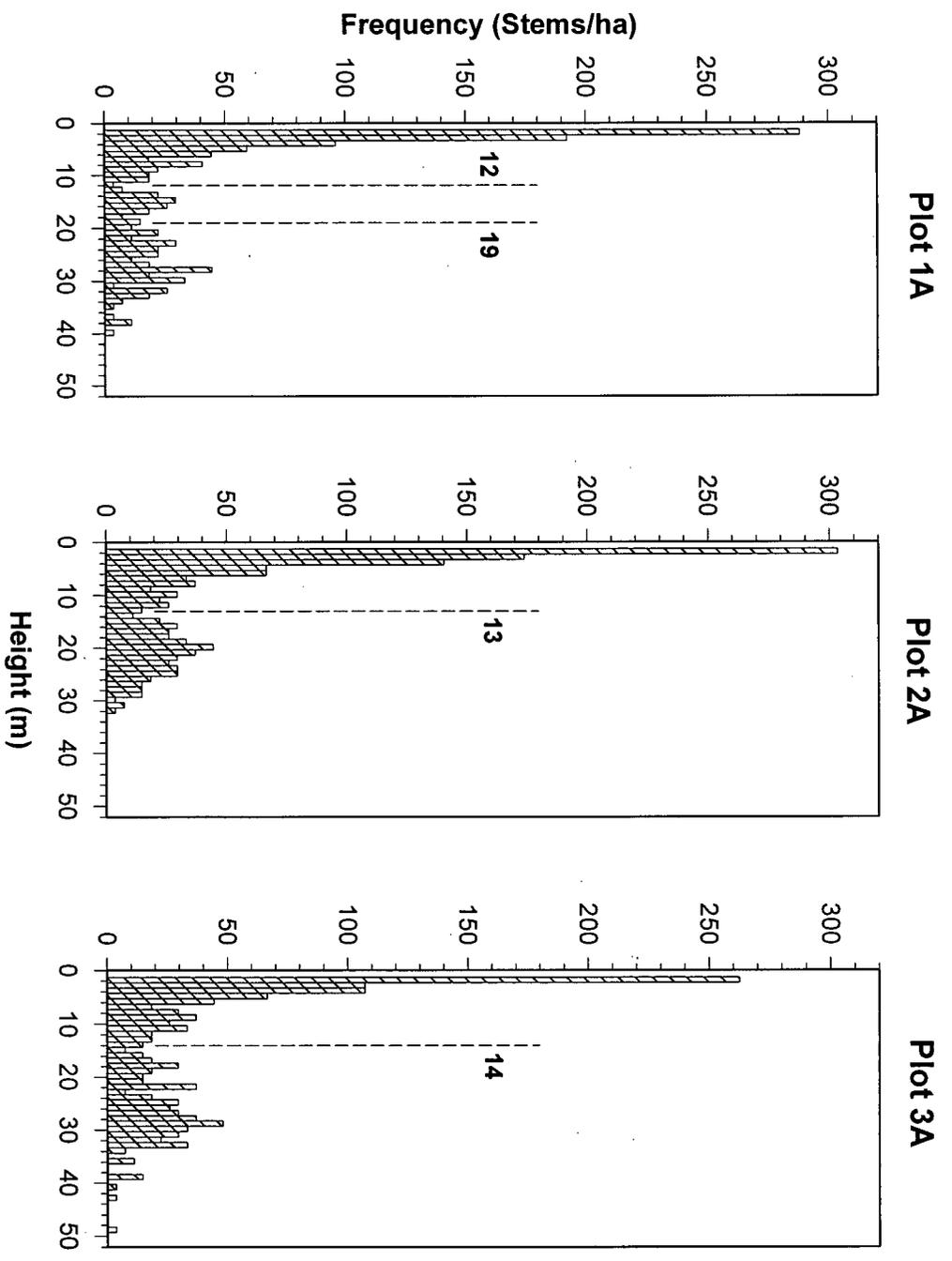


Figure 10. Height frequency distributions of saplings and trees using class width of 1 m. The vertical lines indicate the canopy boundaries.

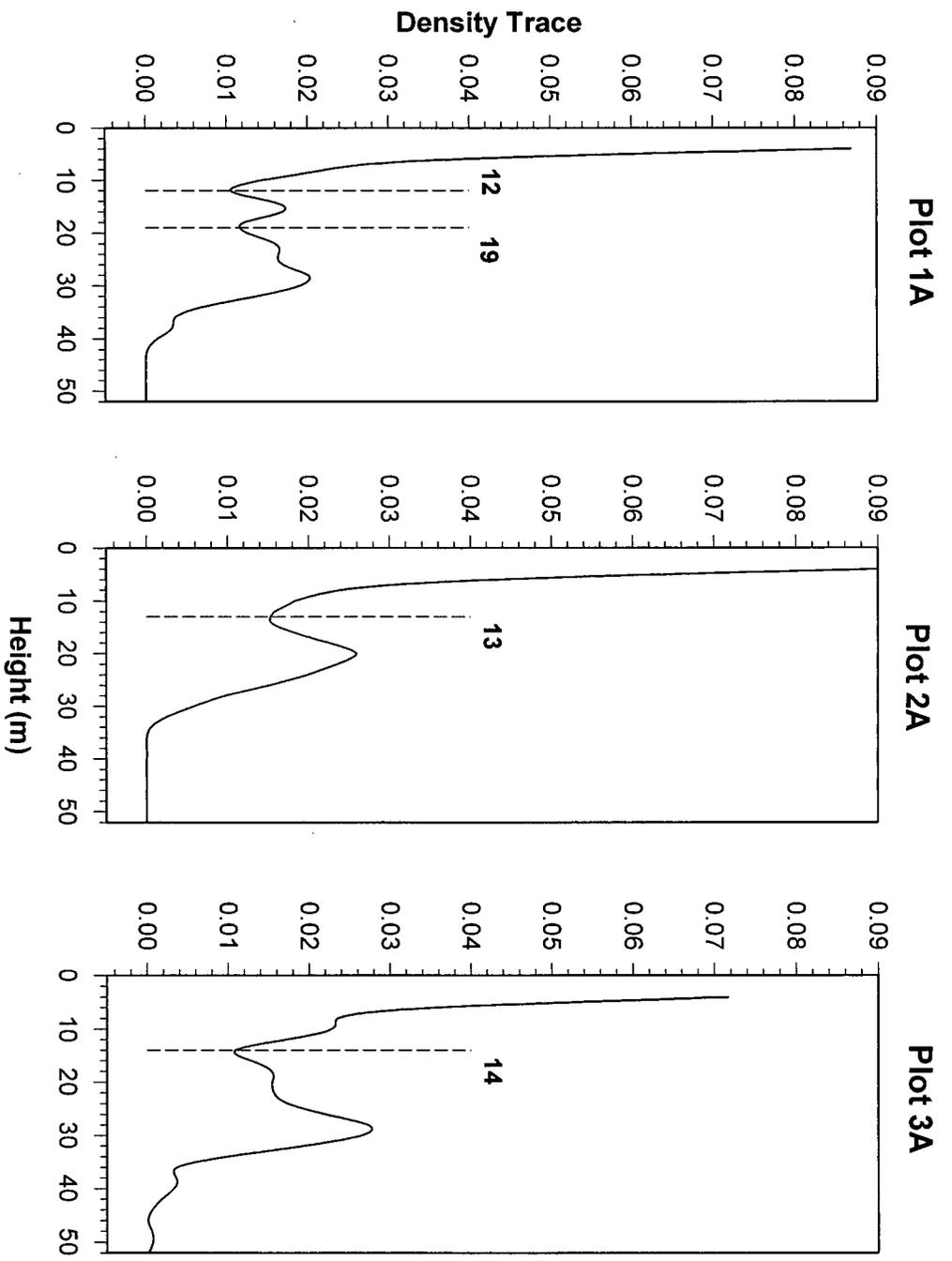


Figure 11. Density trace diagram of heights. The vertical lines indicate the canopy boundaries.

Density trace diagrams with $s = 2$ and $h = 8$ were used to identify minimum values in the frequency distribution, which were regarded as the height of canopy boundaries (Figure 11). Using different s and h values or different starting points generally does not affect the minimum values: the maximum change is 1 m. The height of canopy boundaries were also plotted on the frequency histogram (Figure 10). The lower canopy boundaries were recognizable on the frequency histogram. The second canopy boundary for plot 1A is not as clearly recognizable on the histogram as it is in the density trace diagram. Also, there are low values around 23 m on the histogram for plot 3A. Since the density trace diagram provides a relatively objective way of assessing the shape of a distribution, the canopy boundaries identified on the density trace diagram were used in further analysis.

The maximum crown height of canopy trees was close to the canopy boundary in plot 2A and to the upper canopy boundary in plot 1A (Figure 12). For the canopy boundary in plot 3A and the lower canopy boundary in plot 1A, there is no apparent relationship with the crown height of canopy trees. In all plots, the most frequent height classes (1.3 to 2.3 or 3.3 m classes) were smaller than the minimum crown height of canopy trees.

There was a strong relationship between dbh and height (Table 8, Figure 13). There was no significant lack of fit (details are not shown), all variables were significant, and the intercepts were not significantly different from 1.3 (breast height) (Table 9). Since the dbh - height relationship was strong, the canopy

boundary values were projected to the dbh frequency distribution and the 10 cm dbh value was projected to the height frequency distribution.

The projection of canopy boundary values on the dbh frequency distributions generally did not coincide with the peaks or depressions of the dbh frequency distribution. However, in the case of plot 1A the lower canopy boundary seemed to coincide to a small depression in the dbh frequency curve at dbh \approx 17 cm. In all three plots, the 10 cm dbh corresponded well to the point where the height distribution started to level off. This somewhat justifies the choice of 10 cm dbh as a distinguishing criterion between trees and saplings.

Table 8. Summary of regression statistics for dbh - height relationships. R^2 is the coefficient of determination and SEE is standard error of estimate.

Plot	n	R^2	SEE
1A	338	0.964	2.05
2A	366	0.954	1.87
3A	351	0.942	2.83

Table 9. Parameter values for dbh - height regression models.

