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Boreal Forest Succession: An Intensive Study of a Mixedwood Chronosequence

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**BOREAL FOREST SUCCESSION:
AN INTENSIVE STUDY OF A
MIXEDWOOD
CHRONOSEQUENCE**

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ABSTRACT

To better understand the community structure of boreal forests, it is necessary to examine forest stands in various stages of postdisturbance succession. Studying the effects of disturbance on forest vegetation is necessary to adequately predict the impact of natural and anthropogenic change to the forested ecosystem. An intensive field study of vegetation succession was conducted in 18 mixedwood stands in northern Ontario. Field sampling included measurements of tree and shrub density, plant species composition at 15 height strata, and the abundance of forest floor vegetation types. Results provide a detailed description of the forest community along the successional chronosequence and indicate that age, residual conifer density, and shrub development alone do not control the conifer regeneration of these stands. To adequately predict the postdisturbance vegetative composition of these stands, extensive data are needed on their predisturbance composition, time since disturbance, type of disturbance, intensity of disturbance, and shrub development.

RÉSUMÉ

Pour mieux comprendre la structure des communautés des forêts boréales, il est nécessaire d'examiner les peuplements forestiers à diverses étapes de la succession postperturbation. L'étude des effets des perturbations sur la végétation forestière est essentielle pour prévoir adéquatement l'impact des changements naturels et anthropiques de l'écosystème forestier. Une étude intensive de la succession végétale a été effectuée dans 18 peuplements mixtes du nord de l'Ontario. Les relevés sur le terrain ont comporté des mesures de la densité des arbres, arbustes et arbrisseaux, de la composition spécifique de 15 strates et de l'abondance des types de végétation de la couverture morte. Les résultats fournissent une description détaillée de la communauté forestière ainsi que de la chronoséquence végétale et indiquent que l'âge, la densité résiduelle des conifères et le développement des arbustes et arbrisseaux ne déterminent pas à eux seuls la régénération en conifères de ces peuplements. Pour prévoir adéquatement la composition de la végétation postperturbation, il faut des données considérables sur la composition avant la perturbation, le temps écoulé depuis celle-ci, le type de celle-ci, son intensité et le développement des arbustes et arbrisseaux.

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INTRODUCTION

Succession

Succession, a key ecological process in natural ecosystems, generally refers to observed sequences of vegetation associations or animal groups (Drury and Nisbet 1973). First documented in Europe in the late 1600s, its importance was not recognized until the late 1800s (Clements 1928). Since that time it has received considerable attention in both ecology and forestry. The study of succession has at its basis many different emphases. Among these are monoclimate and polyclimate concepts, a focus on relay floristics and initial floristic composition, and an emphasis on nonselective and selective autosuccession (Matthews 1992). Succession theory has also been based on the processes of facilitation, tolerance and inhibition, chronic disturbances, competitive hierarchies, resource ratios, and evolutionary strategies (Matthews 1992).

Predictions about the nature of successional change vary. For instance, plant species composition may continually evolve in response to random changes in the environment or it may cyclically change in response to an environmental cycle (Horn 1981). As well, succession may involve a rapid convergence toward a stable vegetation composition or it may occur slowly and be dependent on random fluctuations (Horn 1981). Frelich and Reich (1995) summarize five different categories of directional models in the literature: namely, (1) cyclic, (2) convergent, (3) divergent, (4) parallel, and (5) individualistic. In spite of the lack of consensus on the exact role of succession in ecological communities, ecologists generally agree that it plays a key role in the distribution and abundance of species (Odum 1969, Drury and Nisbet 1973, Lietti and Whittaker 1975, Whittaker 1975, Connell and Slatyer 1977, Grime 1979, Horn 1981, Finegan 1984, Glenn-Lewin et al. 1992).

Two types of succession are generally accepted: primary and secondary. Primary succession can be defined as the colonization of new and skeletal habitats that lack developed soil and vegetation. Secondary succession is the process of recolonization of a previously occupied habitat that has been disturbed (Drury and Nisbet 1973, Grime 1979), and involves relationships among establishment and regeneration strategies, life forms, and habitat productivity (Grime 1979). The focus of this study is secondary succession.

Succession in Boreal Forest Ecosystems

Plant succession has been more thoroughly studied and is better understood in temperate zones compared to northern areas. When discussing boreal succession, it is essential to outline the aspects that make it distinct from succession in more temperate areas. First, plant species

diversity in the boreal area is lower (Payette 1992), probably due to lower productivity levels that lead to a large conifer component. The dominant boreal tree species in Canada's eastern boreal area are black spruce (*Picea mariana* [Mill.] B.S.P.), white spruce (*Picea glauca* [Moench] Voss), balsam fir (*Abies balsamea* [L.] Mill.), jack pine (*Pinus banksiana* Lamb.), tamarack (*Larix laricina* [DuRoi] K. Koch.), white birch (*Betula papyrifera* Marsh), balsam poplar (*Populus balsamifera* L.), and trembling aspen (*Populus tremuloides* Michx) (Payette 1992). Second, boreal succession primarily involves changes in species abundance through time, as opposed to species replacement in the community (Wein and El Bayoumi 1982, Carleton and MacLellan 1994). This point is especially true for tree species. The role of abiotic factors relative to biotic factors may be more important in northern regions compared to temperate areas (Wein and El Bayoumi 1982), and can result in cyclical changes in the abundance of species (Wein and El Bayoumi 1982). For instance, in many cases the species that establish in areas after a fire were present in the pre-fire state, just at lower abundance levels (Wein and El Bayoumi 1982).

The boreal forest is ecologically valuable for many reasons. It is the largest surface source of carbon in the world (Shugart et al. 1992), and it plays an important role in climate control and nutrient cycling. In particular, the diversely aged stands and forest types of the boreal region provide habitat for a wide range of wildlife. The boreal forest region of Ontario is the largest forest region in the province and the main resource for its important pulp and paper industry. Therefore, it is subject to extensive industrial forestry activity (Ontario Forest Policy Panel 1993). Prior to the 1920s, the main form of disturbance in the boreal region was wildfire (Ward and Tithecott 1993). All but small pockets of forest frequently burned, resulting in locally similar-aged stands (or extensive patches) in a mixed-age forest (Ontario Forest Policy Panel 1993). In addition, fires that regenerated the boreal forest are thought to have shown a broad distribution of small, medium, and large disturbance patches, with some very large fires (> 10 000 ha) also occurring (Ward and Tithecott 1993). Now most of the fires in intensively managed areas of Ontario's boreal forest are found in the smallest size classes (< 4 ha) (Ward and Tithecott 1993). Before fire suppression began, it is estimated that an average area of roughly 700 000 hectares would have burned annually in Ontario, with a fire interval of 65 years. More recent estimates are close to 80 000 hectares per year, with a fire interval of 580 years (Ward and Tithecott 1993). The prevalence of fire suppression and the increase in forest harvesting since the 1920s, combined with increased insect infestation control, have resulted in tree removal becoming the major form of disturbance in the boreal region (Thompson and Welsh 1993, Ward and Tithecott 1993). Large tracts in the

most accessible areas of the boreal forest have been harvested; other stands that normally would have burned continue to age (Ontario Forest Policy Panel 1993).

It has been argued that clear-cutting mimics wildfire in terms of overall disturbance patterns. The two forms of disturbance are similar in terms of the removal of the tree layer and ensuing seedling light conditions, yet there are important differences between the effects of fire and harvesting on forests (Carleton and MacLellan 1994). First, the boreal forest is rarely burned in a uniform fashion, thereby leaving pockets of fire refugia that provide source plants for recolonization and regeneration. This is very different from the more uniform disturbance of clear-cutting. Second, unlike clear-cutting, fires often leave snags. Species such as pine have serotinous cones that act as seed banks. Jack pine germinates very well on exposed sites where fire has killed other plant species (Burns and Honkala 1990a)—species that would otherwise compete with it for above- and belowground resources. In fact, the natural regeneration of jack pine often exceeds artificial regeneration in northwestern Ontario, and cutovers are typically left to regenerate naturally. In addition, snags cool the forest floor by providing shade. Finally, clear-cutting leaves most of the organic soil behind and promotes the regeneration of understory plants, the seeds of which often survive harvesting but not fire. In addition, root survival of shrubs such as mountain maple (*Acer spicatum* Lam.) and beaked hazel (*Corylus cornuta* Marsh.) lead to extensive shrub regeneration and aspen suckering. In contrast, fire consumes some or all of the organic layers and retards the regeneration of understory plants. In general, fire-disturbed conifer stands tend to reestablish following fire; clear-cut stands do not (Carleton and MacLellan 1994). Forest harvesting and fire suppression have led to the transformation of conifer dominated forest to hardwood/mixedwood forest (Samoil 1988).

Succession and Natural Resource Management

Due to the ecological importance and intensive resource use of boreal forests, a knowledge of boreal forest succession is needed to properly assess the implications of management decisions on the long-term sustainability of all the forest resources in these ecosystems. Plants play key roles in carbon cycling, nutrient cycling, soil composition, and soil fertility. They are primary producers and normally make up the greatest amount of biomass and structural form of a community (Connell and Slatyer 1977). Because plants provide food and shelter to wildlife, changes in plant species composition inevitably lead to changes in wildlife habitat and in turn to changes in wildlife species composition. Present knowledge regarding plant species community composition and how it

changes after harvesting is poor (Robertson 1994). Therefore, increased knowledge on how plant communities change following natural and anthropogenic disturbances is essential in order to predict the effects of forestry practices on forested ecosystems.

Not only is it necessary to know how forest plant communities are affected by different harvesting regimes or by fire, it is also important to understand how the plant species composition of the community changes through time following disturbance. Therefore, one needs to determine the natural patterns of regeneration and plant species composition following the removal of all or some tree species, and how these patterns develop through time following both fire and tree removal.

Forest succession modeling is one tool that can be used to predict forest changes through time. Common features of such models consider growth, recruitment, mortality, resource competition, and geometric composition (Shugart 1984). Tree models focus on the change in tree species composition over a large area, and gap models simulate changes in tree species composition in areas that represent localized sites of regeneration and growth (Shugart 1984). Relatively little data is available on plants for forested areas in varying stages of postdisturbance succession, and very few studies contain the proper controls required to determine the degree to which different forest practices affect the ecosystem. For models to be more realistic and more accurate, extensive plant succession data are needed.

Difficulties in Studying Succession

As with any ecological process, the study of succession is limited by a number of factors. The main limitation is the occurrence of succession across a long time period (hundreds to thousands of years) (Wein and El Bayoumi 1982), whereas most research programs last only 2 to 5 years. Thus it is difficult to establish long term succession studies and equally difficult to compare the few that have been undertaken. Long term succession studies have been conducted in different geographic areas and using different methodologies, thereby limiting general conclusions (Wein and El Bayoumi 1982). An alternative to these long-term studies is to compare spatially distinct but similar sites that represent similar ecosystems which have been disturbed at different times (Crocker and Major 1955, Drury and Nisbet 1973). This commonly used approach has many inherent assumptions. It assumes that communities of different ages in the same area represent a true chronosequence. To be truly comparable, stands must be similar in predisturbance vegetation, site conditions, climatic history, input of propagules, disturbance intensity (e.g., harvesting practices), disturbance type (fire, harvest, insects, disease), postdisturbance environmental histories (Shafi and Yarranton 1973, Finegan

1984), and the season in which the disturbance occurred (Noble and Slatyer 1980). Furthermore, insufficient replication may cause the variation within samples of the same age to be greater than the variation between samples of different ages (Brown 1992). These assumptions are difficult to satisfy because fire and harvesting disturbances can vary tremendously within and among areas, and forested ecosystems are highly variable in terms of their biological and physical composition (Wein and El Bayoumi 1982). Although the results of such studies are often confounded and thus difficult to interpret at a fine scale, overall patterns can be interpreted more easily. Therefore, in spite of its limitations, a chronosequence does provide a snapshot view of forest stands of different ages since the last disturbance. Most of what is known about successional patterns is the result of chronosequence studies, and some of the best successional studies have used chronosequences similar to the one undertaken in this study.

This Study

A chronosequence approach was used in this study. Data were collected to describe the “habitat” for a study of succession in boreal forest birds (Welsh and Fillman 1980, Welsh 1987). In view of the amount of information in the data set and the limited number of studies from this boreal region, it was decided to summarize the vegetation data in a report to ensure future availability. Forest stands representing different successional stages, ranging from recently harvested sites to a 199-year-old uncut site, were studied over two summers. These data provide snapshots of the 18 forest stands in different successional stages. The design was primarily determined by the requirements of the bird study, particularly the choice of mapping census as the means to describe bird species composition and abundance (International Bird Census Committee 1970, Welsh 1983). The experimental design lacks generality because there is no replication within stand ages. Therefore, the study and questions posed are descriptive by nature and the results should be interpreted with this in mind.

Various factors can affect the postdisturbance plant species composition of boreal forest stands, including time since disturbance, nature and intensity of disturbance, shrub development, and residual vegetation, which is defined here as vegetation left behind after a disturbance. Therefore one asks: What are the patterns of association between regenerating tree species composition and age, residual vegetation, and the shrub abundance of the stands sampled? It is also important to understand the impact of disturbance on the understory plant community of regenerating boreal forest stands. Although understory vegetation is a small component of forest biomass, it is extremely

important. The integrity of the forest plant community depends very much upon relationships between tree canopy layers and the plants in the understory (Carleton and Maycock 1981), particularly as the stand develops. Competition among plant species for aboveground resources such as light and space is a key biotic process in forests. In addition, understory vegetation is important to wildlife for foraging and breeding resources. For example, it has been estimated that approximately 30 percent and 29 percent of boreal birds forage on the ground in spruce and fir dominated forests, respectively (Erskine 1977). The herbaceous layer also contains most of the forest plant species diversity and concern over species extinction throughout the world has led to both a political and a scientific focus on the maintenance of the earth’s biodiversity. In spite of the importance of the boreal forest understory, there are few documented studies of under- and overstory relationships in the North American boreal area (Carleton and Maycock 1981). Similarly, few studies evaluate changes in the understory plant community after major disturbances such as fire or harvesting (Robertson 1994). Therefore, a second question can be asked: What are the patterns of association between regenerating understory plant species composition and age, residual vegetation, and the shrub abundance of the stands sampled?