Plot	Intercept	x^2	$x^{2.5}$	x^3
1A	1.4553	0.1044	-0.0212	0.001144
2A	1.0190	0.1281	-0.0279	0.001610
3A	1.3545	0.1146	-0.0234	0.001258

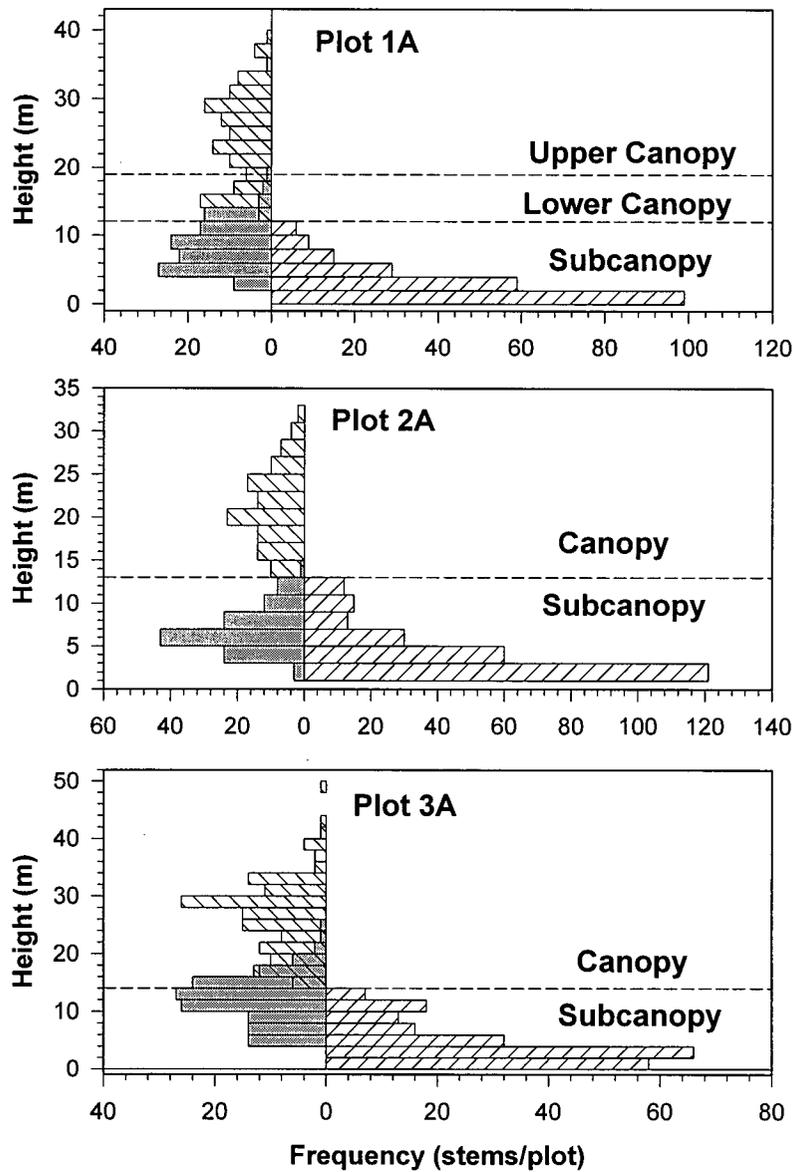


Figure 12. Relationship between canopy boundaries and crown heights. The hatched bars on the left side of 0 are the frequency distribution of numbers of canopy trees and the grey bars are the crown height frequency of the same trees. The hatched bars on the right side of 0 represent the frequency distribution of subcanopy trees.

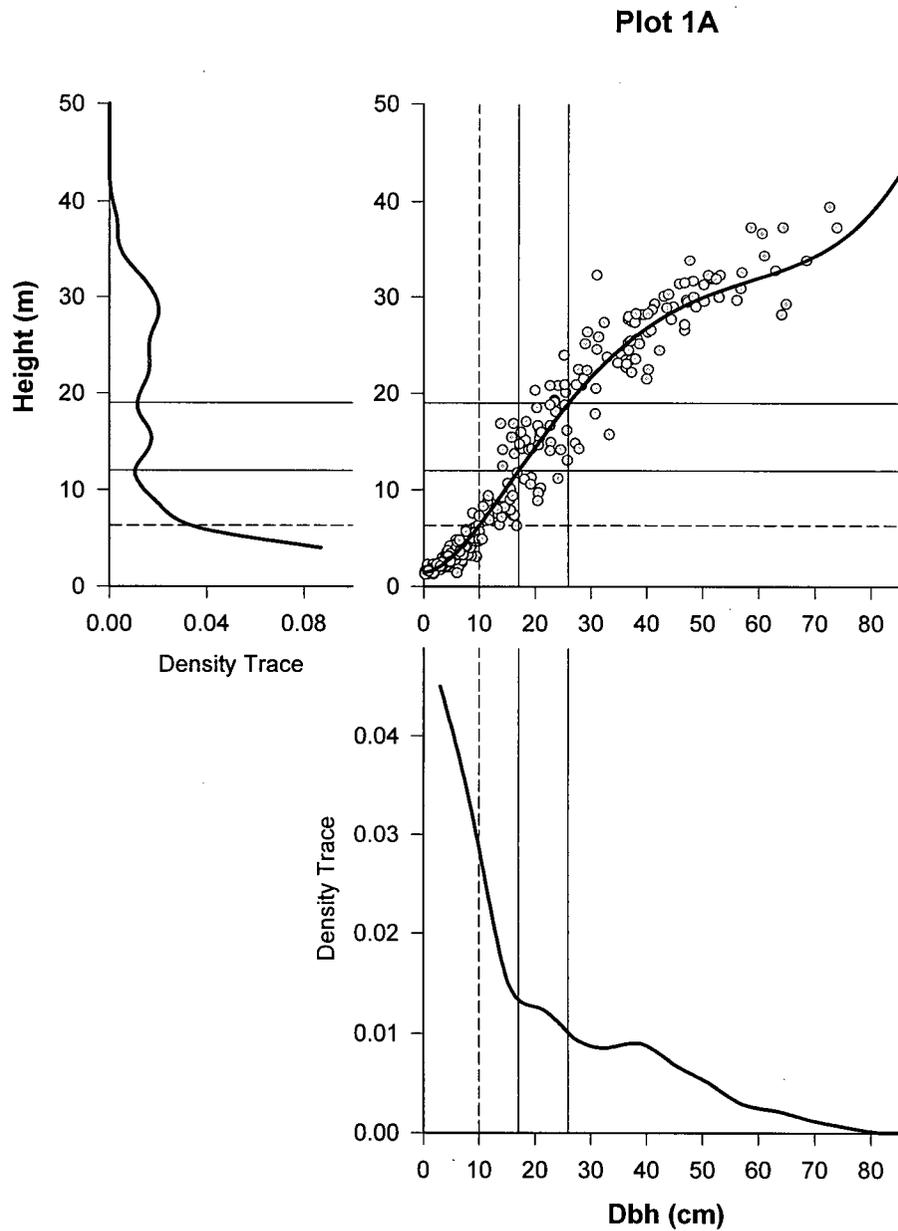


Figure 13. Relationship between the canopy boundary values and the dbh distribution. The thin continuous horizontal and vertical lines mark the canopy boundary values and the corresponding dbh values; the dashed lines mark dbh = 10 and the corresponding height values. The thick continuous line in the dbh - height graph is the fitted equation and the grey dots are the data points.

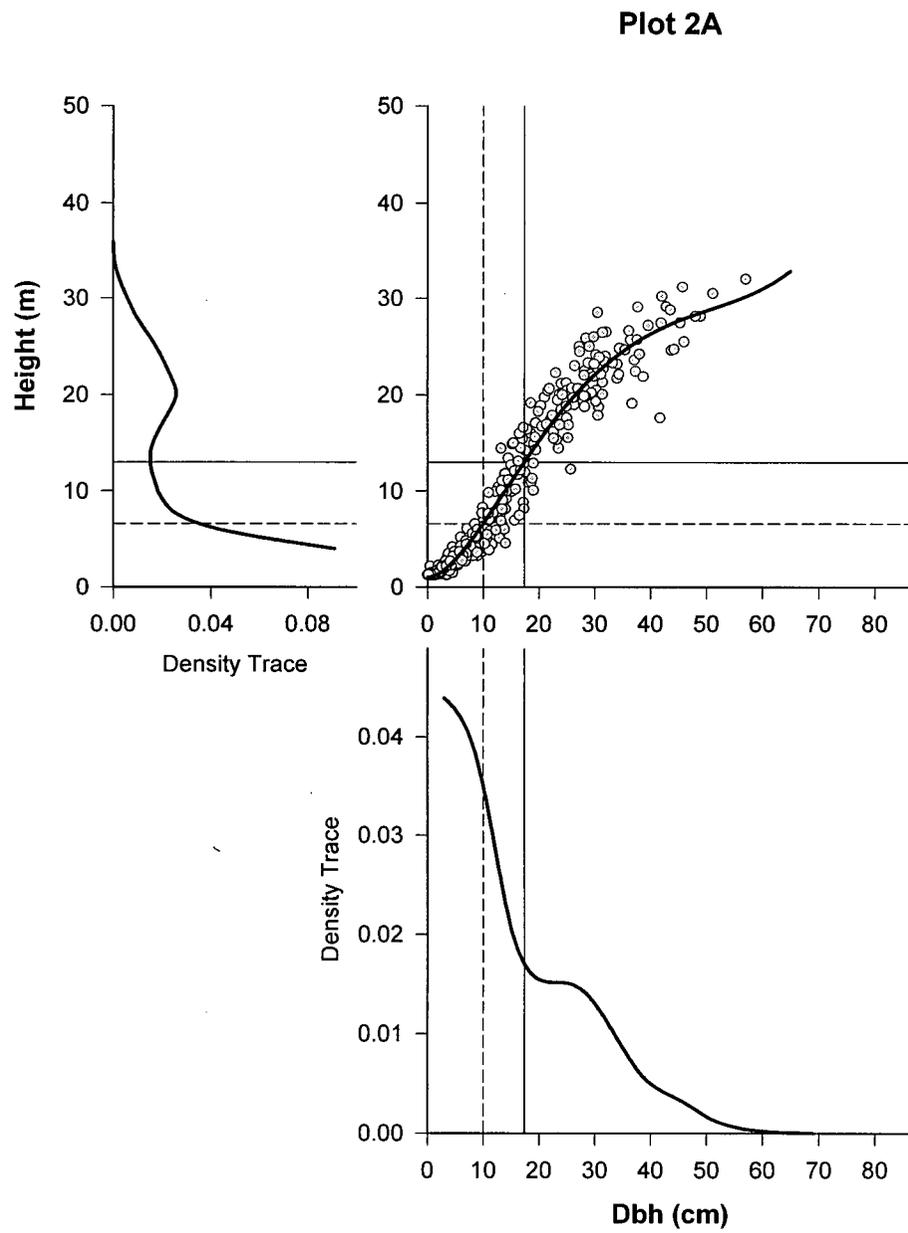


Figure 13. Continued.