METHODS

Study Site

Eighteen mixedwood stands were sampled for this study. Several criteria were used in the selection of the stands. Similarity of the following factors was important: topography, soil composition, and soil moisture regimes. Stands represented an age gradient of naturally regenerating areas cut between 1945 and 1979. Uncut, naturally regenerating stands were also sampled and selected to provide examples of the range of ages of post-fire stands occurring in the area. Stands were generally selected based upon their predisturbance composition (upland black spruce–balsam fir–aspen mixed forest). The stands represent the Forest Ecosystem Classification (FEC) types for northwestern Ontario (Sims et al. 1989), but FEC vegetation types cannot be determined for each stand because they are significantly larger than the 10-m by 10-m scale used in the FEC scheme. The study was conducted during the summers of 1979 to 1983. The 1979 and 1980 data are the focus of this report and represent a snapshot look at succession in 18 stands of different ages: namely, a chronosequence. The study area was located north of Manitouwadge, Ontario (Fig. 1), in the Boreal Shield Ecozone, Ecoregion Lac Matagami, Ecodistrict 27 (Wickware and Rubec 1989), Site Region 3E (Lake Abitibi), Site Districts 1 and 2, and Site Region 3W (Lake Nipigon), Site District 5 (Hills 1951, Burger 1993). The

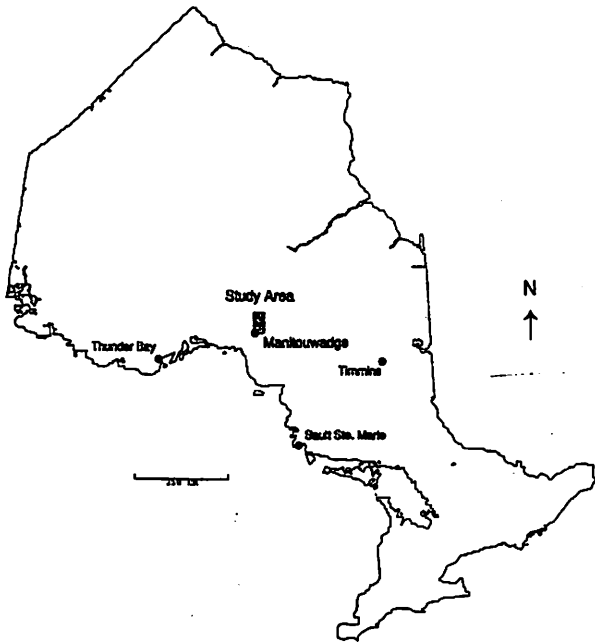


Figure 1. Location of mixedwood study area.

latitudes and longitudes of the individual stands are given in Table 1. Land was licensed by the province of Ontario to American Can of Canada Ltd (Milton, Ontario) at the time of the study. The area is now licensed to Buchanan Forest Products Ltd.

A sampling plot was established in each of the 18 forest stands. All plots were 9 ha (90 000 m²) in size, although their shape varied. Fourteen of the plots were square (300 m X 300 m) and four were rectangular (500 m X 200 m), with an area of 100 m X 100 m missing from one corner. Square and rectangular plots were systematically sampled along seven and five parallel lines, respectively. These were positioned 50 m apart.

Forest stands varied in terms of when they were last harvested or disturbed by fire. Efforts were made to minimize between-stand variation in the intensity of disturbance; however, it was not possible to find stands that were identical in terms of disturbance intensity since they were harvested at different times by different methods. The six oldest stands were uncut sites that varied in age from 56 to 199 years. The 12 youngest stands had been harvested for merchantable conifer and aspen. Their ages

Table 1. Age and geographical location of the eighteen mixedwood forest stands of this study.

Stand age (years) in 1979/1980	Latitude	Longitude
199	49°32'0.4"*	85°48'0.1"
147-2†	49°23'0.0"	85°50'0.8"
147-1†	49°16'0.7"	85°59'0.1"
110	49°21'0.9"	85°45'0.3"
109	49°30'0.3"*	85°44'0.8"
56	49°28'0.0"	85°38'0.7"
33	49°27'0.0"	85°46'0.5"
26	49°21'0.9"	85°47'0.0"
23	49°29'0.8"	85°47'0.6"
20	49°33'0.9"*	85°47'0.5"
18	49°18'0.8"	85°47'0.5"
13	49°31'0.4"*	85°41'0.6"
12	49°33'0.3"*	85°41'0.4"
8	49°35'0.2"*	85°38'0.6"
5-2†	49°15'0.3"	85°53'0.6"
5-1†	49°16'0.9"	85°47'0.6"
3	49°12'0.6"***	85°56'0.8"
0	49°28'0.6"	85°43'0.7"

Note: Longitudes and latitudes were taken from Map 42F/5 (1:50 000) of the National Topographic System, unless otherwise indicated.

† Stands of the same age are distinguished from one another using the numbers "1" or "2".

* Map 42F/12.

** Map 42F/4.

varied from 0 to 33 years. From this point onward, stands will be referred to by their age only. Table 2 provides a summary of the historical information available for the stands used in this study.

Vegetation Sampling

Three vegetation data sets were collected for each of the forest stands. The data sets were complementary and when combined provide an intensive representation (Carleton and MacLellan 1994) of the 18 forest stands used in the study.

Tree and shrub density

One data set was composed of tree and shrub density data. These were collected using a corrected point distance nearest neighbor sampling technique (Batcheler 1973, 1975), which has been shown to consistently yield estimates within 20 percent of the actual population densities (Laycock and Batcheler 1975). Sampling was done separately for three groups of tree size classes and for shrubs. The criteria for the groups of tree size classes are as follows:

- i) saplings (< 2.5 cm diameter at breast height [DBH]);
- ii) small trees (2.5 cm–9.9 cm DBH); and
- iii) large trees (10.0 cm DBH).

A list of plant species sampled and their allocation to vegetation classes are given in Appendix A(1).

In square (rectangular) plots, saplings, small trees, and shrubs were systematically sampled at 31 (47) points located 10 m apart along each of the seven (five) parallel lines, yielding a total of 217 (235) sampling points. Large trees were sampled at every second point, yielding 109 (118) points positioned 20 m apart. At each sampling point, the distance was measured from the point to the center of the closest tree/shrub stem. Stem dimensions were measured (height and/or diameter class were recorded for small trees, saplings, and shrubs and the diameter at breast height was measured for large trees), the species noted, and the number of stems per clump recorded. The distance was then measured from the first stem to the nearest neighbor stem and the same measurements were taken. The process was repeated for the next nearest neighbor. Table 3 provides the height and diameter classes used in sampling the saplings, small trees, and shrub species.

The density of trees and shrubs in stems per hectare and associated measures of variance were then estimated. This

was done by entering the point distance data into a computer program (Welsh 1977) designed to calculate best density estimates and associated probable limits of error for all groups of tree size classes and shrubs at the scales of species and stand.

Plant species composition of the forest strata and understory

The plant species composition of the forest stands was sampled using a point estimate sampling technique. Data were collected at each of 217 (235) points in the square (rectangular) plots. Starting at the same sample point that was used for the density data collection, an imaginary laser-thin line, which theoretically had no area and extended from ground level up through the canopy at right angles to the ground, was visually established. All plant species intercepted by this line at 15 strata were recorded. Therefore species presence/absence data were collected for 15 strata at 217 (235) points per stand. The strata were as follows: ground, <10 cm, 10–25 cm, 25–50 cm, 50 cm–1 m, 1–2 m, 2–3 m, 3–5 m, 5–7.5 m, 7.5–10 m, 10–12.5 m, 12.5–15 m, 15–20 m, 20–30 m, and > 30 m.

Life-form and ground cover

Quadrat data (2-m X 2-m quadrats) were also collected at each of 49 (51) points in the square (rectangular) plots; sampling points were 40 m apart in each plot. The percent cover of 17 life-forms and eight ground cover types were recorded in each of these quadrats. These data appear in the data report.²

Sampling Schedule

Sampling of the stands occurred over two field seasons. Stands that were 199, 109, 56, 26, 20, 13, 5 (5-2), 3, and 0 years old were sampled during the summer of 1979; the remaining stands were sampled in 1980. To better visualize the sampling layout, Figure 2 provides a sketch of a typical sampled forest stand.

DATA ANALYSIS

Data analysis was completed in two phases. The first was a descriptive analysis intended to summarize the plant species composition of the forest communities along the successional chronosequence. The second phase was a statistical analysis of the vegetation data designed to further describe the forest stands at the scale of multispecies communities, and to examine the effects of various factors on the regenerated plant species composition.

² Twolan-Strutt, L.; Welsh, D.A. An intensive study of a mixedwood chronosequence: A data report. Nat. Resour. Can., Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, ON. NODA/NFP File Rep. No. 30. 67 p.

Table 2. Summary of the historical information available for the eighteen mixedwood forest stands of this study. Some of the information was collected at the time of stand selection and field sampling from the Ministry of Natural Resources and American Can of Canada Ltd. Additional information was recently obtained from D. Fry (Buchanan Forest Products Ltd.) and the Forest Resource Inventory Maps (Ontario Ministry of Natural Resources 1974).

Year of disturbance	Estimated age (years)	Time of the year harvested	Nature of disturbance	Residual/regeneration information
1780	199–250+		fire	
1833	147-2		fire	
1833	147-1		fire	
1870	110		fire	
1870 and 1980	109		fire	
1923	56		fire	
1947 (1946)	33 (34)	Spring or summer	Clear-cut; manually felled; delimited, bucked into 8-foot logs and piled, hauled in winter by horse and sleigh	Very little timber remaining; natural regeneration
1953 (1951/1952)	26 (27–28)	Spring or summer and spring	Clear-cut; manually felled; delimited at the stump; trees cable yarded to roadside and slashed	Some white birch left; natural regeneration
1957 (1956)	23 (24)	Spring or summer	Clear-cut; manually felled; delimited at the stump; trees cable yarded to roadside and slashed	Patches of white birch and balsam poplar left scattered around plot area; natural regeneration
1959 (1957 or 1957/1958)	20 (21–22)	Winter or summer	Clear-cut; manually felled; delimited at the stump; appears to have been bucked and hand piled and bundle yarded to roadside	Few scattered patches of white birch and perhaps balsam poplar left standing; natural regeneration
(1962)	18	Spring/summer	Clear-cut; manually felled; delimited at the stump; trees skidded to roadside for slashing	Part of plot covers roads and skidways where all trees were felled; otherwise there were varying amounts of residual white birch; natural regeneration
1966 (1965)	13 (14)	Spring or summer	Clear-cut; trees manually felled; delimited at the stump; moved by wheeled skidders to roadside for slashing	Residual white birch; hand-planted to black spruce and white spruce in fall 1968 (no site preparation); most regeneration is probably natural due to high mortality of planted stock

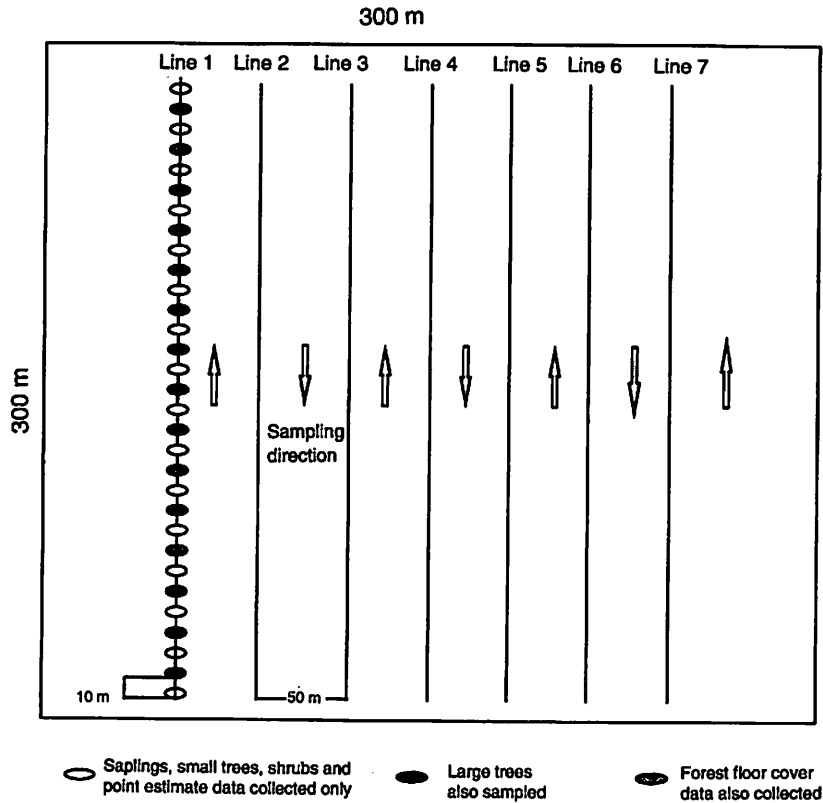
Year of disturbance	Estimated age (years)	Time of the year harvested	Nature of disturbance	Residual/regeneration information
1968 (1967)	12 (13)	Summer	Clear-cut; trees manually felled; delimbed at the stump; moved by wheeled skidders to roadside for slashing	Residual white birch, heavy in places; natural regeneration
1972 (1971)	8 (9)	Spring	Clear-cut; trees manually felled; delimbed at the stump; moved by wheeled skidders to roadside for slashing	Fairly heavy residual white birch left standing; although parts of the harvest area were prescribed burned and planted in 1972, area occupied by plot was likely natural regeneration
1974 (1973)	5-2 (6)	Spring or summer	Clear-cut; trees manually felled; delimbed at the stump; moved by wheeled skidders to roadside for slashing	Some patches of white birch and a small patch of 15-year old mixedwood along road were left standing; thought to be natural regeneration
1975 (1974)	5-1 (6)	Summer	Clear-cut; trees manually felled; delimbed at the stump; moved by wheeled skidders to roadside for slashing	Light to heavy patches of white birch left standing; natural regeneration
1976	3	Summer	Clear-cut; trees manually felled; delimbed at the stump; moved by wheeled skidders to roadside for slashing	Few scattered white birch left standing; unknown regeneration; parts of the harvest area were site prepared and hand planted several years later and may have been ground sprayed
1979 (1978)	(1) 0	Spring	Clear-cut; trees manually felled; delimbed at the stump; moved by wheeled skidders to roadside for slashing	Few standing residuals left, perhaps balsam poplar or white birch; unknown regeneration

* When ages derived from recently collected data (shown in brackets) were not consistent with data gathered at the time of the study, the latter were used because they were estimated using first-hand harvest data and information.