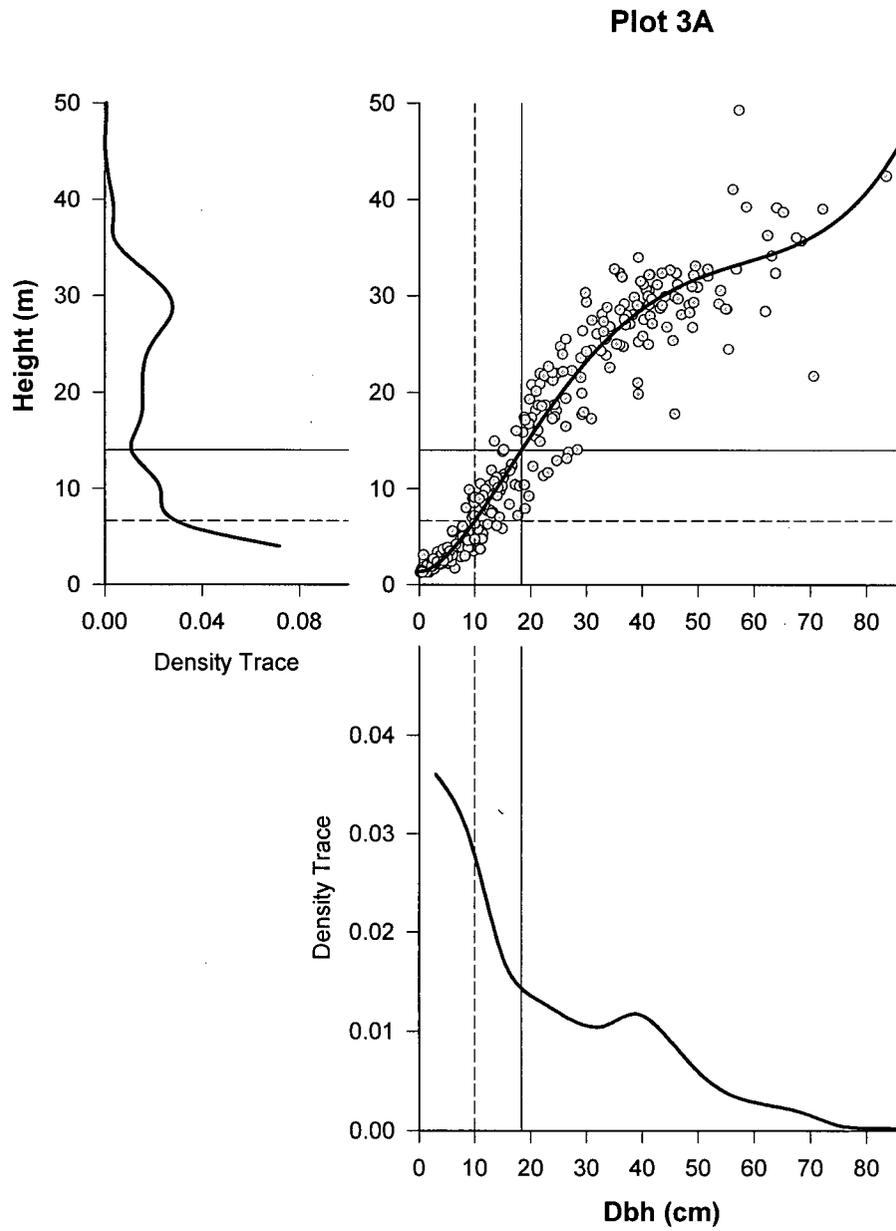


Figure 13. Continued.

3.1.3. Age Structure

The box plots of sapling ages determined at base and tree ages determined at bh (1.3 m) indicated symmetrical, rather than skewed distributions as was the case for the size distributions (Figure 14 and 15). The frequency histograms also confirmed the symmetry (Figure 16 and 17). The age distribution of saplings was unimodal in all plots, approximating a normal distribution. Some saplings were over 200 years old and still had a dbh < 10 cm. The slow growth could be explained by extended periods of suppression.

The shape of the age distribution of trees appears to be slightly bimodal with a small peak in the oldest age classes. In the case of tree ages caution should be exercised because: (1) a high number of cores could provide only minimum age; (2) the distinction between saplings and trees was based on dbh, and as a result, the frequency in the youngest age classes might be underestimated, compared to the complete census of bh ages.

The time required to reach 1.3 m varied from a minimum of 11 years to a maximum of 140 years (Figure 18). The average was 50 years for plot 1A, 70 years for plot 2A, and 30 years for plot 3A. For plots 1A and 2A the time required to reach 1.3 m was significantly and positively correlated with the base age: for plot 1A the correlation coefficient was 0.64 ($P < 0.01$), and for plot 2A, 0.44 ($P < 0.01$).

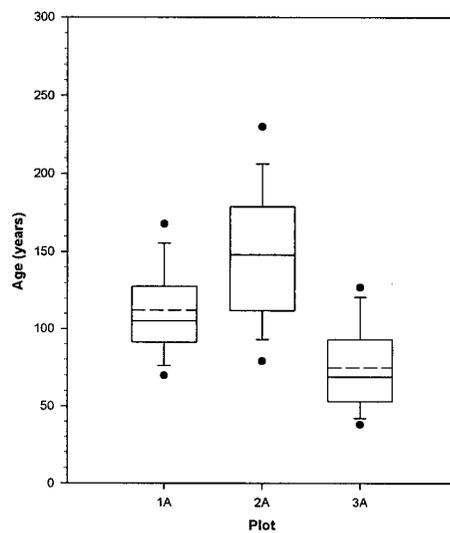


Figure 14. Box plot of sapling ages determined at the base. The extent of the box indicates the 25th and 75th percentiles of the data. Inside the box the solid line indicates the median, the dashed line shows the mean. Circles note 5th and 95th percentiles.

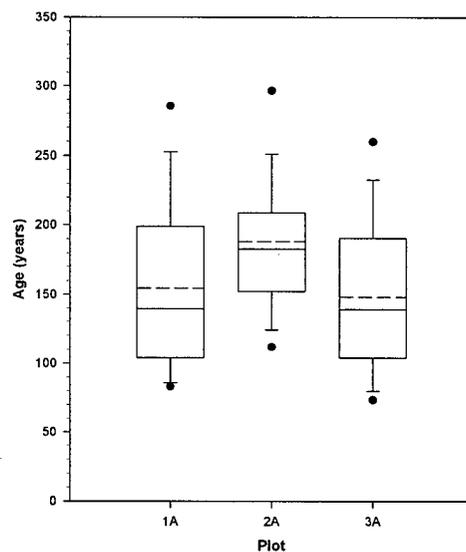


Figure 15. Box plot of tree ages determined at 1.3 m. The extent of the box indicates the 25th and 75th percentiles of the data. Inside the box the solid line indicates the median, the dashed line shows the mean. Circles note 5th and 95th percentiles.

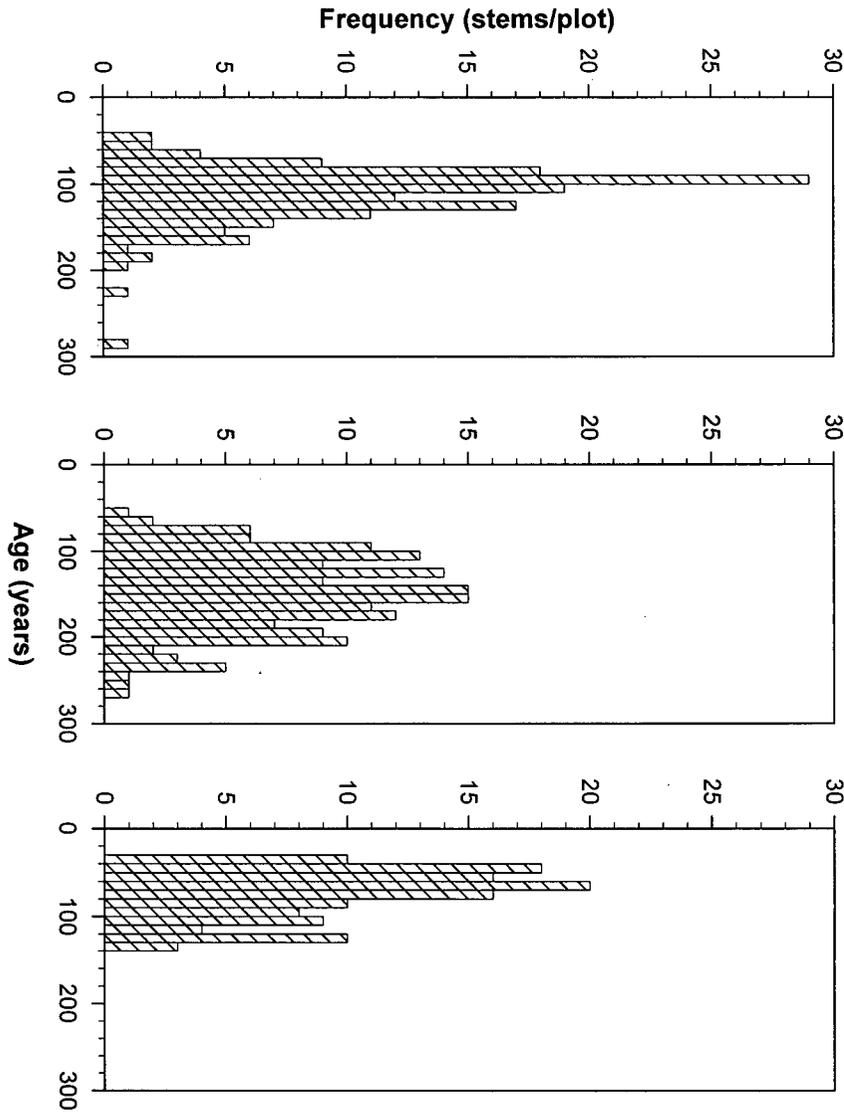
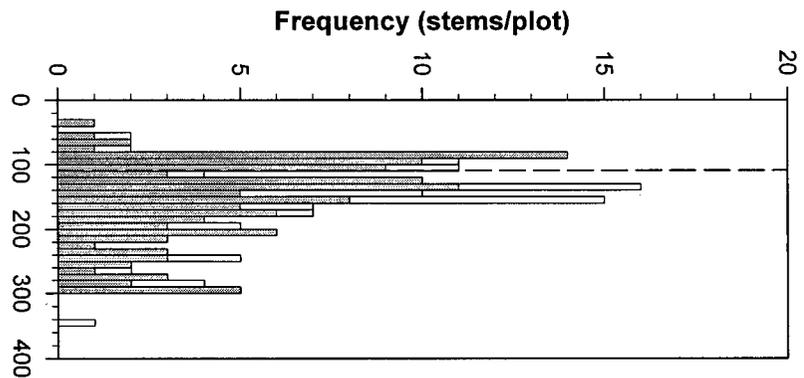
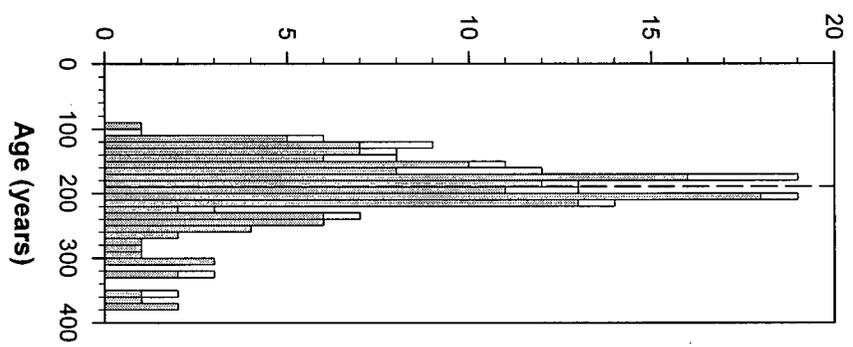


Figure 16. Age (determined at base) frequency distributions of saplings using class width of 10 years.

1A



2A



3A

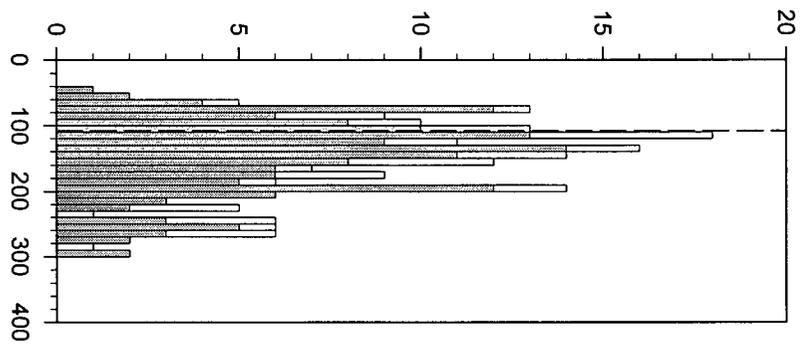


Figure 17. Age (determined at 1.3 m) frequency distributions of trees using class width of 10 years. The open bars represent minimum ages. The dashed lines indicate the maximum sapling age at breast height (1.3 m).

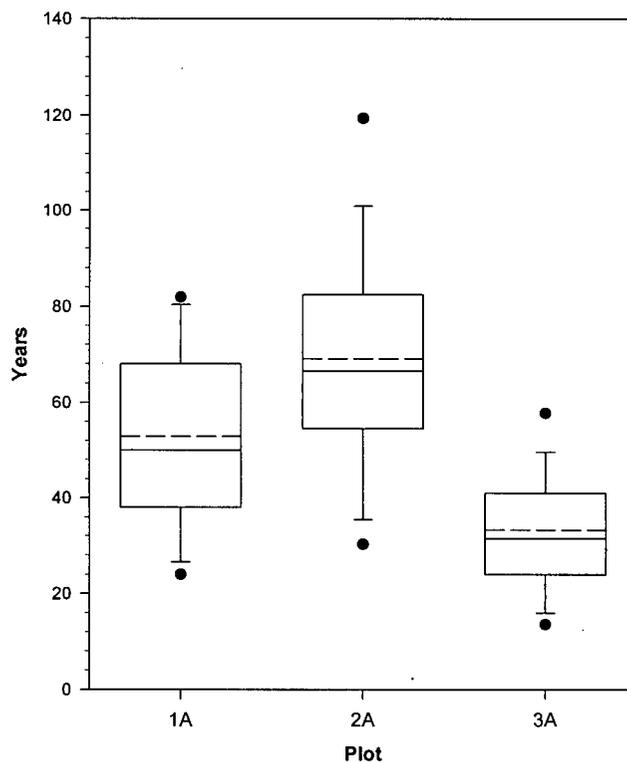


Figure 18. Box plot of time required to reach breast height. The extent of the box indicates the 25th and 75th percentiles of the data. Inside the box the solid line indicates the median, the dashed line shows the mean. Circles note 5th and 95th percentiles.

The dbh - age and height - age relationships are not suitable for predictive purposes because of the high variation of the data. Although for all plots, the relationships were significant at $\alpha = 0.05$ level, the coefficient of determination was around 0.2, and the standard error of estimate was large, about 50 years. This means that the 95% confidence interval for age predictions is about 200 years wide, half of the total age range.

3.1.4. Spatial Pattern

The spatial pattern varied from highly aggregated, to random, to regular with increasing size (Table 10). The saplings represented the smallest class for dbh (0 - 10 cm) and most of the individuals in the subcanopy height class. The spatial pattern of saplings was aggregated for all plots and all quadrat sizes, which means the aggregates of saplings were also aggregated. The scale of regularity for trees in the largest dbh classes was close to the maximum crown diameter (8 m), but trees in the upper canopy show regularity at smaller scales (2 - 4 m) as well.

In relation to age, young- and medium-aged trees had aggregated and random spatial patterns respectively, as was the case for size. However, for the oldest trees, the spatial pattern was regular only in plot 1A, while highly aggregated for plots 2A and 3A.

Table 10. Summary of spatial pattern analysis. *A* denotes aggregated and *R* regular spatial patterns which were significant ($\alpha = 0.05$). The numbers indicate the side length of the quadrats in metres. In all other cases the spatial pattern is random.

Dbh Class	Plot 1A	Plot 2A	Plot 3A
0 - 10	A: All sizes	A: All sizes	A: All sizes
10 - 20	A: 7, 10		
20 - 30	A: 8		
30 - 40		R: 6	
40 - 50		R: 10, 12, 13	
50 <	R: 8	-	

Height Class	Plot 1A	Plot 2A	Plot 3A
Subcanopy	A: All sizes	A: All sizes	A: All sizes
Lower canopy		-	-
Upper canopy	R: 2, 4, 5, 11-16	R: 2, 4, 12, 21, 22	R: 3

Age Class (Trees)	Plot 1A	Plot 2A	Plot 3A
0 - 100	A: 7, 8, 10	-	A: 3, 5-7, 9-13, 24
100 - 150		A: 3, 8, 13, 16	
150 - 200	R: 11		
200 <		A: 5, 6, 10	A: 5, 7, 8, 10

3.2. Regeneration Pattern

The canopies of the study stands were quite open, especially in plot 2A (Table 11, Figure 19). Because of the openness of the entire canopy, it was difficult to delineate individual canopy openings. The crown transect maps indicate that (1) the location of downed coarse woody debris (decaying logs) is

quite well delineated by the seedlings established on them, and (2) the number of subalpine fir seedlings in plot 3A is considerably less than in the other two plots.

In all plots the percent of seedlings established beneath the canopy on the forest floor was closely related to the percent of the total canopy cover even where the z -test indicated significant differences between the observed and expected frequencies (Table 11). Compared to the percent of the total canopy cover, the percent of seedlings established beneath the canopy on decaying wood was lower in plot 1A and 3A and the same in plot 2A. There were significant differences between the observed and expected frequencies for these seedlings in plots 1A and 3A.

The snow accumulation pattern was similar to what was expected: the average snow water equivalent and snow depth were consistently higher in the canopy openings than under the canopy, but there was no difference in snow density. Generally more seedlings occurred in the earlier snow melt time zones than was expected with the exception of 22 April, but the differences were significant only for the three snow melt time zones (Table 12). (The total number of seedlings in Table 12 and Table 11 are different because 23 seedlings occurred on MS).

Table 11. Number and percent (calculated column-wise) of fir seedlings under the canopy and in canopy openings in the crown transects. z values were used to test the null hypothesis of no difference between percentage of seedlings under canopy and canopy cover. Values printed in bold indicate a significant difference at $\alpha = 0.05$.

Plot 1A				
	DW	FF	Total	Canopy cover
C. opening	473 (50%)	131 (23%)	604 (40%)	
Canopy	474 (50%)	432 (77%)	906 (60%)	
Total	947	563	1510	75%
z value	-17.73	0.95	-13.46	

Plot 2A				
	DW	FF	Total	Canopy cover
C. opening	397 (41%)	148 (43%)	545 (42%)	
Canopy	561 (59%)	196 (57%)	757 (58%)	
Total	958	344	1302	58%
z value	0.35	-0.38	0.10	

Plot 3A				
	DW	FF	Total	Canopy cover
C. opening	115 (31%)	34 (24%)	149 (29%)	
Canopy	256 (69%)	106 (76%)	362 (71%)	
Total	371	140	511	74%
z value	-2.19	0.46	-1.63	

Table 12. Number and percent of seedlings in different snow melt time zones in the crown transect of plot 3A. The z values are the statistics to test whether the ratios of number of seedlings in different snow melt time zones is different from the percent cover of each snow melt time zone. The critical values for $\alpha = 0.05$ are ± 1.96 and $n = 534$. Significant values are marked in bold.

	Time of snow melt					
	15 Apr.	22 Apr.	29 Apr.	6 May	13 May	20 May
No. of fir seedlings	-	27 (5%)	92 (17%)	216 (40%)	153 (29%)	46 (9%)
% cover of snow melt time zones	0%	8%	13%	36%	32%	11%
z - value	-0.65	-2.16	2.53	2.22	-1.64	-1.77

Plot 1A

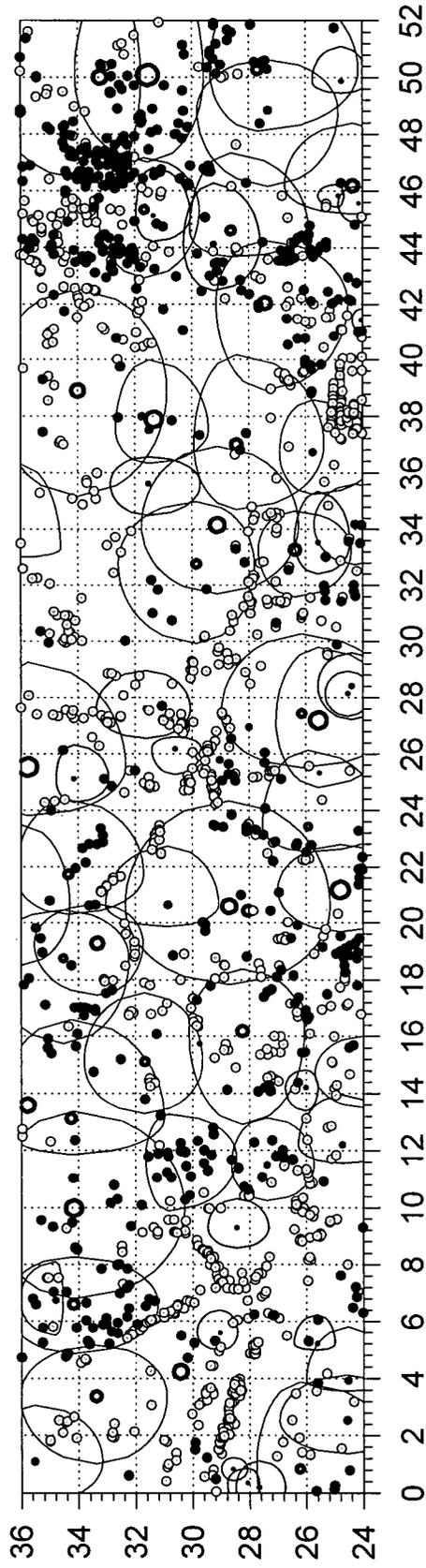


Figure 19. Crown transect maps. The lines indicate crown boundaries, the thick lines stems, the grey dots seedlings on DW and the black dots seedlings on FF. The measurements on the axes are in metres.

Plot 2A

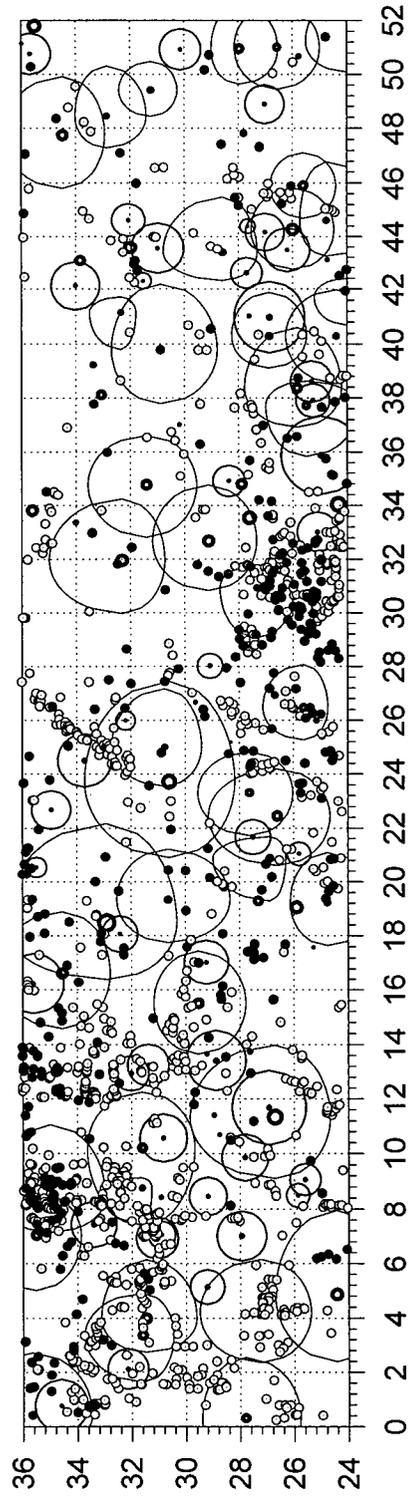


Figure 19. Continued.