Table 3. The height and diameter classes and respective size ranges recorded for all trees and shrubs sampled in the eighteen mixedwood forest stands of this study.

Size class	Size range
Sampling^{***}	
1	0.5 m–0.9 m in height
2	1.0 m–1.9 m in height (1.0 m in height–2.5 cm DBH) [*]
3	2.0 m in height–2.5 cm (DBH) ^{**}
Small trees	
1	2.5 cm– 4.9 cm DBH
2	5.0 cm–9.9 cm DBH
Large trees	
	≥10.0 cm DBH (actual diameter measured)
Shrubs	
1	0.5–0.9 m in height
2	1.0–1.9 m in height
3	2.0–2.9 m in height
4	3.0–3.9 m in height
5	≥4.0 m in height

* Size range in brackets is a different size range used in 1980 only.
 ** Size range not used in 1980.
 *** A list of shrub and tree species appears in Appendix A(1).



Phase I. Descriptive Analysis

Size and density of trees and shrubs

Tree density data were summarized at three different scales using a combination of tables and graphs. First, data were summarized for all trees greater than 10 cm DBH (hereafter referred to as large trees), all trees > 2.5 cm and < 10 cm DBH (hereafter referred to as small trees), and all trees < 2.5 cm DBH and > 0.5 m in height (hereafter referred to as saplings) for all forest stands. Next, the densities of all coniferous and deciduous large trees, small trees, and saplings were summarized for all stands. Finally, the density of each species was summarized for three sapling size classes, two small tree diameter classes, and 15 large tree diameter classes. The sapling and small tree classes were specified in Table 3. Large tree diameter classes were created by classifying the tree diameter data, which ranged from 10 to 85 cm DBH, into fifteen 5-cm-diameter intervals. An explanation of how the density of tree species for different size classes was calculated is included in Appendix B(1). In addition to density, tree diameters were summarized for all large trees and for large coniferous and deciduous trees. The analyses in this report are based on the number of stems in a given area as the measure of abundance. Volume, an alternative abundance measure, is essentially an estimate of species biomass. Volume has been estimated for each tree sampled in the stands, but, given the additional space required in the report to include all analyses as volume-based analyses, it was decided to include only density-based analyses. The volume data are available from the authors.

Shrub density was summarized at three levels: namely, density of all shrubs in each stand, density of selected shrub species for each stand, and density of shrub species in five size classes.

Plant species composition of the forest strata and understory

Percent vegetative cover, calculated as the percentage of points sampled at which vegetation occurred, was summarized for all strata of all stands. It should be noted that nonvegetative features, such as litter and slash, were not included in these values. Similarly, percent cover of life-form groups, including conifers, deciduous growth, shrubs, flowering herbs, ferns and fern allies, bryophytes, and lichens, were summarized.

Measures of diversity are now being used as indicators of ecosystem health or anthropogenic effects on natural systems. Biodiversity can be measured at many scales (i.e., genetic, species, intraspecies, community, ecosystem, etc.) (McKenney et al. 1994). The authors looked at measures of species diversity (Crites and Dale 1995).

Species richness was calculated by counting the number of species occurring in each stratum level of each forest stand. The Brillouin Index was used to measure diversity because of its suitability when it is not certain that the community richness has been fully sampled (Pielou 1975, Magurran 1988). The abundance measure used in the diversity measure was the percent cover for each species in each stratum. Diversity summaries and analyses appear in the data report.³

Phase II. Statistical Analysis

Description of forest plant communities—a multivariate analysis

To complement the descriptive summary analyses of the chronosequence, two classification techniques, two-way indicator species analysis (TWINSPAN) (Hill 1979) and clustering, were used to further describe the postdisturbance plant communities and to look for natural patterns in the species data. Ordination techniques, Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) (ter Braak 1988), were used for descriptive purposes and for testing the effects of age since disturbance, type and intensity of disturbance, and residual vegetation on the postdisturbance plant communities.

Tree and shrub density

SAHN clustering techniques, including UPGMA, complete-link, and single-link methods based on the Bray-Curtis coefficient of similarity (Rohlf 1992), were conducted for the small tree and sapling density data, large tree density data, and shrub density data. TWINSPAN analyses using equal cut levels were also run for each of the three sets of density data. A DCA of tree species density in 17 diameter classes was performed. The data matrix was 18 plots X 97 pseudo species. Mean percent cover of eight ground cover variables and age since the last major disturbance were used as passive environmental data. In other words, these variables did not constrain ordination analysis and were only included to look for possible relationships between underlying gradients and measured external variables. A CCA was done on the same species data. Percent cover of eight ground cover variables and age since the last disturbance were used as environmental data.

Plant species composition of the forest strata and understory

A DCA of species cover data for the 15 forest strata was completed. Percent cover of each species per stratum constituted the species data. The data matrix was 237 samples X 79 species. Separate analyses for each stratum were also run.

³ Ibid.

Effects of various factors on tree regeneration after a disturbance

Simple linear regression was used to test for the effect of residual conifers on conifer regeneration. Similar analyses were done to test for the effect of shrub development on conifer regeneration of the stands. Multiple regression analysis was used to test for effects of residual conifer abundance, age since disturbance, and shrub abundance simultaneously on the conifer regeneration in the study area. This analysis was done for groups of tree size classes and for all shrubs. Therefore, entire groups of tree size classes were designated as residual or regenerated vegetation across all stands. The density of all trees > 10 cm DBH in the 12 youngest stands was used as a measure of residual vegetation, the sum of sapling and small tree density was used as a measure of regenerated vegetation, and the density of all shrubs was used as a measure of shrub abundance. Because stands were of different ages and species growth rates vary, dividing regenerated and residual vegetation based on groups of tree size classes alone may be somewhat inaccurate (i.e., all saplings and small trees may not be regenerated vegetation). Therefore, it was decided to complete a more detailed analysis. This analyses and its results are described in the associated data report.⁴ In addition, the effects of residual vegetation of boreal tree species on tree regeneration at the level of individual species was also studied. Again, these analyses are presented only in the associated data report.

RESULTS

Phase I. Descriptive Analysis

Size and density of trees and shrubs

Trees

It is important to point out that the following analyses of tree data used density (number of stems per hectare) as the measure of tree abundance. Volume-based measures of tree abundance have been estimated and are available from the authors. Figure 3 shows the densities of saplings (Fig. 3a), small trees (Fig. 3b), large trees (Fig. 3c), and shrubs (Fig. 3d). Overall, peak density tended toward the older end of the successional chronosequence as size class increased. Sapling density peaked in the 3- to 12-year-old forest stands, where density was approximately 7 000 stems/hectare in the 5-year-old stand (5-2) (Fig. 3a). Small tree density peaked in the 18- to 26-year-old stands, where density was close to 4 000 stems/hectare in the 26-year-old stand (Fig. 3b). Density of large trees was highest in some of the older stands, with the maximum density reached in the 56-year-old stand (Fig. 3c). Sapling density showed a clear bimodal distribution with a second peak at a lower density, approximately 2 500 stems/hectare, in the

147-year-old (147-1) stand. Small and large tree density did not show a bimodal trend (Fig. 3). Finally, sapling density was very low in the older harvested stands (Fig. 3a).

When examining vegetation trends at the conifer/deciduous level (Fig. 4), a few overall trends become visible. First, where vegetation density is highest, the vegetation is dominated by deciduous cover. Next, numbers of deciduous saplings and small trees show large fluctuations in density; conifer saplings and small tree numbers tend to be less variable (Figs. 4a and 4b). Finally, younger stands are dominated by deciduous cover and older stands are dominated by coniferous cover. Conifer sapling density was also greater than deciduous sapling density in the older stands. In fact, deciduous density was close to zero in three of the six oldest stands. The reverse was true for younger stands (Fig. 4a). Conifer sapling density was greatest (2 500 stems/hectare) in the 147-year-old (147-1) stand. A smaller peak was seen in the 8- to 18-year-old stands. In contrast, deciduous saplings peaked close to 7 000 stems/hectare in the 3- and 5-year-old (5-2) stands (Fig. 4a). Small trees showed similar patterns (Fig. 4b). Small deciduous tree density was highest in the 18- to 26-year-old stands. In fact, almost all of the small trees in the 26-year-old stand were deciduous. On the other hand, small conifers were most dense in the 56- to 199-year-old stands and lowest in the youngest stands (Fig. 4b). Trends in large trees further highlight this pattern (Fig. 4c). Conifer density peaked at 600 stems/hectare in the 56- to 199-year-old stands, whereas the density of deciduous trees peaked in the 33- and 56-year-old stands. Finally, the clear bimodal density distribution is only evident when examining conifer saplings (Fig. 4a).

The densities of saplings, small trees, and large trees are summarized for all species in Tables 4 and 5. To highlight species density trends, maximum and minimum densities for four dominant tree species in the study area are marked in bold and underlined, respectively. Figure 5 summarizes the sapling results for all conifer tree species. Conifer regeneration in the older, uncut stands was mainly balsam fir and to a lesser extent black spruce. In addition, most of the conifer regeneration in the harvested stands was also balsam fir. Balsam fir saplings were more abundant than were black spruce saplings in all harvested stands, except the three youngest (Fig. 5).

The density of tree species is also summarized for individual size classes. Appendix B(1) shows tree species density in 17 diameter size classes. To facilitate interpretation of these figures, Appendices B(2) and B(3) summarize the trends in the data across stands and across species, respectively.

⁴ Ibid.

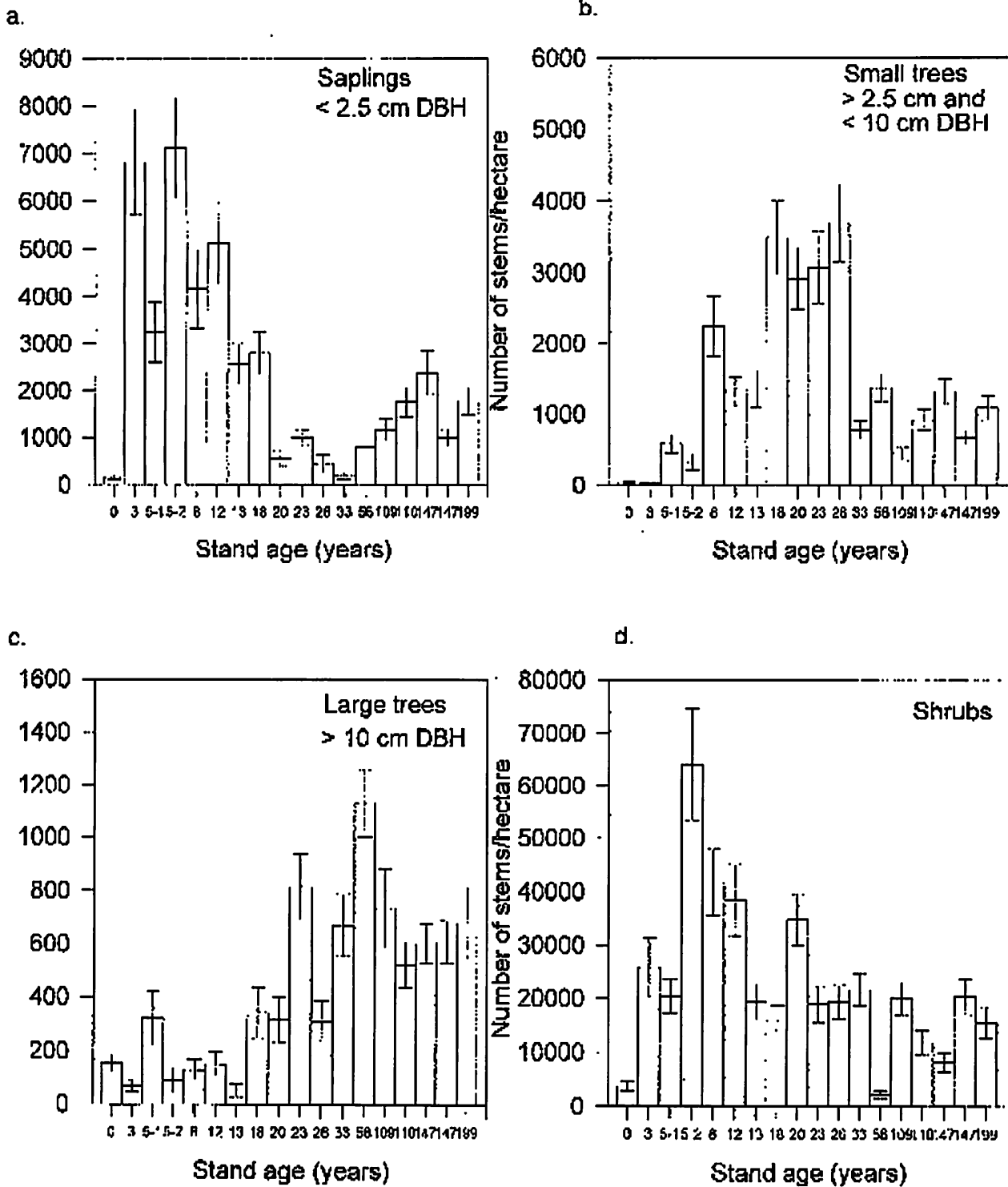


Figure 3. Density of trees and shrubs in the mixedwood forest stands of this study. Densities are given for three size classes of trees and for all shrubs.