Plot 3A

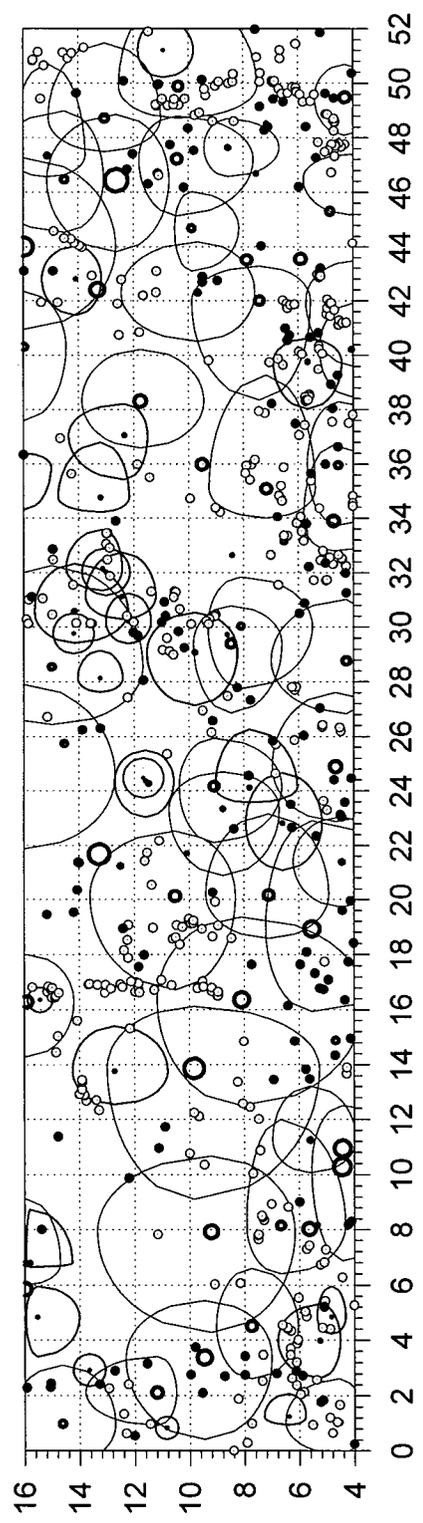


Figure 19. Continued.

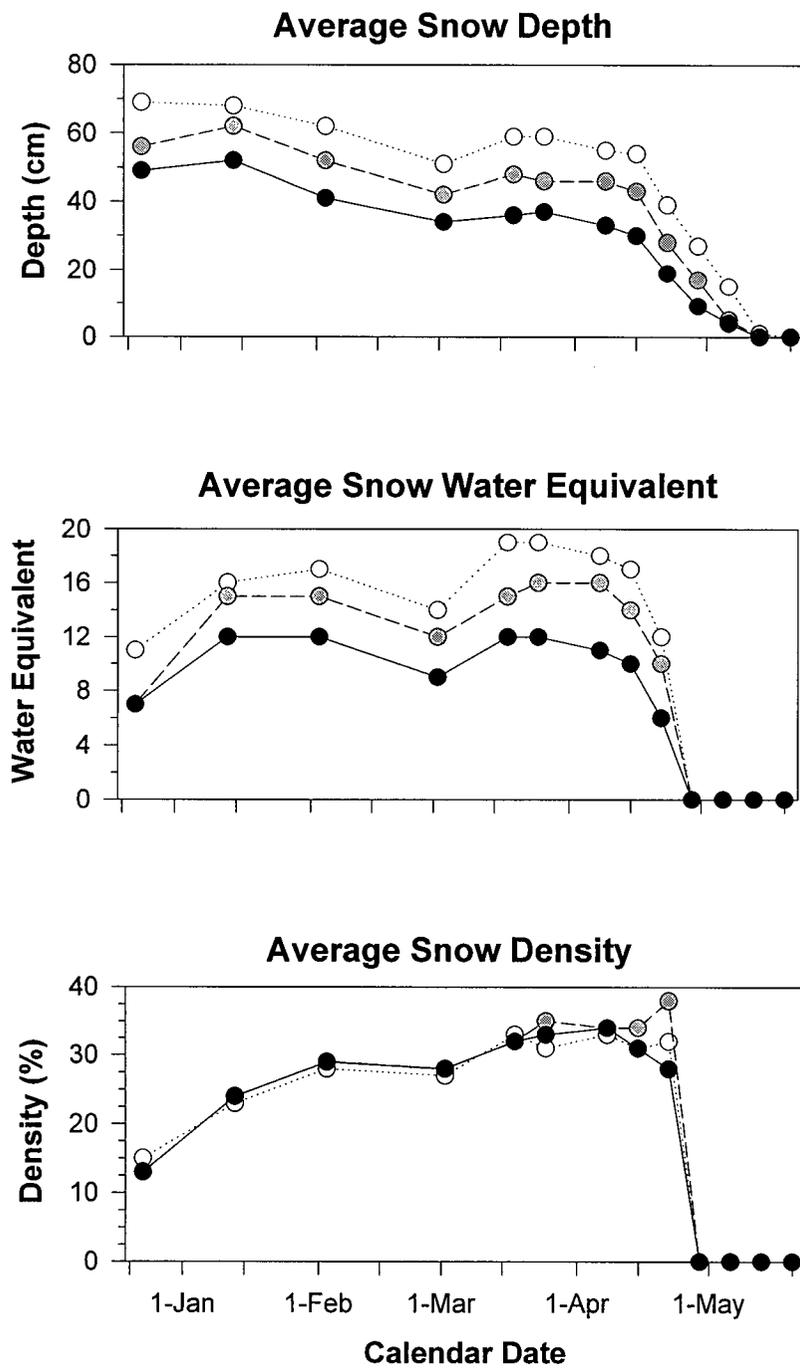


Figure 20. Average snow depth, snow water equivalent and snow density measured in canopy openings (open circle), at canopy edge (grey circle) and under canopy (black circle).

The frequency distribution of substrate covers showed similar trends for all plots (Figure 21): DW had a low coverage (< 40%, Table 2), while FF often covered the whole quadrat. The mean FF and DW covers were significantly different between plots 1A and 3A (Table 13).

The Pearson correlation between the number or mean vigour of seedlings and site factors was very low for all plots (Table 14). However, the FF, DW and moss covers were consistently correlated with the regeneration variables - FF was negatively and DW and moss cover were positively correlated. Shrub and fern cover were consistently negatively correlated, and herb and lichen cover were consistently positively correlated with the regeneration variables.

The multiple correlation analysis showed weak relationships between regeneration variables and site factors (Table 15) and the residual plots also indicated poor fit (not shown). The variables selected for this analysis were those which had the highest Pearson correlations. The variables that were found significant were mainly related to vegetation layers and substrates, and in two plots to available light.

As a consequence of the previous results, it was not surprising that canonical correlation analysis also indicated weak relationships between regeneration and site variables. The canonical correlation for the first canonical variable was around 0.4 for all plots. The redundancy analysis showed that about 14% of the variation in regeneration variables was explained by the first site canonical variable in all plots.

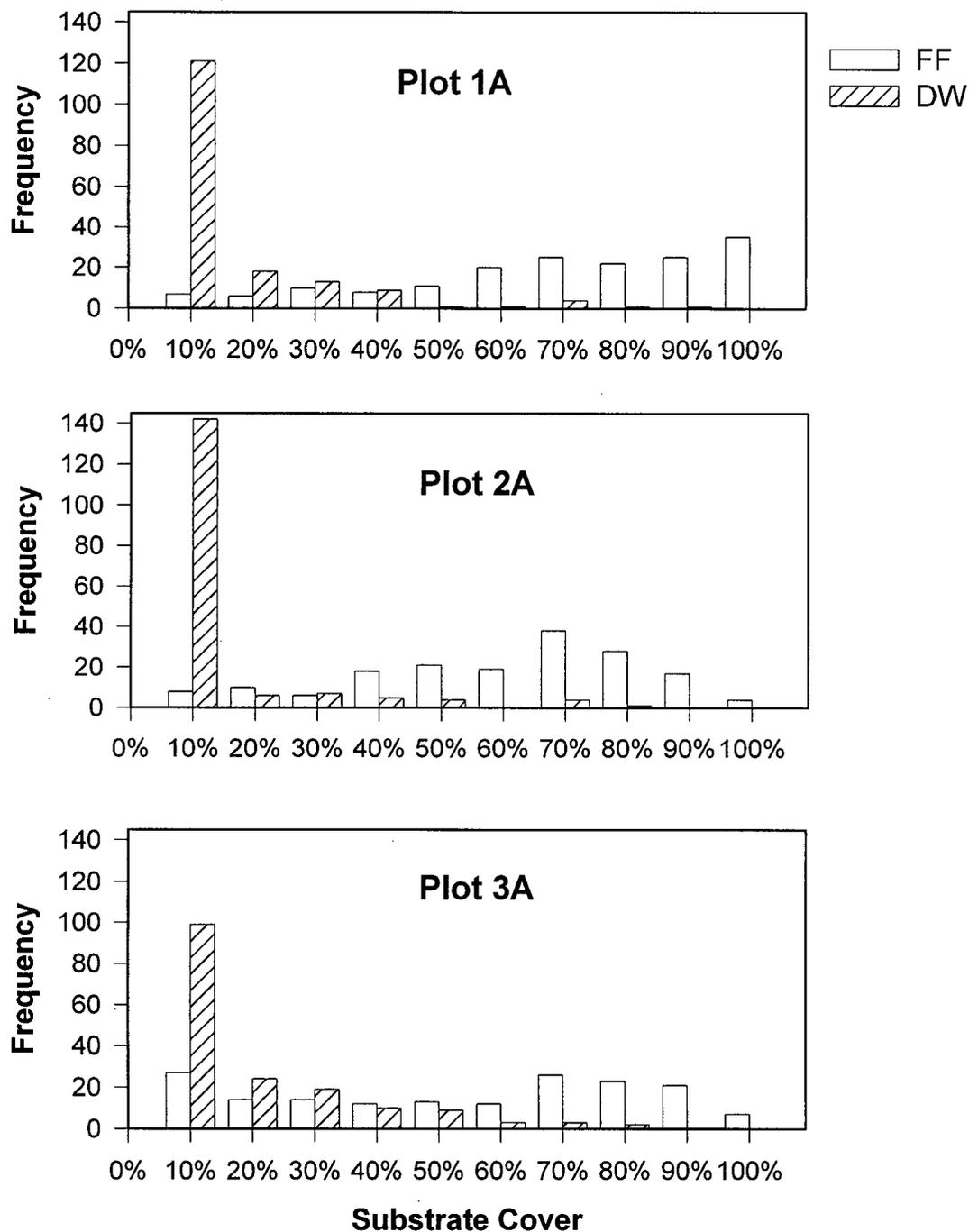


Figure 21. Frequency of substrate covers in quadrats for the three A plots. FF = forest floor, DW = decaying wood.

Table 13. Summary of average percent substrate covers and number of spruce and fir seedlings encountered in the quadrats within plots. The percent covers do not add up to 100, because of the presence of trees in the quadrats. (Bl = subalpine fir, Se= Engelmann spruce.)

	Plot 1A	Plot 2A	Plot 3A
FF (%)	67.8	58.4	56.4
DW (%)	26.3	37.4	34.2
MS (%)	0.0	0.8	2.0
Total number of Se seedlings	3	5	7
Total number of Bl seedlings	369	392	169

Table 14. Pearson correlation coefficients between number (noBl) and mean vigour (mVig) of fir seedlings and site variables, which were significant at $\alpha = 0.05$. (See methods section for variable abbreviations.) Number of observations = 169.

	Plot 1A		Plot 2A		Plot 3A	
	noBl	mVig	noBl	mVig	noBl	mVig
FF	-0.20			-0.23		-0.22
DW	0.24			0.22	0.16	0.22
Shrub		-0.16	-0.19	-0.16		
Fern						-0.23
Herb		0.17				
Moss	0.30	0.28	0.16		0.18	0.20
Lichen			0.24			
mPACL					0.16	0.21

Table 15. Summary statistics and the final set of variables (all of them significant at $\alpha = 0.05$) of the multiple regressions. R^2 = coefficient of determination, SEE = standard error of the estimate and $n = 169$ for all plots.

		R^2	SEE	Variables
Plot 1A	noBl	0.11	4.76	FF, Moss
	mVig	0.14	1.42	Shrub, Herb, Moss
Plot 2A	noBl	0.10	4.52	Shrub, Moss, Lichen
	mVig	0.09	1.23	FF, L
Plot 3A	noBl	0.06	1.93	Moss, mPACL
	mVig	0.14	1.30	DW, Fern, mPACL

Table 16. Correlation of the variables with canonical variables. REG1 and REG2 are the regeneration canonical variables, SITE1 and SITE2 are the canonical variables of site factors.

	Plot 1A		Plot 2A		Plot 3A	
	REG1	REG2	REG1	REG2	REG1	REG2
noBl	0.835	-0.550	-0.719	0.695	0.627	-0.779
mVig	0.844	0.537	-0.923	-0.386	1.000	-0.006
	SITE1	SITE2	SITE1	SITE2	SITE1	SITE2
FF	-0.312	0.588	0.486	0.283	-0.472	0.065
DW	0.418	-0.614	-0.500	-0.159	0.480	-0.152
MS	-	-	-0.116	-0.123	0.327	0.281
L	-0.316	-0.107	0.413	0.207	-0.231	-0.003
F	-0.222	-0.026	0.294	0.119	0.027	0.370
H	-0.167	-0.113	0.228	0.021	0.118	0.478
Shrubs	-0.266	-0.429	0.460	-0.204	-0.256	0.148
Ferns	-0.265	-0.243	0.292	0.107	-0.498	-0.016
Herbs	0.338	0.298	-0.163	-0.474	0.181	0.206
Mosses	0.779	-0.085	-0.313	0.264	0.426	-0.426
Lichens	0.269	0.336	-0.351	0.564	0.325	0.055
mPACL	-0.009	0.170	0.354	-0.103	0.449	-0.272

Table 17. Coefficient of determination between regeneration variables (noBl = number of fir seedlings; mVig = mean vigour of fir seedlings) and the canonical variables (SITE1 and SITE2) of site factors.

	Plot 1A		Plot 2A		Plot 3A	
	SITE1	SITE2	SITE1	SITE2	SITE1	SITE2
noBl	0.136	0.158	0.096	0.146	0.083	0.099
mVig	0.139	0.160	0.158	0.173	0.212	0.212

Substrate variables (FF and DW) generally had the highest correlations with site canonical variables in all plots, but always with the opposite sign (Table 16). Humus form variables (L, F, and H) played a role only in 2A (L) and 3A (H) plots. Among the vegetation variables, shrub cover was highly correlated with site canonical variables in plots 1A and 2A; herb cover only in plot 2A, moss cover in plots 1A and 3A, and lichen cover in plot 2A. Light as a variable seemed to be important only in plot 3A. The important variables in canonical analysis were about the same as those which were significant in the multiple correlation analysis. However, the thickness of H horizon was not important in multiple correlation analysis and the fern cover was not important in canonical analysis.

The site canonical variables generally correlated better with the mean vigour than the number of seedlings (Table 17). This trend is most pronounced in plot 3A. The low number of seedlings in plot 3A might have contributed to

the low R^2 in multiple correlation analysis as well as to the low correlation with site canonical variables.

The regeneration efficiency coefficient showed values of 2 to 4 for DW for all plots (Table 18). This means that at least twice as many seedlings occurred on DW than was the percent cover of DW. In other words, downed coarse woody debris was utilized by regeneration of subalpine fir to a much greater extent than the forest floor.

Table 18. Mean value and 95 % confidence intervals for regeneration efficiency coefficient of seedlings calculated for each quadrat. reFF = regeneration efficiency on FF, reDW = regeneration efficiency on DW.

	Plot 1A		Plot 2A		Plot 3A	
	reFF	reDW	reFF	reDW	reFF	reDW
n	68	68	97	97	61	61
Mean	0.40	3.56	0.27	2.64	0.22	3.09
St. error	0.074	0.618	0.064	0.263	0.097	0.404
Upper limit	0.25	2.33	0.14	2.12	0.03	2.28
Lower limit	0.54	4.80	0.40	3.16	0.42	3.89

The regeneration efficiency of saplings less than 100 years old was different from that determined for the seedlings (Table 19). The regeneration efficiency of saplings on DW was lower than the regeneration efficiency of seedlings on DW and on FF it was higher; but saplings were still utilizing DW better than FF. As the variance of regeneration efficiency coefficients for saplings can not be calculated, the regeneration efficiency values between seedlings and samplings

can not be compared. However, the regeneration efficiency coefficients for saplings are outside of the 95% confidence interval of the regeneration efficiency coefficients for seedlings. This would mean that the seedling and sapling regeneration efficiency coefficients are significantly different if the variance of the sapling efficiency coefficient were known.

Table 19. Number and regeneration efficiency of saplings in plots 2A and 3A that were less than 100 years old.

	Plot 2A	Plot 3A
Number of saplings on DW	17	34
on FF	10	18
Regeneration efficiency on DW	1.54	1.89
on FF	0.57	0.61

4. DISCUSSION

4.1. Stand Structure

The structure of all study stands could be described as follows: marginally mixed species, at least two-storied, and uneven-aged. The low number of Engelmann spruce trees did not permit a detailed analysis, but all plots had both spruce saplings and trees (Appendix). In all A plots the spruce trees had dominant positions (belonged to the canopy), and their age ranged from 180 to 360 years, therefore, they had the potential to produce viable seed (Alexander and Shepperd 1990). The spruce sapling ages at the base ranged from 31 to 104 years in the A plots (Appendix), indicating recent establishment of regeneration. However, the present study can not evaluate whether the established spruce regeneration could survive to reach the canopy. There was no evidence of recent spruce mortality, since there were only three dead spruce trees and no dead spruce saplings in all of the study plots. The snag-bole decay rate (Harmon *et al.* 1986) for Engelmann spruce is 0.012 and the half-time of decay is 67 years; for snag-bark the decay rate is the same and the half-time is 57 years (Mielke 1950). Based on the decay rates it takes roughly 70 years for spruce snags to decompose so that the species would not be easily identifiable any more, which means there was very little mortality of spruce trees in the past 70 years. Spruce had a much lower mortality rate compared to fir, since fir snags were abundant and their decay rate is higher (decay constant is 0.317 and half-time is 4 years) (Lyon 1977). Higher fir mortality was also observed in other studies (Oosting and

Reed 1952, Day 1972, Veblen 1986) and it represents one of the arguments for coexistence of spruce and fir (Oosting and Reed 1952, Miller 1970, Whipple and Dix 1979).

The structure of the study stands was generally very similar despite some differences in site quality and, possibly in stand history. This would imply that the findings of this pilot study will likely be valid for other stands on similar sites in the ESSFmc subzone. On the other hand, there was just as much within-stand as between-stand variation in the dbh distribution. This means that within-stand processes are just as important in influencing dbh distributions as are site differences.

The dbh distribution and spatial pattern of trees and saplings showed characteristics of the old-growth stage, but the height and age distributions did not. The dbh distributions become inverse-J shaped very early after disturbance, therefore, they are not reliable indicators of the old-growth stage (Harper 1977, Aplet *et al.* 1989). In this study plot 3C had the closest fit with the negative exponential function while stand 3 had the youngest saplings and trees (assuming that ages in plot 3A are representative for the whole stand). One possible explanation is that on the more productive site (stand 3) competition is more intensive resulting in greater differentiation (Platt *et al.* 1988, Knox *et al.* 1989, Begon *et al.* 1990). The spatial pattern of trees with different sizes might be subject to differentiation due to competition as well;

therefore, spatial pattern may not be a reliable indicator of old-growth processes (Williamson 1975, Nakashizuka and Numata 1982, Cale *et al.* 1989).

The height distributions were not consistent with the old-growth stage, because they indicated canopy strata (Roovers and Rebertus 1993). Similar height structure in old-growth stage was observed only for the less shade-tolerant Engelmann spruce (Roovers and Rebertus 1993). It was assumed that trees either make it to the upper canopy and continue growing, or remain suppressed in the lower canopy without any further growth. This in turn would cause a depression in the height distribution where the canopy boundary occurs. Since the stands are quite open, the canopy strata can not be attributed to canopy closure (Oliver and Larson 1990). The modal height distribution was most prominent in the plot (2A) with the oldest trees, which may indicate that it is a steady state distribution for the study stands.

The age distributions in the old-growth stage were different from the age distributions of the study stands in (1) the unimodal distribution of sapling ages and (2) the bimodal distribution of tree ages. For subalpine fir, the expected age distribution is inverse-J in the later stages of stand development (Whipple and Dix 1979, Aplet *et al.* 1988, Roovers and Rebertus 1993). The sapling age distribution indicated a peak in regeneration establishment about 100 - 150 years ago and a decline since then. The lack of established regeneration might be due to lack of ingress or high mortality (Johnson *et al.* 1994). However, there were no apparent reasons why the ingress should decrease, since with increasing

age sites suitable for regeneration increase (gaps, decaying wood, exposed mineral soil from blowdown) (Knapp and Smith 1982). Also, the seedling mortality probably decreased with increasing stand age, since the time to reach bh (1.3 m) was lower for younger seedlings, which may indicate better growing conditions. The shape of the tree age distributions should be interpreted with caution as the number of incomplete cores is high. The age distributions did not show inverse-J shape which means they were not in a steady state assuming that the mortality rate is independent of age (Hett and Loucks 1976).

The future stand structure, especially in terms of size and spatial pattern, probably will only conform closer to what is expected in a steady state (Meyer 1952, Aplet 1988, Oliver and Larson 1990). The future height distribution can not be predicted, because the reasons for canopy stratification are not known, so its change with time can not be evaluated. The future age distribution is also difficult to predict, because the relationships between size and age are very weak, and growth and mortality are more related to size than to age (Harper 1977, Peet 1981, Parker 1988).