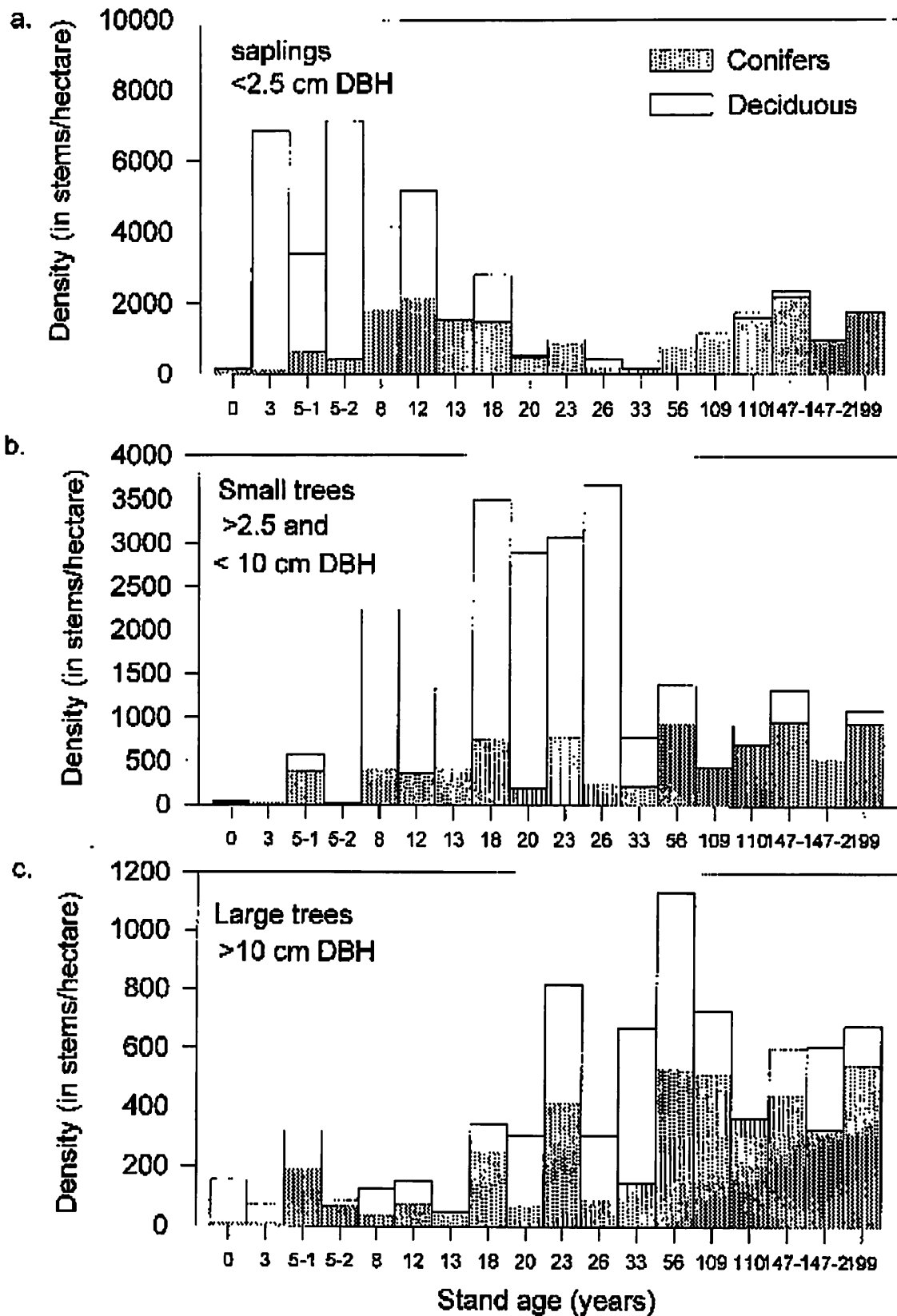


Figure 4. Density of trees in the mixedwood forest stands of this study. Density is summarized for three size classes and for conifers and deciduous trees separately. Bars correspond to total densities divided into conifer and deciduous densities.

Table 4. The density (in stems/hectare) of all tree species in the harvested mixedwood stands of this study. Densities are presented for three groups of tree size classes and total densities are provided for conifers and deciduous trees. Latin nomenclature and common names for trees are provided in Appendix A(1).

Species		Stand age (in years)											
		0	3	5-1	5-2	8	12	13	18	20	23	26	33
Conifers													
PICE MAR	saplings	118.5	73.8	304.8	<u>12.7*</u>	190.0	574.1**	449.5	174.7	146.8	58.0	<u>42.1</u>	100.3
	small trees	20.1	15.9	130.2	<u>1.3</u>	<u>5.3</u>	24.8	48.2	33.7	35.5	16.9	112.9	159.3
	large trees	11.8	1.2	75.2	1.2	<u>0.4</u>	<u>1.1</u>	<u>1.1</u>	4.7	18.7	11.4	2.0	53.3
PICE GLA	saplings	4.3	5.6	A***	6.3	193.7	44.7	292.4	67.7	4.1	7.2	16.2	13.4
	small trees	0.1	0.1	A	0.4	32.6	4.4	6.7	28.1	A	22.6	A	11.9
	large trees	0.2	1.5	1.0	A	5.6	2.1	A	38.2	2.5	46.7	2.3	8.7
PINU BAN	saplings	A	A	48.2	6.3	A	A	10.1	A	A	1.5	0.9	0.5
	small trees	A	A	A	A	A	27.1	30.2	A	A	11.3	27.5	6.1
	large trees	A	A	A	A	A	A	A	0.9	A	11.4	19.0	42.5
ABIE BAL	saplings	<u>30.5</u>	<u>38.9</u>	294.1	411.1	1384.2	1543.4	747.3	1253.6	340.1	817.7	154.1	69.5
	small trees	<u>Δ</u>	<u>16.0</u>	262.3	21.8	374.7	314.0	333.6	689.7	166.9	736.3	121.9	50.8
	large trees	<u>0.2</u>	<u>11.9</u>	116.7	65.2	33.4	74.0	38.5	208.6	52.7	346.8	71.2	42.4
THUJ OCC	saplings	A	A	A	A	75.8	4.0	58.5	A	A	A	A	A
	small trees	A	A	A	0.1	10.7	A	10.1	A	A	A	A	A
	large trees	A	A	A	A	1.1	A	0.6	A	A	A	A	A
Total	185.7	164.9	1232.5	526.4	2307.5	2613.7	2026.8	2499.9	767.3	2087.8	570.1	558.7	
Deciduous													
LARI LAR	saplings	A	A	A	A	A	4.0	A	A	A	A	A	A
	small trees	A	A	A	A	A	2.2	A	A	A	A	A	A
POPU TRE	saplings	2.5	6523.7	636.1	6490.4	820.4	429.2	274.7	133.4	15.9	1.0	1.7	0.5
	small trees	<u>0.1</u>	<u>0.1</u>	101.9	307.1	1470.6	546.6	831.5	1158.6	2241.4	1954.3	2687.0	415.6
	large trees	0.5	A	0.5	A	A	2.0	A	56.6	61.2	223.3	157.9	325.6
BETU PAP	saplings	2.2	203.8	2094.0	119.1	1366.3	2150.2	505.0	1155.6	34.8	103.4	230.5	A
	small trees	24.1	<u>0.4</u>	87.5	<u>0.4</u>	199.4	362.2	69.2	1585.0	301.1	304.0	611.4	A
	large trees	140.2	56.2	125.2	21.2	86.2	69.2	<u>10.5</u>	32.3	161.2	138.1	48.9	A
POPU BAL	saplings	0.4	5.6	18.6	100.5	133.9	400.1	244.2	19.7	5.7	9.0	4.6	1.0
	small trees	A	A	A	0.4	148.3	42.9	17.7	A	136.6	29.3	114.1	131.9
	large trees	A	0.2	A	1.8	0.7	1.4	0.1	A	8.8	38.9	2.8	197.3
FRAX NIG	saplings	A	A	A	A	A	A	A	A	8.5	A	0.9	A
	small trees	0.1	A	A	A	A	A	A	A	25.3	A	2.8	4.0
	large trees	A	A	A	A	A	A	A	A	1.7	A	A	A
Total	170.1	6790.0	3063.8	7040.9	4225.8	4010.0	1952.9	4141.2	3002.2	2801.3	3862.6	1075.9	

* Minimum density for a species across all stands in this table and Table 5 is underlined.

** Maximum density for a species across all stands in this table and Table 5 appears in bold.

*** Tree species class absent from a given stand is marked with an "A".

Table 5. The density (in stems/hectare) of all tree species in the uncut mixedwood stands of this study. Densities are presented for three groups of tree size classes and total densities provided for conifers and deciduous trees. Latin nomenclature and common names of trees are provided in Appendix A(1).

Species		Stand age (years)					
		56	109	110	147-1	147-2	199
Conifers							
PICE MAR	saplings	94.7	242.9	304.0	322.9	79.3	108.7
	small trees	505.1	98.9	117.8	114.5	23.5	102.4
	large trees	403.2	349.5	71.7	94.1	11.2	140.5
PICE GLA	saplings	30.4	8.7	47.3	38.9	32.2	50.0
	small trees	109.0	4.0	43.0	68.6	22.9	0.9
	large trees	59.1	1.3	18.6	43.1	42.4	12.4
PINU BAN	saplings	A	A	A	A	A	A
	small trees	A	A	A	2.6	A	A
	large trees	3.8	2.6	A	A	59.0	A
ABIE BAL	saplings	668.9	813.3	1138.6	1247.1	866.4	1094.7
	small trees	327.3	326.3	520.5	742.5	499.0	798.7
	large trees	68.3	160.9	272.8	295.5	213.3	354.8
THUJ OCC	saplings	A	7.0	132.0	618.8	2.1	521.5
	small trees	A	2.5	21.4	30.7	A	41.7
	large trees	A	A	3.0	12.0	1.2	39.3
Total		2269.8	2017.9	2690.7	3631.3	1852.5	3265.6
Deciduous							
LARI LAR	saplings	A	1.0	A	A	A	A
	small trees	A	A	A	A	A	A
POPU TRE	saplings	0.7	86.5	11.3	A	11.0	A
	small trees	163.0	0.4	7.9	10.3	29.1	A
	large trees	355.6	131.6	42.1	11.4	111.5	A
BETU PAP	saplings	<u>1.1</u>	8.0	126.8	144.1	5.7	5.6
	small trees	242.5	10.9	211.7	352.9	95.6	147.7
	large trees	70.6	45.0	111.4	147.4	171.0	129.4
POPU BAL	saplings	A	9.9	A	3.3	A	A
	small trees	31.9	2.1	1.7	2.6	A	A
	large trees	170.1	38.2	2.0	A	A	A
FRAX NIG	saplings	A	A	A	A	A	A
	small trees	A	A	A	A	A	A
	large trees	A	A	A	A	A	A
Total		1035.5	333.6	514.9	672.0	423.9	282.7

* Minimum density for a species across all stands in this table and Table 4 is underlined.

** Maximum density for a species across all stands in this table and Table 4 appears in bold.

*** Tree species class absent from a given stand is marked with an "A".

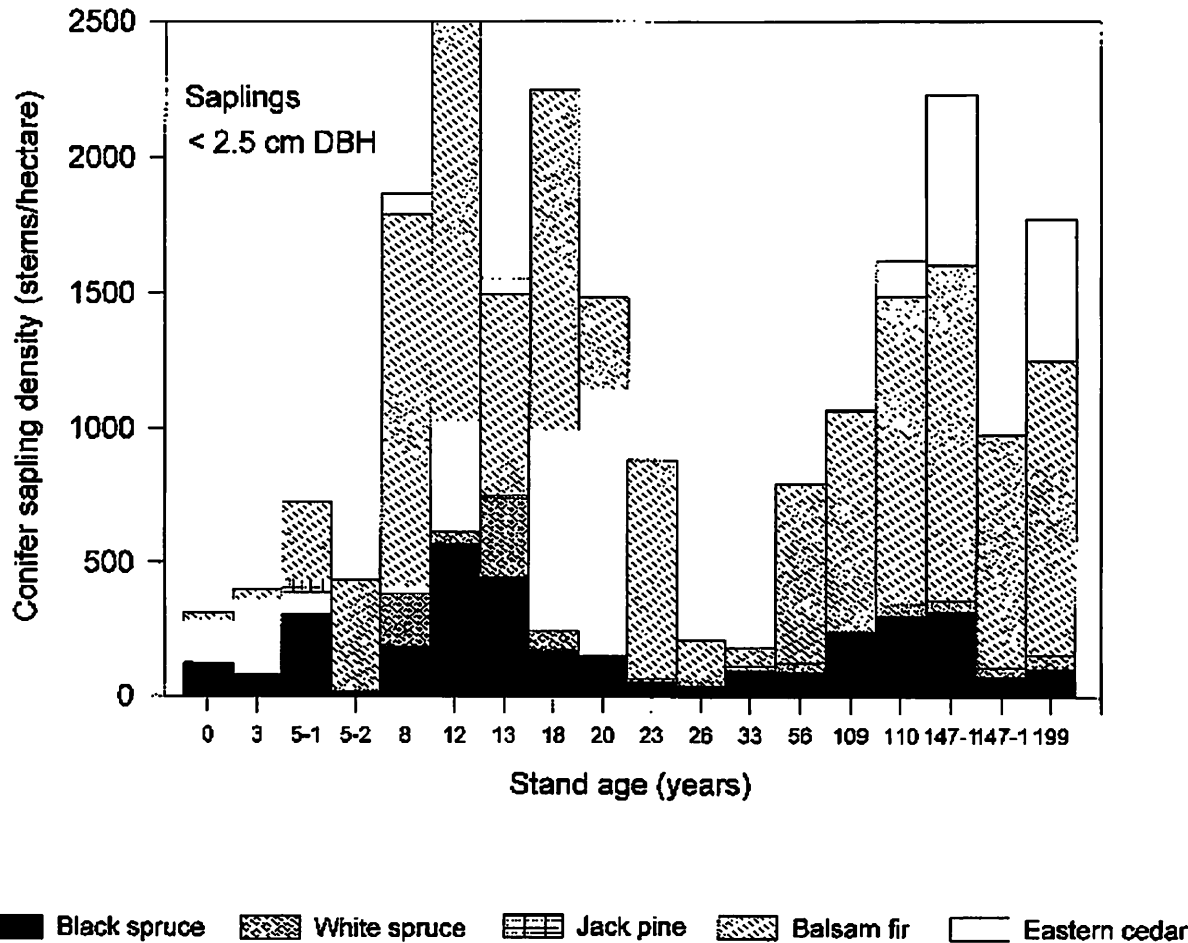


Figure 5. Density of conifer saplings in the mixedwood forest stands of this study. Bars correspond to total sapling densities divided into the densities of each species.