4.2. Regeneration Pattern

For Engelmann spruce seedlings, a similar pattern was found as for spruce saplings, and trees: the number of spruce seedlings was very low but they were present in all A plots. Almost all (90%) spruce saplings and seedlings encountered occurred on DW which is consistent with the findings of Knapp and Smith (1981), Harmon *et al.* (1986), and Geier-Hayes (1987). The seedlings were

spread out along the whole length of the crown transect in all A plots, which indicates that the spruce trees in or around the plot are sufficient in seeding the plots. In clearcuts, about 50 to 70% of spruce seeds fall within 30 m of the stand edge and about 95% within 100 m (Noble and Ronco 1978, Alexander and Edminster 1983), which compares well with the plot size of 52 m. The ages of spruce seedlings which were encountered in the quadrats varied from 3 years to 154 years, but most were younger than 40 years. This indicates that spruce seedlings have established in the recent past. However, the future of spruce regeneration can not be predicted because the mortality rate of seedlings in the study stands is unknown.

The distribution of subalpine fir seedlings was independent of canopy opening with the exception of plot 1A. This result contrasts with findings of Shea (1985), Qinghong and Hytteborn (1991), Kneeshaw (1992), Yamamoto (1993), and Kneeshaw and Bergeron (1996) who found that gaps were important in determining the location of seedlings. Although gaps are usually defined as canopy openings caused by tree mortality, in this study no distinction was made between canopy openings caused by mortality or other factors. However, the study plots are relatively homogeneous and there are no apparent edaphic reasons for canopy openings.

The percent of seedlings under canopy was only significantly different from the canopy cover for seedlings rooting in DW in plots 1A and 3A where there were more seedlings on DW in canopy openings than expected. This result is consistent with the results of Harmon and Franklin (1989) who suggested that

competition could be the reason for high percentage of seedlings occurring on DW. Since plots 1A and 3A are more productive than 2A, the competition is more intense especially in canopy openings. The DW in canopy openings can provide a relatively competition free environment (from the root competition of both trees and understory vegetation) which would explain the higher percent of seedlings. But on FF, the distribution of seedlings is independent of the canopy cover. This result may question the applicability of gap dynamics (Runkle 1981) for the study stands.

The relative number of seedlings in canopy openings might have been relatively low because of the late snowmelt. The intermediate snow melt time zones had relatively the highest number of seedlings which roughly corresponds to the snow accumulation trend of canopy edges. However, the results should be interpreted with caution, since the measurements were made only in one plot and only through one snow melt period.

The correlation between site variables and the abundance of seedlings was low. Bradfield and Scagel (1984) found similarly low correlation between vegetation strata (including tree species) and environmental variables using canonical correlation analysis. Possible explanations for the weak relationship are: (1) a high variation in site variables, or (2) non-linear relationships between the variables which the analysis could not detect (Bradfield and Scagel 1984), or (3) some other factor is determining the occurrence of regeneration, like soil temperature or seed predation (Farnden 1994). The relative importance of DW compared to FF in seedling establishment was the only statistically

supported relationship. The observed mean regeneration efficiency coefficient values (2.6-3.5) for decaying wood corresponded well to the value 3.0, determined by Knapp and Smith (1982). However, Kneeshaw (1992) found that substrate was not a determining factor for the regeneration of subalpine fir in the Sub-Boreal Spruce zone (the zone below ESSF) - in the same area as this research was conducted in - although he did not provide data on the relative importance of substrates.

If competition is the main reason for the high regeneration efficiency on DW, as was suggested by Harmon and Franklin (1989), then one would expect a strong negative correlation with competing vegetation, especially with shrubs in the most productive 3A plot. In fact, the regeneration efficiency on DW was higher for 3A plot than for the least productive 2A plot. However, the vegetation cover was a weak predictor of both seedling abundance and vigour.

The seedling survival, judged by the presence of saplings, indicated a higher survival on the FF than DW substrate. This means that DW might be more favourable for seedling establishment than FF, but FF may be more favourable for long-term seedling survival than DW.

5. CONCLUSIONS

The study stands showed similar general structure despite some differences in site and possibly in stand history. The observed structure was similar to old-growth structure of spruce - fir forests in Colorado in terms of diameter distribution and spatial pattern but different in terms of height and age distributions.

The diameter distribution of trees and saplings was close to a steady state distribution as indicated by the constancy of neighbouring dbh class ratios. The spatial pattern of trees and saplings changed from aggregated to regular with increasing size which was observed in other old-growth stands.

On the other hand, the height distributions consistently indicated modal distribution which was taken as evidence for canopy layers. Since the canopy stratification is most pronounced in the oldest stand, the modal height distribution may represent the steady state condition in these forests.

The most important factor determining fir seedling establishment was the presence of DW: the percent of seedlings and saplings on DW were consistently higher than what is proportional to the relative cover of DW. This can not be explained by competition because vegetation correlated poorly with either number or vigour of seedlings. Other site factors, like humus form and light also showed poor correlation with regeneration. The percent of seedlings in the intermediate snow melt time zone was higher than the relative cover of this snow melt time zone. However, the spatial distribution of seedlings was

independent of canopy openings. Therefore, gap dynamics was not an important factor in seedling establishment in the study stands, but it may play a role in the survival of seedlings.

The future dbh structure and spatial pattern are expected to remain the same since they are close to a steady state. The modal character of the height distribution is also expected to remain unchanged considering that the oldest stand exhibited it most clearly. The future age distribution is difficult to predict because (1) the age distribution is not in a steady state; and (2) the amount of established regeneration has declined in the last 100 years.

The number of Engelmann spruce seedlings, saplings and trees was consistently low, but they were present in all plots and they had much lower mortality rates than fir. Since spruce seedlings are establishing in the present conditions, the spruce trees in the upper canopy are likely sufficient for seeding. However, it is unlikely that the spruce component would increase in the future.

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APPENDIX

Summary of structural attributes of live trees and saplings. (Bl = subalpine fir, Se= Engelmann spruce, Ht = height, Cr. diam. = average crown diameter, BA = basal area, No. of obs. = number of observations, B. diam. = diameter at base, BH Age = age at breast height)

TREES	Bl	Stems	Dbh (cm)	Ht (m)	Age (yrs)	Cr. diam (cm)	BA (m ²)	Volume (m ³)
1A	No. of obs.		155	155	118	155	155	155
	Mean		31.4	20.7	157	367	0.096	1.05
	St. dev.		15.3	8.8	62	86	0.090	1.22
	Min.		10.0	4.9	62	155	0.008	0.02
	Max.		73.9	39.5	295	595	0.429	6.13
	Sum/plot	155					14.855	163.04
	Total/ha	573					54.94	603
1B	No. of obs.		149	149			149	149
	Mean		26.3	16.7			0.068	0.66
	St. dev.		13.4	8.1			0.066	0.81
	Min.		10.2	4.7			0.008	0.02
	Max.		60.2	32.7			0.285	3.50
	Sum/plot	149					10.194	97.88
	Total/ha	551					37.70	362
1C	No. of obs.		171				171	
	Mean		26.3				0.067	
	St. dev.		12.7				0.061	
	Min.		10.0				0.008	
	Max.		61.5				0.297	
	Sum/plot	171					11.469	
	Total/ha	632					42.41	
Stand 1	No. of obs.		475	304			475	304
	Mean		28.0	18.7			0.077	0.86
	St. dev.		14.0	8.7			0.074	1.06
	Min.		10.0	4.7			0.008	0.02
	Max.		73.9	39.5			0.429	6.13
	Sum/plots	475					36.517	260.92
	Total/ha	586					45.02	482

Appendix Continued.

TREES Plot	Bl	Stems	Dbh (cm)	Ht (m)	Age (yrs)	Cr. diam (cm)	BA (m ²)	Volume (m ³)
2A	No. of obs.		174	174	145	174	174	174
	Mean		23.9	16.9	188	331	0.053	0.48
	St. dev.		10.2	7.2	55	79	0.045	0.53
	Min.		10.2	3.9	88	160	0.008	0.02
	Max.		57.0	32.0	403	560	0.255	3.16
	Sum/plot	174					9.195	83.58
	Total/ha	643					34.01	309
2B	No. of obs.		214	212			214	212
	Mean		23.9	17.2			0.056	0.54
	St. dev.		12.1	7.1			0.059	0.70
	Min.		10.0	4.1			0.008	0.02
	Max.		64.5	33.8			0.327	4.20
	Sum/plot	214					12.004	113.73
	Total/ha	791					44.39	421
2C	No. of obs.		174				174	
	Mean		25.9				0.066	
	St. dev.		12.8				0.063	
	Min.		10.1				0.008	
	Max.		66.9				0.352	
	Sum/plot	174					11.436	
	Total/ha	643					42.29	
Stand 2	No. of obs.		562	386			562	386
	Mean		24.5	17.0			0.058	0.51
	St. dev.		11.8	7.1			0.057	0.63
	Min.		10.0	3.9			0.008	0.02
	Max.		66.9	33.8			0.352	4.20
	Sum/plot	562					32.634	197.31
	Total/ha	693					40.23	365

Appendix Continued.

TREES Plot	Bl	Stems	Dbh (cm)	Ht (m)	Age (yrs)	Cr. diam (cm)	BA (m ²)	Volume (m ³)
3A	No. of obs.		195	195	150	195	195	195
	Mean		31.4	21.5	147	328	0.097	1.10
	St. dev.		15.7	9.5	57	104	0.093	1.30
	Min.		10.0	3.7	45	114	0.008	0.02
	Max.		83.5	49.3	291	725	0.548	8.57
	Sum/plot Total/ha	195 721					18.840 69.67	214.74 794
3B	No. of obs.		205	204			204	204
	Mean		26.6	19.9			0.068	0.73
	St. dev.		12.8	8.2			0.065	0.84
	Min.		10.0	5.7			0.008	0.02
	Max.		61.8	37.4			0.300	3.78
	Sum/plot Total/ha	205 758					13.971 51.67	147.82 547
3C	No. of obs.		266				266	
	Mean		25.3				0.064	
	St. dev.		13.0				0.071	
	Min.		10.0				0.008	
	Max.		83.9				0.553	
	Sum/plot Total/ha	266 984					16.906 62.52	
Stand 3	No. of obs.		666	399			666	399
	Mean		27.5	20.7			0.075	0.91
	St. dev.		14.0	8.9			0.077	1.10
	Min.		10.0	3.7			0.008	0.02
	Max.		83.9	49.3			0.553	8.57
	Sum/plot Total/ha	666 821					49.716 61.29	362.56 670
All Stands	No. of obs.		1703	1089	413	524	1703	1089
	Mean		26.6	18.8	164	341	0.070	0.75
	St. dev.		13.4	8.4	60	92	0.071	0.96
	Min.		10.0	3.7	45	114	0.008	0.02
	Max.		83.9	49.3	403	725	0.553	8.57
	Sum/plot Total/ha	1703 700					118.868 48.84	820.79 506

Appendix Continued.