Appendix B(4) depicts the mean DBH of large trees. In general, there was a bimodal trend in diameter with stand age. Mean diameter was highest in the 8- and the 147-year-old (147-2) stands where it was 26 and 24 cm DBH, respectively. Appendix B(5) also provides the mean diameter and associated standard deviation of coniferous and deciduous trees. The mean diameter of deciduous trees was greater than that of conifers in all but two of the stands, the 33-year-old stand and the 147-year-old (147-1) stand. Appendix 2(E) also shows that the ratio of mean conifer diameter to mean deciduous tree diameter generally increased with age along the chronosequence. In the younger harvested stands, the mean diameter of conifers was roughly one-half that of deciduous trees; the mean diameter of conifers was similar to the diameter of deciduous trees in the older harvested stands and the uncut stands.

Shrubs

The density of shrubs is given in Fig. 3d. Shrub density was highest in the 5- to 12-year-old stands and the 20-year-old stand, reaching 65 000 stems/hectare in the 5-year-old stand (5-2). The density of shrub species is summarized for all stands in Appendix C. Trends of four common shrub species are presented in Figure 6. Most notably, the densities of *Acer spicatum* Lam. and *Corylus cornuta* Marsh. show three peaks along the chronosequence: one peak in the 5- to 8-year-old harvested stands, another in the 20- to 26-year-old stands, and a third peak in the older stands. When comparing these two species, it is noteworthy that *Acer spicatum* Lam. is more prevalent in the older stands than is *Corylus cornuta* Marsh.; the reverse is true in the younger stands. Finally, *Diervilla lonicera* Mill. and *Rubus strigosus* Michx. show very different trends along the chronosequence. They both peak in the 5-year-old stand (5-2) and then decrease in the older stands.

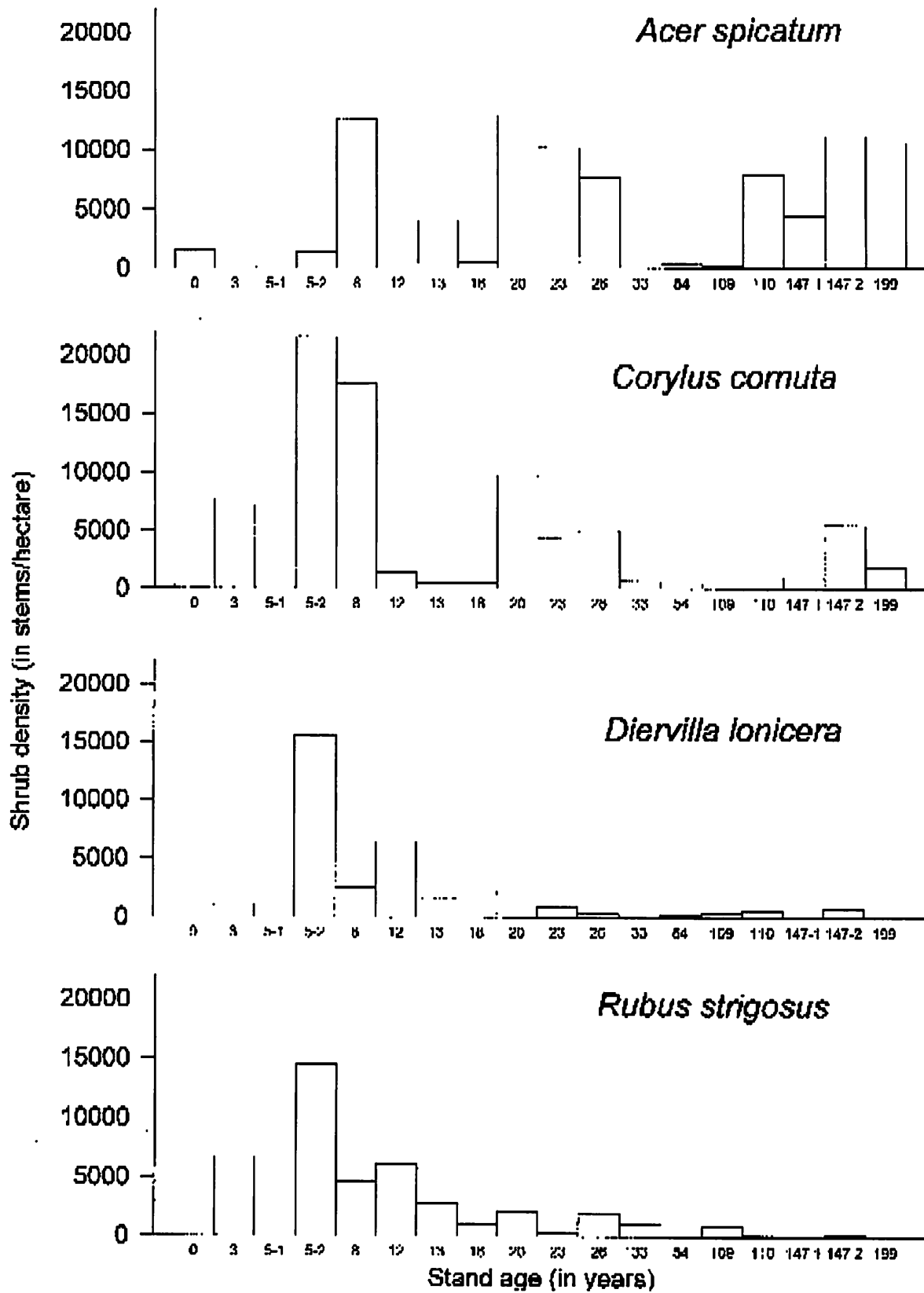


Figure 6. Density of four shrub species in the mixedwood forest stands of this study.

Plant species composition of the forest strata and understory

The percent cover data of all vegetation in each forest stratum are summarized in Tables 6 and 7. Percent cover of vegetation did not reveal a clear increase or decrease along the chronosequence, although there were trends within groups of height strata. For the forest herbaceous layer (i.e., ground through 1 m), the shrub/sapling layer (1–3 m), and the tree layer (3–10 m) stratum, the greatest percent cover of vegetation occurred in the 5- to 13-year-old stands, the 8-, 20-, and 26-year-old stands and the 20-, 23-, 56-, and 147-year-old stands, respectively. The highest percent cover of vegetation in the strata above 10 m occurred in the uncut stands.

Appendix D provides a summary of the percent cover of life-forms in each stratum. The conifer component was minor in most of the harvested stands (except the 18- and 23-year-old stands), but was a major component in all of the older stands. Conifer cover was quite different in the 33-year-old stand compared to the 56-year-old stand. Even though there is only one sample for each age and therefore comparisons must be interpreted with caution, it is noteworthy that conifer cover was present in a low abundance in five strata in the harvested stand, whereas it was present at a higher abundance in 11 strata of the uncut stand. Shrubs were a major component of the harvested stands, especially some of the older ones (> 20 years of age). Shrubs were still present but less abundant in the older uncut stands. Lastly, the older uncut stands clearly revealed a higher percent cover of conifers, deciduous growth, shrubs, flowering herbs, ferns and fern allies, bryophytes, and lichen life-forms compared to younger harvested stands.

All species found in the 18 forest stands, along with their seven letter species codes, are listed in Appendix A(1). A summary of percent cover of each species in each stratum of each stand appears in Twolan-Strutt and Welsh.⁵

Phase II. Statistical Analysis

Description of forest plant communities—a multivariate analysis

Tree and shrub density

Clustering of the large tree density data did reveal some groups of similarly aged stands but did not show a clear age gradient (Fig. 7a). Although the UPGMA, single, and complete link clustering methods yielded slightly different results, the three methods produced the following distinct groups of stands (Rohlf 1992): the four oldest stands; the 56- and 33-year-old stands; and the 5- (5-2), 12-, and 13-year-old stands. TWINSpan analysis of the

same data revealed a clearer age gradient (Fig. 7b). After the first cut, the 18- to 109-year-old stands separated from the oldest and the youngest stands. After the second division, the four oldest stands, the seven youngest stands, the two youngest uncut stands, and the older stands were grouped together.

Detrended correspondence analysis of large and small tree density in seventeen 5-cm diameter size classes revealed a clear separation of the harvested and uncut forest stands ($\bar{\epsilon} = 0.45$ for Axis 1 and $\bar{\epsilon} = 0.17$ for Axis 2). Forty-two percent of the variance in the species data was accounted for by the first two axes (Fig. 8a), and species distributions were somewhat separated along the first ordination axis. It was noteworthy that the 0 and the 5-year-old (5-1) stands were situated between the harvested and uncut groups in ordination space. A CCA of the same data using age and ground cover variables as environmental data was comparable in its ability to describe the forest stands ($\bar{\epsilon} = 0.41$ for Axis 1 and $\bar{\epsilon} = 0.21$ for Axis 2) (Fig. 8b). The environmental variables most highly correlated with the first two ordination axes were litter ($r = 0.72$, can coef. = 0.99) and age ($r = -0.54$, can coef. = -0.48).

Clustering of the small trees and saplings together revealed an obvious age gradient (Fig. 9a). The two youngest stands and the 5-year-old stand (5-2) separate from the remaining ones at a high dissimilarity value (> 75 percent) using all three clustering techniques. The oldest harvested stand separated out next when using two of the three clustering techniques. Finally, the six oldest stands were clustered together at 75 percent dissimilarity, as were the 20- to 26-year-old stands and the 8-, 12-, and 18-year-old stands (Fig. 9a). TWINSpan analyses of the same data did not reveal such a clear gradient (Fig. 9b). The 3- and the 5-year-old stands again separated from the rest after the first cut, but the resulting TWINSpan groups had mixed-aged groups. For example, the 13-year-old stand was grouped with three of the oldest stands (Fig. 9b).

Clustering of shrub density data revealed only a slight age gradient, and the results varied somewhat among the three clustering techniques (Fig. 10a). The general trends are as follows: the 5-year-old (5-2) stand separated from all other stands with 70 percent dissimilarity, the 109- and the 33-year-old stands separated from remaining stands with 60 percent dissimilarity. As well, the 3-, 5- (5-1), 12-, 13-, and 18-year-old stands separated out together with more than 55 percent dissimilarity. The 8-year-old stand, the 20- to 26-year-old stands, the 110-year-old stand, one of the 147-year-old stands, and the 199-year-old stands separated from remaining stands with 50 percent dissimilarity. As well, TWINSpan analyses showed only a slight age

⁵ Ibid.

Table 6. Percent cover of vegetation in 15 strata of the harvested mixedwood stands of this study. Cover values are the percentage of sampling points at which vegetation occurs in a given stratum (including trees, shrubs, herbs, fern and fern allies, bryophytes, and lichens).

Stratum	Stand age (years)											
	0	3	5-1	5-2	8	12	13	18	20	23	26	33
Ground	6.9	15.3	20.4	35.5	6.5	5.1	31.8	19.8	8.8	12.0	12.8	8.3
10 cm	17.5	43.1	41.3	44.2	15.7	42.9	57.3	41.5	32.3	19.8	31.9	31.3
10–25 cm	8.5	37.0	37.4	56.2	51.2	65.4	55.5	50.2	59.0	39.2	51.1	34.1
25–50 cm	5.3	24.5	22.6	47.5	31.8	59.0	35.9	24.4	35.0	30.0	33.2	12.4
50 cm–1 m	3.2	17.6	20.0	48.4	38.2	49.3	26.4	15.2	32.3	30.4	14.5	12.9
1–2 m	1.1	6.9	16.6	38.7	56.7	37.3	34.1	31.8	43.3	27.7	29.4	18.4
2–3 m	1.1	1.9	14.5	15.7	26.3	32.3	26.8	38.7	43.8	41.5	43.0	28.1
3–5 m	4.2	1.9	17.4	3.7	16.6	27.2	19.1	51.6	47.5	67.3	58.3	17.1
5–7.5 m	5.8	3.7	8.1	3.2	4.1	6.9	6.8	29.0	32.7	50.7	40.4	29.0
7.5–10 m	5.8	4.6	4.3	1.4	5.1	5.1	0.9	7.8	29.0	26.7	28.5	22.1
10–12.5 m	5.3	2.3	2.1	1.4	3.2	2.3		1.4	16.1	8.3	12.3	12.4
12.5–15 m	1.4	0.9	1.4	1.4	1.4			7.8	1.8	5.1	1.8	
15–20 m	1.6	0.5	0.4	1.8					4.6		0.4	
20–30 m		0.5	0.9	1.4				0.5	0.5			
≥ 30 m												

Table 7. Percent cover of vegetation in 15 strata of the uncut mixedwood stands of this study. Cover values are the percentage of sampling points at which vegetation occurs in a given stratum (including trees, shrubs, herbs, fern and fern allies, bryophytes, and lichens).

Stratum	Stand age (years)					
	56	109	110	147-1	147-2	199
Ground	21.7	27.6	18.9	32.7	13.4	28.1
10 cm	42.3	41.0	23.0	23.0	22.3	30.0
10–25 cm	18.9	40.6	38.2	16.6	19.9	22.6
25–50 cm	6.3	25.3	24.9	8.8	19.4	16.1
50 cm–1 m	2.3	21.2	24.9	11.5	23.2	14.3
1–2 m	4.6	36.4	27.2	17.1	24.6	33.2
2–3 m	16.0	27.6	35.0	26.7	36.5	31.8
3–5 m	34.3	24.0	60.4	61.3	46.4	47.0
5–7.5 m	37.1	14.7	37.3	43.8	21.3	34.6
7.5–10 m	30.9	12.4	22.6	25.3	16.1	25.8
10–12.5 m	23.4	9.2	12.9	10.1	10.4	20.7
12.5–15 m	21.1	10.1	9.2	6.5	9.0	21.2
15–20 m	12.6	20.3	6.5	2.3	6.6	20.3
20–30 m		12.4	7.8	1.4	15.6	9.2
≥ 30 m			1.4		1.4	0.5

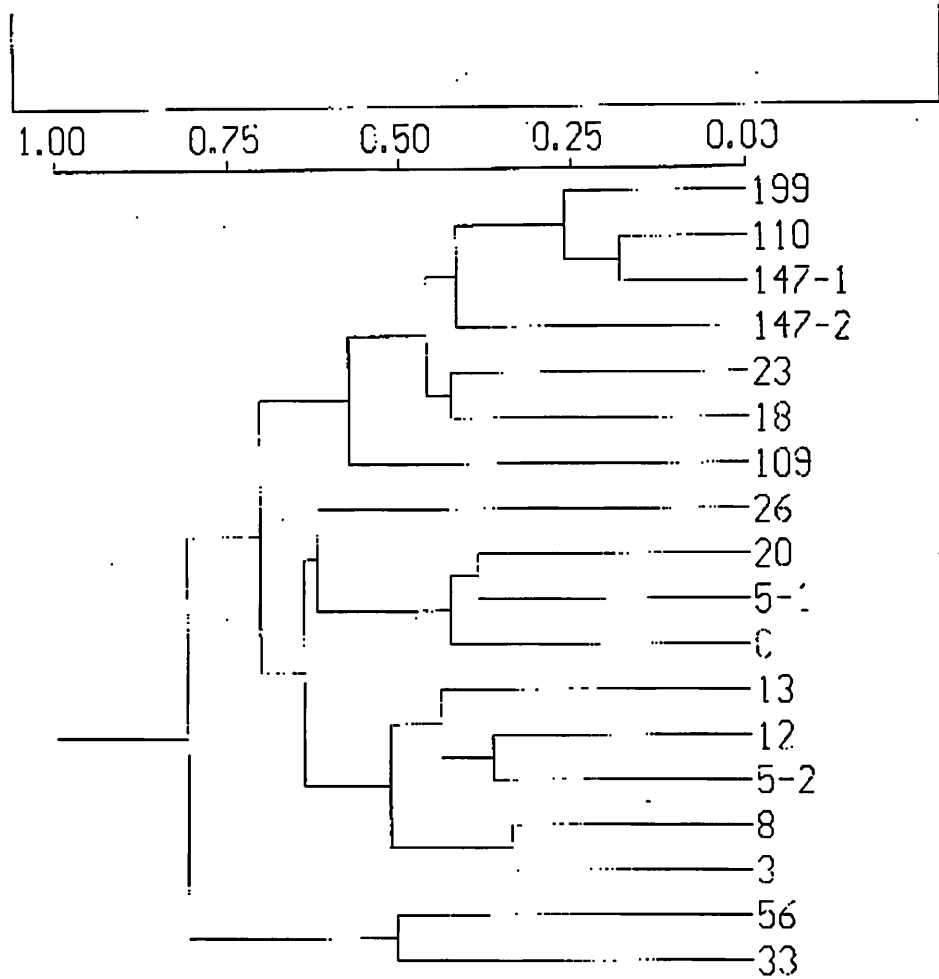


Figure 7. (a) Cluster diagram showing the mixedwood forest stand grouped together based on trends in large tree density. SAHN clustering techniques included UPGMA, complete-link and single-link methods and were based on the Bray-Curtis coefficient of similarity (Rolf 1992).

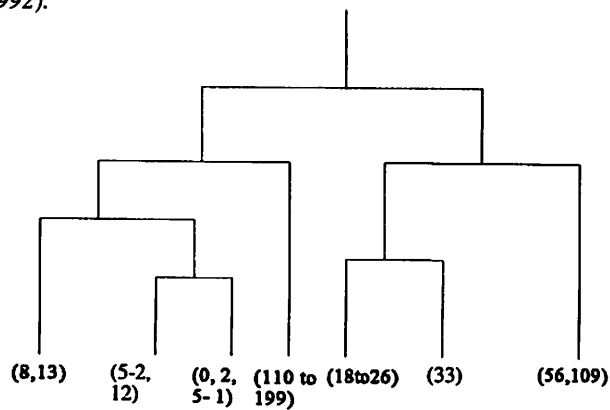


Figure 7. (b) TWINSPAN diagram showing the similarity of mixedwood forest stands in terms of the density of large trees in the stands. Equal cut levels were used in the analysis.

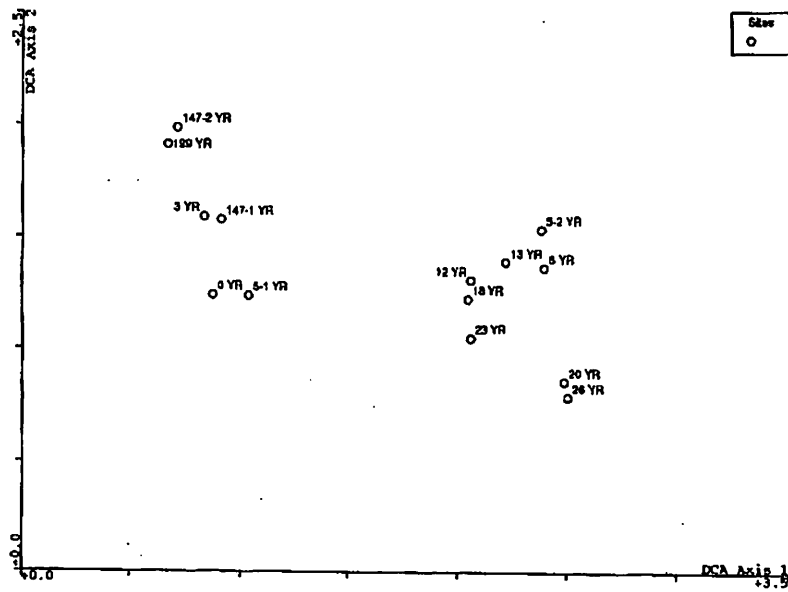


Figure 8. (a) A Detrended Correspondence Analysis (DCA) biplot showing the large tree density of the mixedwood stands plotted along the first two DCA axes.

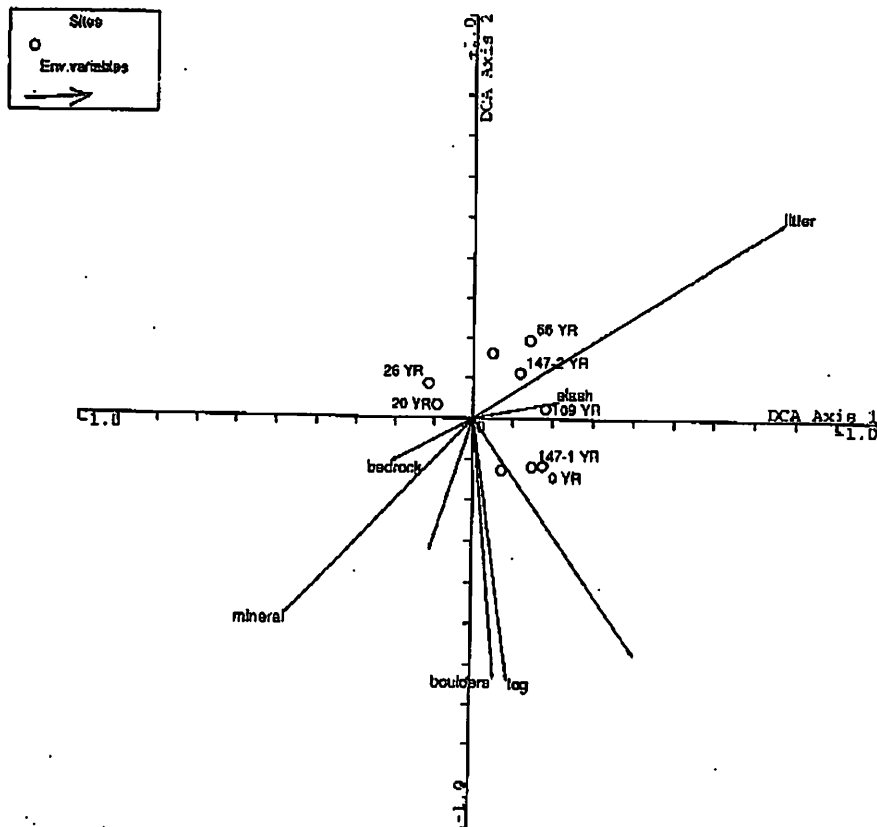


Figure 8. (b) A Canonical Correspondence Analysis (CCA) triplot showing the large tree density of the mixedwood stands plotted along the first two CCA axes.

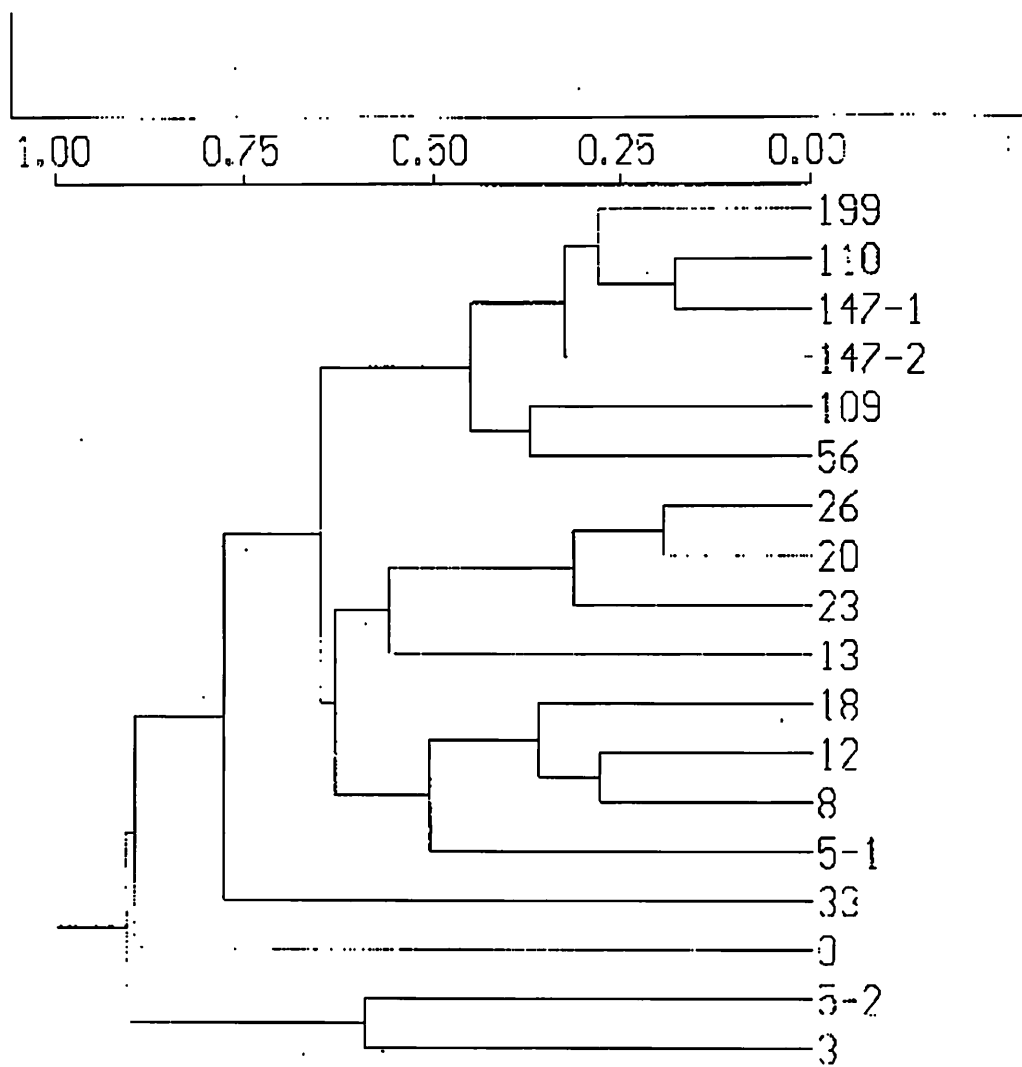


Figure 9. (a) Cluster diagram showing the mixedwood forest stands grouped together based on trends in the density of trees < 10 cm DBH. SAHN clustering techniques included UPGMA, complete-link and single-link methods and were based on the Bray-Curtis coefficient of similarity (Rolf 1992).

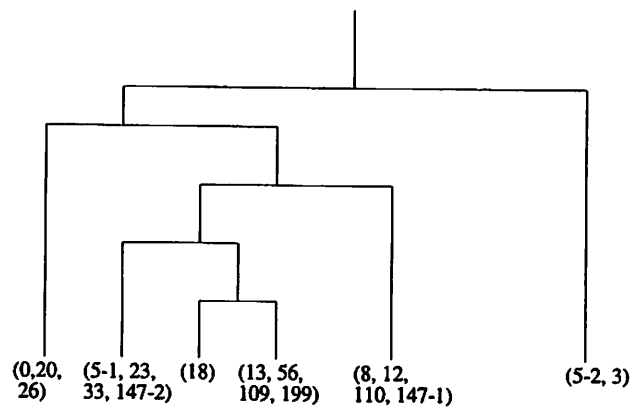


Figure 9. (b) TWINSPAN diagram showing the similarity of mixedwood forest stands in terms of the density of trees < 10 cm DBH in the stands. Equal cut levels were used in the analysis.