TREES Plot	Se	Stems	Dbh (cm)	Ht (m)	Age (yrs)	Cr. diam (cm)	BA (m ²)	Volume (m ³)
1A	No. of obs.		2	2	2	2	2	2
	Mean		32.8	22.2	114	268	0.089	0.90
	St. dev.		10.2	11.0	40	67	0.052	0.83
	Min.		25.6	14.4	86	250	0.051	0.31
	Max.		40.0	29.9	142	345	0.126	1.48
	Sum/plot		2				0.177	1.79
	Total/ha		7				0.65	7
1B	No. of obs.		6	6			6	6
	Mean		23.7	14.2			0.081	0.97
	St. dev.		24.0	11.1			0.162	2.22
	Min.		12.5	8.8			0.012	0.05
	Max.		72.5	36.8			0.413	5.51
	Sum/plot		6				0.489	5.85
	Total/ha		22				1.81	22
1C	No. of obs.		6				6	
	Mean		28.7				0.080	
	St. dev.		15.4				0.070	
	Min.		103.0				0.008	
	Max.		49.5				0.192	
	Sum/plot		6				0.480	
	Total/ha		22				1.78	
Stand 1	No. of obs.		14	8			14	8
	Mean		27.1	16.2			0.082	0.96
	St. dev.		18.2	10.9			0.111	1.91
	Min.		10.3	8.8			0.008	0.05
	Max.		72.5	36.8			0.413	5.51
	Sum/plots		14				1.146	7.64
	Total/ha		17				1.41	14

Appendix Continued.

TREES Plot	Se	Stems	Dbh (cm)	Ht (m)	Age (yrs)	Cr. diam (cm)	BA (m ²)	Volume (m ³)
2A	No. of obs.		2	2	2	2	2	2
	Mean		31.1	22.1	233	303	0.083	0.81
	St. dev.		13.7	5.7	180	32	0.067	0.75
	Min.		21.4	18.1	105	280	0.036	0.28
	Max.		40.8	26.1	360	325	0.131	1.34
	Sum/plot	2					0.167	1.62
	Total/ha	7					0.62	6
2B	No. of obs.		13	13			13	13
	Mean		21.5	14.4			0.041	0.25
	St. dev.		8.0	5.7			0.032	0.21
	Min.		10.7	4.4			0.009	0.02
	Max.		38.2	21.4			0.115	0.84
	Sum/plot	13					0.530	3.23
	Total/ha	48					1.96	12
2C	No. of obs.		4				4	
	Mean		13.0				0.014	
	St. dev.		3.8				0.007	
	Min.		10.0				0.008	
	Max.		17.6				0.024	
	Sum/plot	4					0.056	
	Total/ha	15					0.21	
Stand 2	No. of obs.		19	15			19	15
	Mean		20.7	15.4			0.040	0.32
	St. dev.		9.0	6.1			0.036	0.34
	Min.		10.0	4.4			0.008	0.02
	Max.		40.8	26.1			0.131	1.34
	Sum/plot	19					0.753	4.85
	Total/ha	23					0.93	9

Appendix Continued.

TREES Plot	Se	Stems	Dbh (cm)	Ht (m)	Age (yrs)	Cr. diam (cm)	BA (m ²)	Volume (m ³)
3A	No. of obs.		3	3	3	3	3	3
	Mean		37.2	27.9	193	225	0.114	1.31
	St. dev.		9.5	5.4	8	45	0.052	0.71
	Min.		26.5	21.8	186	180	0.055	0.50
	Max.		44.4	32.1	202	270	0.155	1.79
	Sum/plot		3				0.341	3.94
	Total/ha	11				1.26	15	
3B	No. of obs.		1	1			1	1
	Mean		67.9	33.5			0.362	4.44
	St. dev.	-	-				-	-
	Min.	-	-				-	-
	Max.	-	-				-	-
	Sum/plot		1				0.362	4.44
	Total/ha	4				1.34	16	
3C	No. of obs.		4				4	
	Mean		43.2				0.177	
	St. dev.		23.0				0.191	
	Min.		25.6				0.051	
	Max.		76.5				0.460	
	Sum/plot		4				0.710	
	Total/ha	15				2.63		
Stand 3	No. of obs.		14	4			14	4
	Mean		27.1	29.3			0.082	2.10
	St. dev.		18.2	5.2			0.111	1.67
	Min.		10.3	21.8			0.008	0.50
	Max.		72.5	33.5			0.413	4.44
	Sum/plot		14				1.146	8.38
	Total/ha	17				1.41	16	
All Stands	No. of obs.		41	27	7	7	41	27
	Mean		27.4	17.7	182	268	0.081	0.77
	St. dev.		16.8	8.9	90	57	0.106	1.33
	Min.		10.0	4.4	86	180	0.008	0.02
	Max.		76.5	36.8	360	345	0.460	5.51
	Sum/plot		41				3.311	20.87
	Total/ha	17				1.36	13	

Appendix Continued.

SAPLINGS Plot	Bl	Stems	Dbh (cm)	B. Diam. (cm)	Ht (m)	BH Age (yrs)	Base Age (yrs)	Cr. diam (cm)
1A	No. of obs.		183	148	183	62	147	183
	Mean		4.1	6.2	2.8	68	112	150
	St. dev.		2.7	2.8	1.3	20	34	63
	Min.		0.2	1.6	1.3	31	45	25
	Max.		9.9	13.0	7.6	109	290	330
	Sum/plot		183					
Total/ha		677						
1B	No. of obs.		348					
	Mean		3.0					
	St. dev.		2.5					
	Min.		0.2					
	Max.		9.9					
	Sum/plot		348					
Total/ha		1287						
1C	No. of obs.		174					
	Mean		3.7					
	St. dev.		2.7					
	Min.		0.2					
	Max.		9.9					
	Sum/plot		174					
Total/ha		643						
Stand 1	No. of obs.		705					
	Mean		3.4					
	St. dev.		2.7					
	Min.		0.2					
	Max.		9.9					
	Sum/plots		705					
Total/ha		869						

Appendix Continued.

SAPLINGS Plot	Bl	Stems	Dbh (cm)	B. Diam. (cm)	Ht (m)	BH Age (yrs)	Base Age (yrs)	Cr. diam (cm)
2A	No. of obs.		192	172	192	63	163	192
	Mean		4.4	5.7	2.8	92	148	151
	St. dev.		2.6	2.3	1.4	36	45	55
	Min.		0.0	2.1	1.3	15	58	50
	Max.		9.9	11.7	8.3	189	266	290
	Sum/plot	192						
	Total/ha	710						
2B	No. of obs.		301					
	Mean		4.2					
	St. dev.		2.7					
	Min.		0.2					
	Max.		9.8					
	Sum/plot	301						
	Total/ha	1113						
2C	No. of obs.		178					
	Mean		4.5					
	St. dev.		2.7					
	Min.		0.2					
	Max.		9.9					
	Sum/plot	178						
	Total/ha	658						
Stand 2	No. of obs.		705					
	Mean		3.4					
	St. dev.		2.7					
	Min.		0.2					
	Max.		9.9					
	Sum/plot	705						
	Total/ha	869						

Appendix Continued.

SAPLINGS Plot	Bl	Stems	Dbh (cm)	B. Diam. (cm)	Ht (m)	BH Age (yrs)	Base Age (yrs)	Cr. diam (cm)
3A	No. of obs.		156	128	156	44	124	156
	Mean		4.1	5.4	3.0	61	75	172
	St. dev.		3.0	2.8	1.6	24	28	62
	Min.		0.2	1.2	1.3	23	31	65
	Max.		9.9	12.3	9.9	108	137	335
	Sum/plot Total/ha		156 577					
3B	No. of obs.		212					
	Mean		4.4					
	St. dev.		2.7					
	Min.		0.2					
	Max.		9.9					
	Sum/plot Total/ha		212 784					
3C	No. of obs.		173					
	Mean		4.8					
	St. dev.		2.5					
	Min.		0.2					
	Max.		9.7					
	Sum/plot Total/ha		173 640					
Stand 3	No. of obs.		541					
	Mean		4.4					
	St. dev.		2.7					
	Min.		0.2					
	Max.		9.9					
	Sum/plot Total/ha		541 667					
All Stands	No. of obs.		1917	448	531	169	461	531
	Mean		4.0	5.8	2.9	75	114	157
	St. dev.		2.7	2.6	1.4	31	46	60
	Min.		0.0	1.2	1.3	15	31	25
	Max.		9.9	13.0	9.9	189	290	335
	Sum/plot Total/ha		1917 788					

Appendix Continued.

SAPLINGS Plot	Se	Stems	Dbh (cm)	B. Diam. (cm)	Ht (m)	BH Age (yrs)	Base Age (yrs)	Cr. diam (cm)
1A	No. of obs.		7		7	1	5	7
	Mean		2.5		2.3	44	74	104
	St. dev.		2.5		1.2	-	30	51
	Min.		0.4		1.3	-	31	40
	Max.		6.7		4.3	-	104	190
	Sum/plot	7						
	Total/ha	26						
1B	No. of obs.		24					
	Mean		3.5					
	St. dev.		2.9					
	Min.		0.2					
	Max.		8.5					
	Sum/plot	24						
	Total/ha	89						
1C	No. of obs.		6					
	Mean		0.6					
	St. dev.		0.5					
	Min.		0.3					
	Max.		1.5					
	Sum/plot	6						
	Total/ha	22						
Stand 1	No. of obs.		37					
	Mean		2.8					
	St. dev.		2.8					
	Min.		0.2					
	Max.		8.5					
	Sum/plots	37						
	Total/ha	46						

Appendix Continued.

SAPLINGS Plot	Se	Stems	Dbh (cm)	B. Diam. (cm)	Ht (m)	BH Age (yrs)	Base Age (yrs)	Cr. diam (cm)
2A	No. of obs.		8		8	3	6	8
	Mean		2.4		2.0	30	58	124
	St. dev.		1.5		0.4	19	20	53
	Min.		1.0		1.6	8	36	75
	Max.		5.4		2.8	44	83	235
	Sum/plot		8					
Total/ha		30						
2B	No. of obs.		9					
	Mean		3.9					
	St. dev.		3.4					
	Min.		0.2					
	Max.		9.0					
	Sum/plot		9					
Total/ha		33						
2C	No. of obs.		6					
	Mean		1.8					
	St. dev.		1.4					
	Min.		0.2					
	Max.		3.6					
	Sum/plot		6					
Total/ha		22						
Stand 2	No. of obs.		23					
	Mean		2.8					
	St. dev.		2.5					
	Min.		0.2					
	Max.		9.0					
	Sum/plot		23					
Total/ha		28						

Appendix Continued.

SAPLINGS Plot	Se	Stems	Dbh (cm)	B. Diam. (cm)	Ht (m)	BH Age (yrs)	Base Age (yrs)	Cr. diam (cm)
3A	No. of obs.		14		14	-	13	14
	Mean		2.9		2.6		47	138
	St. dev.		2.0		1.1		12	48
	Min.		0.9		1.4		30	70
	Max.		7.2		5.2		69	255
	Sum/plot Total/ha		14 52					
3B	No. of obs.		4					
	Mean		2.0					
	St. dev.		1.2					
	Min.		0.4					
	Max.		3.3					
	Sum/plot Total/ha		4 15					
3C	No. of obs.		1					
	Mean		3.3					
	St. dev.		-					
	Min.		3.3					
	Max.		3.3					
	Sum/plot Total/ha		1 4					
Stand 3	No. of obs.		19					
	Mean		2.8					
	St. dev.		1.8					
	Min.		0.4					
	Max.		7.2					
	Sum/plot Total/ha		19 23					
All Stands	No. of obs.		29	24	29	7	24	29
	Mean		2.7	4.8	2.4	32	56	126
	St. dev.		1.9	3.1	1.0	13	20	50
	Min.		0.4	1.8	1.3	8	30	40
	Max.		7.2	15.6	5.2	44	104	255
	Sum/plot Total/ha		29 12					