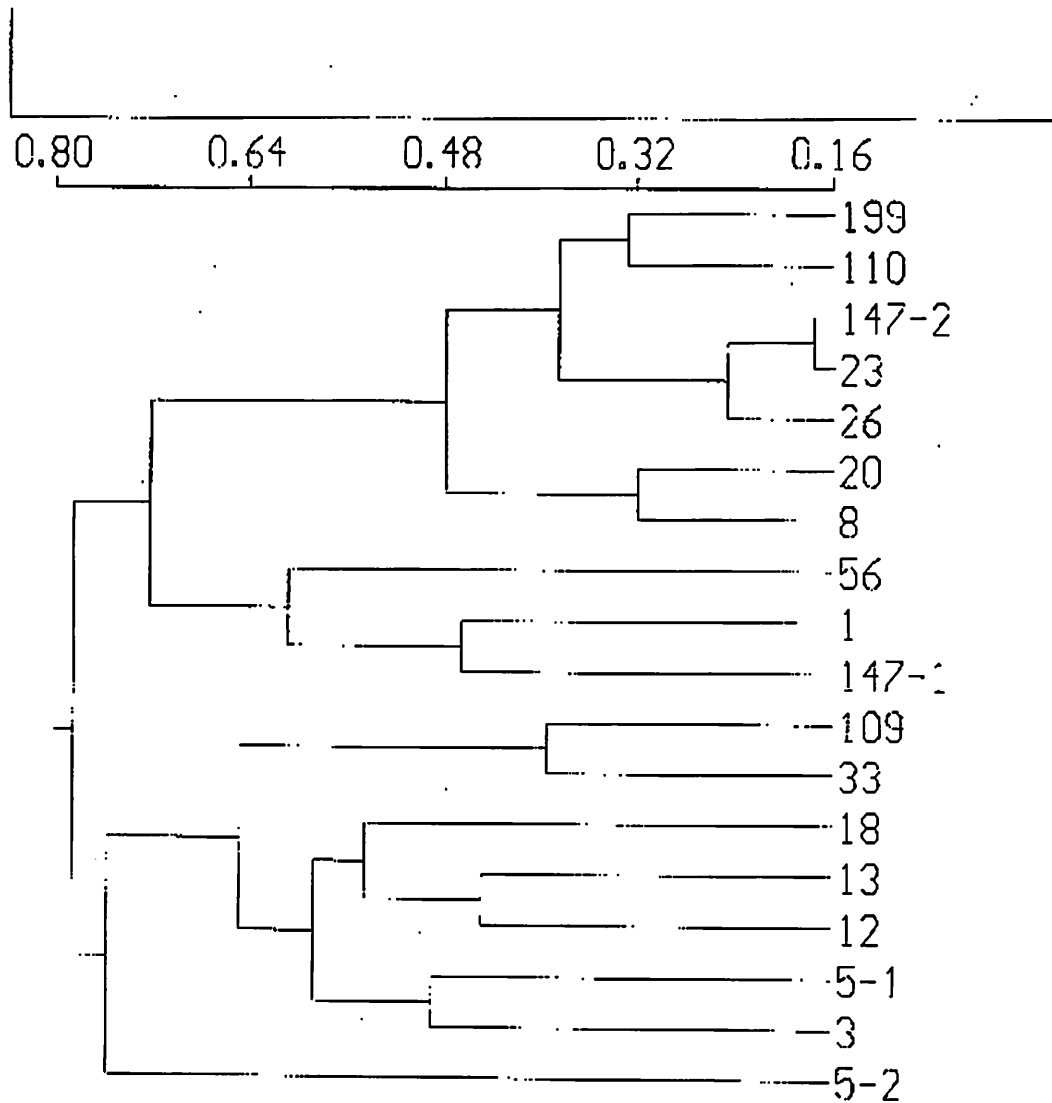


Figure 10. (a) Cluster diagram showing the mixedwood forest stands grouped together based on trends in shrub density. SAHN clustering techniques included UPGMA, complete-link and single-link methods and were based on the Bray-Curtis coefficient of similarity (Rohlf 1992).

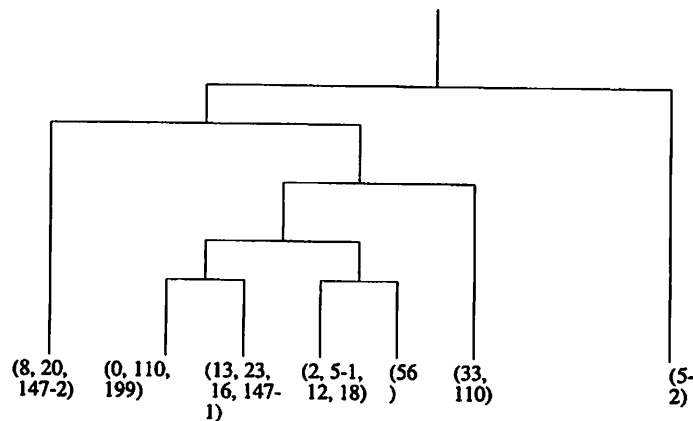


Figure 10. (b) TWINSPAN diagram showing the similarity of mixedwood forest stands in terms of shrub density. Equal cut levels were used in the analysis.

gradient in the shrub abundance data (Fig. 10b). Again the same 5-year-old stand was separated from all other stands at the first cut level, and the 109- and the 33-year-old stands were grouped together.

Plant species composition of the forest strata and understory

A DCA of the forest strata plant data revealed that species distributions were highly separated along the first ordination axis ($\bar{e} = 0.87$ for Axis 1 and $\bar{e} = 0.28$ for Axis 2) (Appendix E[1]). These first two axes accounted for 19 percent of the variance in the species data. A height gradient was obvious in the data, as was a general age trend within the stratum groups. DCA analyses of each stratum further revealed an age gradient. In general, strata greater than 25 cm and less than 20 m showed evidence of an age gradient along the second ordination axis. The results for the 25- to 50-cm and the 1- to 2-m strata are shown in Appendices E(2) and E(3).

Effects of various factors on tree regeneration after the disturbance

No significant relationship was found between the density of residual conifers and conifer regeneration ($R^2 = 0.09$, $p = 0.36$, $F = 0.92$; Fig. 11). Nor was there a significant effect of shrub density on the density of conifer regeneration ($R^2 = 0.05$, $p = 0.40$, $F = 0.76$; Fig. 12). A step-wise multiple regression analysis showed that there were no significant effects of age, residual tree abundance, or shrub abundance on conifer regeneration ($F = 0.20$, $p = 0.90$).

DISCUSSION

Phase I. Descriptive Analysis

Size and density of trees and shrubs

Trees

In keeping with well documented successional trends, the younger stands in this chronosequence were dominated by deciduous cover and the older stands by coniferous cover. In the boreal forest, conifers are more shade tolerant, produce larger seeds, are larger in size, and have longer life spans than do deciduous trees. They also have slower growth rates and use resources more efficiently (Grime 1979, Brumelis and Carleton 1989, Burns and Honkala 1990a, Freedman et al. 1994). These traits permit species like black spruce and balsam fir to establish under an existing canopy, and also to persist in the understory until they are released from competition (Brumelis and Carleton 1989). Even though there are limited data on resource competition in boreal forests, there is a widespread assumption that conifer species grow best in sites where resources are not limited (Newton et al. 1992). Conifers have poorly dispersed seeds, and, with the exception of

black spruce and white cedar (*Thuja occidentalis* L.), which can reproduce by layering (Frelich and Reich 1995), they rely solely on seed production for reproduction (Fowells 1985). In newly disturbed sites where light is not limited, conifer regeneration is less aggressive than are deciduous trees and shrubs. Therefore, competition is thought to play a key role in conifer abundance and distribution. Apart from competition, conifer dominance is reduced in younger stands because of poor seed dispersal, destruction of advance growth, and unsuitable seedbed conditions (Brumelis and Carleton 1989). For instance, conifers do not dominate in the younger stands of this study because they generally have smaller light-compensation thresholds that restrict their productivity in the high light conditions of recently disturbed sites (Freedman et al. 1994).

Deciduous trees, like aspen, are early successional, shade-intolerant species (Freedman et al. 1994) that establish very well on disturbed sites with unlimited light (Grime 1979, Burns and Honkala 1990b). For instance, most postdisturbance aspen are the result of suckering from damaged roots. This trait, among others, permits hardwoods to out-compete conifers in recently disturbed areas. Studies comparing conifer growth before and after hardwoods were reduced using herbicides (Newton et al. 1992) have demonstrated that hardwoods do negatively impact conifer growth.

The trends in deciduous and conifer cover may also relate to the fact that the six older stands were not harvested. A study by Carleton and MacLellan (1994) found that a higher percentage of mechanically harvested and skidded study stands were dominated by trembling aspen and balsam poplar than by conifers. In addition, Harvey and Bergeron (1989) showed an increase in the proportion of deciduous trees and shrubs after harvest and a shift in dominance from advance softwood regeneration to a mixedwood forest. Furthermore, Robertson (1996) found softwood/hardwood and spruce/hardwood ratios to be higher in stands where either hardwoods were poisoned and stands were deferred "softwood" cut or stands were just deferred "softwood" cut, than in stands that were clear-cut or softwood cut. Low sapling numbers in the 20- to 33-year-old stands are likely due to competition from shrubs and deciduous trees. Low numbers of saplings and small conifers in the older harvested stands (Fig. 4) are unlikely to lead to high conifer levels as harvested stands age further, at least in the first generation of trees. Although the lack of harvested stands older than 50 years does not enable confirmation, data from this study strongly suggest that harvesting these mixedwood stands is shifting the vegetation composition toward deciduous/shrub dominated stands.

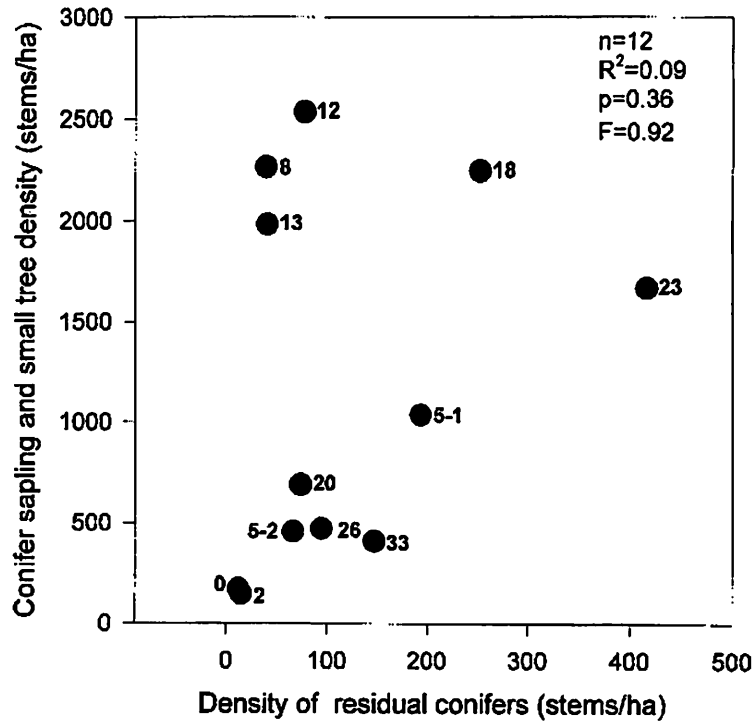


Figure 11. Simple linear regression of residual conifer density and conifer regeneration density for the twelve harvested mixedwood stands of this study. Numbers beside symbols correspond to stand age.

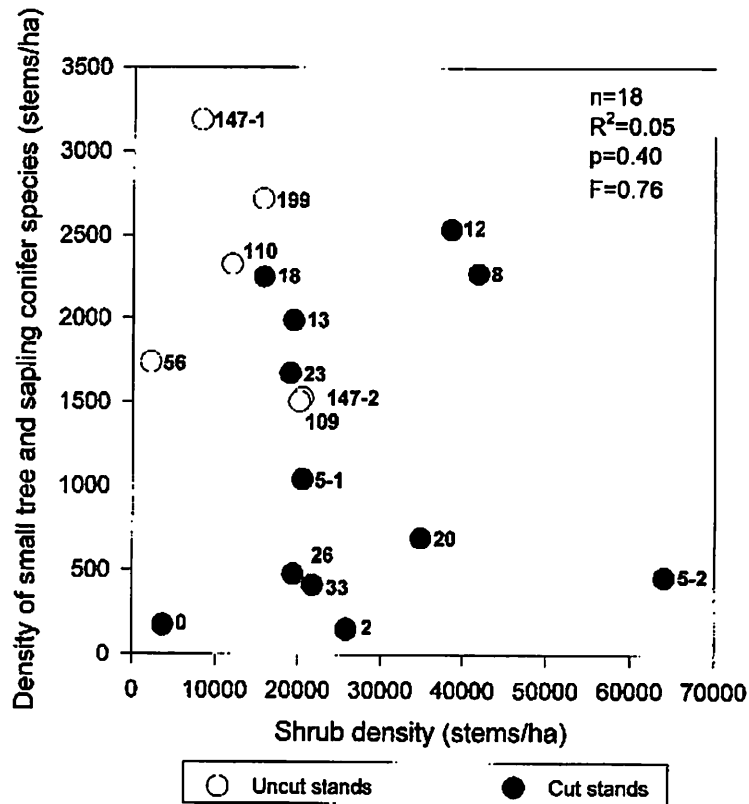


Figure 12. Simple linear regression of shrub density and conifer regeneration density for the mixedwood forest stands of this study. Numbers beside symbols correspond to stand age.

Lastly and perhaps most importantly, the density of conifers > 2.5 cm DBH did not show the bimodal trend in density through time that conifer saplings did. This indicates that the postharvest density of conifers is not controlling their regeneration. A relationship between residual conifers and conifer regeneration is expected because seed from residual conifers would lead to sapling establishment, rather than conifer regeneration being dependent on the seedbank and low rates of dispersal from unlogged adjacent areas.

Most saplings in the older stands were balsam fir and to a lesser extent black spruce; most conifer saplings in the harvested stands were balsam fir (Fig. 5). Balsam fir dominance in the older stands is not surprising. This species can readily establish in the shade of larger trees and it is more shade tolerant than is black spruce. It can also develop beneath pioneer deciduous canopies and invade spruce stands that are beginning to break up (Carleton and MacLellan 1994). Balsam fir seeds may germinate in less than 10 percent full sunlight (Burns and Honkala 1990a), but after germination require 50 percent full sunlight for optimum growth (Burns and Honkala 1990a). Therefore, balsam fir saplings in the oldest stands were probably occurring in small forest gaps created by windfall, insects, disease, or natural tree senescence. Canopy openings are important for moving the succession of even-aged stands, such as pine-aspen, forward to uneven-aged stands, such as old-growth mixtures of balsam fir, black spruce, white cedar, and white birch (Frelich and Reich 1995). Shaded conditions and canopy gaps are therefore leading to balsam fir and black spruce regeneration in the older stands. The dominance of balsam fir in most of the younger stands related to the nature of disturbance. The 12 youngest stands would have been dominated by black spruce had they originated from fire, because it is a post-fire pioneer species with semiserotinous seeds, massive seedling recruitment after fire, and can maintain continuous seed dispersal in the absence of fire (Bonan and Shugart 1989, Frelich and Reich 1995). In contrast, balsam fir seeds are not serotinous or fire-tolerant (Burns and Honkala 1990a) and the species is usually eliminated by fire. Black spruce is more abundant than balsam fir immediately following harvest (i.e., two youngest stands) (Fig. 5). This indicates that there were black spruce saplings in the stands before harvest and either no balsam fir saplings or they were damaged during harvest. The balsam fir saplings in the slightly older stands may have seeded in from residual balsam fir left behind after harvest, or they may be seedlings whose growth was delayed after harvest.

Small and large conifers (> 2.5 cm DBH) were mainly balsam fir, but small black spruce were relatively more abundant than were small balsam fir in the two oldest

harvested stands and in two of the uncut stands (Appendix A[2]). Aside from the 56-year-old stand, where black spruce regenerated before balsam fir, it is difficult to determine a reason for this. Disturbance intensity is likely an important factor. For instance, black spruce was more abundant than was balsam fir in the 15- to 45-cm size range in the 109-year-old uncut stand. This diameter range included both residual trees and regeneration, so high levels of black spruce may in part be due to black spruce left in the stand after fire.

The density of trembling aspen was very high in the young stands and low in the older stands. This is consistent with aspen life history traits. Aspen is an early successional, competition-intolerant species. It produces a large number of light seeds that are wind-dispersed (Fowells 1985, Bonan and Shugart 1989, Burns and Honkala 1990b), can be carried many kilometers, and germinate well in exposed mineral soils (Burns and Honkala 1990b). Aspen trees have high resource acquisition rates (Finegan 1984), can produce seed after 2 to 3 years, and have large seed crops when they are 10 to 20 years old. Aspen also reproduce extensively through the production of sucker shoots (root sprouting) following harvest (Fowells 1985, Bonan and Shugart 1989, Burns and Honkala 1990b).

White birch was the other dominant deciduous species considered in this study. This species also has wind-dispersed seeds that germinate well on mineral soils. Birch begins seed production later than aspen, at 15 years of age, and the optimum seed production age is 40–70 years (Burns and Honkala 1990b). Aspen saplings were dominant in stands less than 8 years of age, while white birch was dominant in older stands. Trembling aspen appeared to regenerate before white birch in the harvested stands. This is probably due largely to aspen suckers that would have developed immediately after harvest. Similar to the sapling trend, small trembling aspen trees were more dense than were white birch in the 18- to 33-year-old stands; the reverse was true in the older uncut stands.

Again, sapling and small tree species data generally support work by Carleton and MacLellan (1994) in which the vegetative composition of post-logged stands displayed a strong conversion from a needle-leaved conifer dominated ecosystem to broad-leaved deciduous forest and shrub ecosystems. The current work supports their conclusion that logging conifer trees does not ensure the persistence of the same dominant species (Carleton and MacLellan 1994).

The density of trembling aspen > 10 cm DBH was highest in the 23- to 56-year-old stands. This species then dropped off in abundance. This complements general trends of small aspen, which peak in 18- to 33-year-old stands. Most of the residual trees left behind after cutting were

white birch. Therefore, white birch patterns in the harvested stands reflect the effects of harvesting more than ecological successional patterns.

The mean diameter of trees in some of the youngest stands was comparable to the mean diameter of trees in some of the oldest stands. Clearly, this figure reflects the extent to which residual trees were left behind more than it does a successional gradient in tree size across the chronosequence. Dividing the diameter distribution into conifers and deciduous trees shows that most of the trees left behind after harvesting were deciduous. This supports the historical data.

Shrubs

Shrubs were most abundant in the 20-, 12-, 8-, and 5-year-old (5-2) stands (Fig. 3d). The species that composed most of the shrub biomass in the 20-year-old stand were: *Acer spicatum* Lam. (which has intermediate tolerance of competitive stress, survives disturbance, and persists until later successional stages [Freedman et al. 1994]) and *Corylus cornuta* Marsh. *Diervilla lonicera* Mill. (an early successional, competition-intolerant species [Freedman et al. 1994] at the northern edge of its range in this study) and *Rubus strigosus* Michx. (a widespread, early successional, competition-intolerant species [Freedman et al. 1994]) were most dominant in the 12-year-old stand. *Corylus cornuta* Marsh. and *Acer spicatum* Lam., and *Corylus cornuta* Marsh. and *Diervilla lonicera* Mill. (Fig. 6) were most abundant in the 8-, and 5-year-old stands, respectively. Shrub density was generally lower in the very young stands, where shrubs have not yet established as the dominant understory vegetation, and in some of the older stands, where trees have become the dominant vegetation. The oldest stands were never harvested and this also leads to lower shrub abundance. Fires may leave conifer snags, whose serotinous cones act as seedbanks (Carleton and MacLellan 1994) and they may remove most or all of the organic soil layer, thereby retarding the regeneration of understory plants (Carleton and MacLellan 1994). Therefore, low shrub cover in the older stands was probably related both to stand age and disturbance type. The communities of recently harvested stands in this study were composed mainly of broad-leaved saplings and shrubs, and supported previous successional studies (Carleton and MacLellan 1994). This study, like many others (e.g., Carleton and MacLellan 1994), lacks representation of young fire-disturbed stands because increased fire suppression has made it very difficult to find such sites in potential study areas. Therefore, it was not possible to determine the extent of the broad-leaved sapling/shrub community type in post-fire stands. The 56-year-old uncut stand had the lowest shrub cover. A stand can develop into a closed canopy in approximately 50 years. At that

time, trees are not old enough for the stand to become highly prone to windfall, insects, disease, or natural senescence. Therefore, unlike the older stands that have canopy gaps, shrubs in the 56-year-old stand may not have suitable habitat for shrub establishment and development.

By examining trends for these shrub species, it was apparent that species had quite different abundance patterns along the chronosequence. *Acer spicatum* and *Corylus cornuta* both show small abundance peaks (greater than 500 stems/hectare) in some of the older stands, whereas the abundance of *Diervilla lonicera* Mill. and *Rubus strigosus* Michx. peak in the younger stands, generally decrease with age along the chronosequence, and almost disappear by 25 years of age. Certain shrub species may establish easily and grow in the forest gaps of the older stands, thereby increasing their abundance. As well, these intermediate successional species, unlike early successional species, may be present at low abundance levels in the understory of mature stands and increase in numbers when gaps form (Freedman et al. 1994). The abundance of within-shrub species and the relative abundance of different shrub species vary among stands. This variation may be due largely to predisturbance vegetative composition, so this should be kept in mind when interpreting shrub abundance trends across the chronosequence.

Plant species composition of the forest strata and understory

Vegetative cover

The plant species composition of the stands' upper strata supports the shrub and tree density patterns (Appendix D). Vegetation cover data of the 3- to 10-m height range complement density data for large trees. Vegetation cover of the upper strata was higher in uncut stands, which is not surprising given that age and height are highly correlated. Vegetation abundance of the 1- to 3-m height range is highest in the 8-, 20-, and 26-year-old stands, which corresponds well with peak densities of saplings, small trees, and shrubs. In terms of herbaceous vegetation (< 1-m strata) of the forest stands, vegetation cover was generally highest in the 5- to 13-year-old stands. Herbaceous and small shrub abundance would be lower in the youngest stands because herbs and shrubs require several growing seasons to become established following a disturbance.

Cover of life-forms

Dividing the plant species composition data into life-form groups permits a more thorough interpretation of the successional trends. The trends in conifer and shrub cover will be discussed in detail. Trends in the remaining life form cover types are presented in Appendix F.

Shrubs possess certain life history traits, which, once established, give them a competitive advantage over herbaceous vegetation following a disturbance. They have high rates of dry matter production, continuous leaf production, and stem extension (Grime 1979). They can also quickly adjust phenotypic traits such as shoot morphology and leaf area as shade increases (Grime 1979). Therefore, they outcompete herbaceous annuals and perennials that invade recently disturbed habitats. Shrubs were a major component of the harvested stands, having the highest percent cover of all life-forms in all stands except the 0-year-old stand. In harvested stands 20 years of age and older, shrubs were the major vegetation component of the ground through 5-m strata. In particular, the 33-year-old harvested stand and the 56-year-old uncut stand showed dramatic differences in shrub cover. Shrubs were present in the < 10-cm through 5-m strata in the oldest harvested stand, whereas they were significantly reduced in the 56-year-old uncut stand. Shrubs and their propagules often survive harvesting but not fire, quickly spread in stands in the absence of tree cover, and reach extremely high abundance levels. These high abundance levels rarely occur in burned sites where shrubs develop with trees. Eventually, shrubs are replaced in older stands by deciduous tree species. Shrubs become too shaded to be reproductively successful and reach the end of their life span as the tree species reach maturity (Grime 1979). In this study, trembling aspen and white birch were the first tree species to increase in numbers, and thus compete with shrubs and herbaceous vegetation for resources.

In this study, conifers comprised the highest proportion of all vegetative cover in the uncut stands. Conifer density of the younger stands was relatively low with a dramatic increase in the uncut stands. In addition, all uncut stands showed high levels of conifer abundance throughout the forest layers, whereas harvested stands did not. There was a general increase in conifer cover with age, but the trend did not appear to be based strictly on this criterion. Conifer abundance and the number of strata where it occurred increased quite suddenly in the older, uncut stands. Although replication of the stands for each age class would be required to reach a definitive conclusion, the data suggest that the increase in conifer cover may be related to both age and disturbance type.

In general, the tree, shrub, and herbaceous trends of this study follow commonly observed successional trends, which are summarized in the following simplification: encrusting prostrate life-forms, decumbent or emergent life-forms, ephemeral herbaceous life-forms (often annuals and biennials), taller perennial herbs (grasses, sedges, perennial wildflowers) and low thickets, tall shrubs and scattered taller trees, and canopy of trees with an understory of saplings and a ground cover of several levels

(Drury and Nisbet 1973, Grime 1979, Noble and Slatyer 1980, Carleton and MacLellan 1994).

Phase II. Statistical Analysis

Description of forest plant communities—a multivariate analysis

Tree and shrub density

Large trees

Multivariate analysis revealed that similarly aged forest stands were alike in terms of large tree density (Fig. 7a). This was illustrated by the TWINSpan results, which yielded six groups of similarly aged stands. As well, the CCA analysis revealed age to be one of the top two environmental variables explaining variation in large tree density data (Fig. 8b). In spite of these general trends, age is clearly not the only factor controlling the large tree species composition of a stand. First, clustering results showed that the largest percent dissimilarity was between the 33- and 56-year-old stands and all other stands. Data containing a clear age gradient would have shown that the oldest or the youngest stands were most different from all others. It is important to note that an age trend may have been somewhat reduced by the choice of index. The Bray-Curtis index is a species presence driven index, meaning that species occurrence in stands dominates the cluster results. A stronger age gradient may have been seen using an abundance-driven index and by using volume based size intervals instead of diameter based size intervals. Secondly, the TWINSpan analyses separated the 26-through 109-year-old stands from all other stands after the first cut (Fig. 8a). Not only is age likely just one of a group of factors controlling the postdisturbance composition of mixedwood stands, it may not be the main factor. Multivariate results indicate that disturbance type may be playing a role in postdisturbance plant species composition. All uncut stands are grouped with one another or singly in the final TWINSpan groupings (Fig. 8a). Furthermore, there was a clear separation of the six uncut stands from all harvested stands greater than 8 years of age using DCA analyses (Fig. 8a). In spite of this, some uncut stands were similar in large and small tree density to some harvested stands. For example, the 2-year-old stand was grouped with all uncut stands, and the two other most recently cut stands are closest to the oldest stands in ordination space.

The intensity of disturbance may also account for trends in large tree composition, because most of the large trees sampled in the 0 to 33-year-old stands would have been left behind after trees in the original stand were removed. The only source of information about the intensity of disturbance is the historical data. Lack of detailed information about the impact of harvesting (e.g., *skidding* impact on soil) and fire behavior may contribute to inconsistencies in perceived general trends between vegetation

and disturbance type and intensity (e.g., relationships between skidding process and vegetation) (Carleton and McLellan 1994). Residual vegetation (mainly white birch) was left behind following tree harvest. Because not all stands were entirely clear-cut, it is not surprising that a clear age gradient was not found for the large tree data. It may be that the conditions of the large tree species composition of the most recently harvested stands were more similar to those of the older uncut stands than would be expected because of residual vegetation being left behind after harvest. As well, less residual vegetation was left in the 18- to 33-year-old stands; the 20- to 33-year-old stands were the only ones in which trees were cable yarded to the roadside instead of wheel skidded. This could explain why these four stands were more similar to the 56- and 109-year-old stands than to the remaining harvested stands. The reason why the 33- and 56-year-old stands were quite dissimilar from all other stands could have something to do with the fact that the 33-year-old stand was horse skidded and therefore probably more similar to the 56-year-old stand than if it had been wheel skidded. Multivariate analyses showed evidence of their effects on plant species composition, but do not reveal that either is the overall underlying factor.

The effect of predisturbance vegetation on the results is also critical (Carleton and MacLellan 1994, Robertson 1996). Unfortunately, predisturbance plant species composition of the study stands is not available. Therefore it is not possible to evaluate its effect on the postdisturbance plant species composition of the stands.

Small trees and saplings

Multivariate clustering analyses of trees less than 10-cm DBH revealed an age gradient in the data (Fig. 9a). Two of the youngest stands were most dissimilar to all other stands, as demonstrated in Figure 9b. As well, the six uncut stands were similar to each other in terms of small tree and sapling species composition. Furthermore, the 20- to 26-year-old stands were similar to one another, as were the 8-, 12-, and 18-year-old stands. Disturbance type (wildfire/harvesting) was shown to be an important factor in the sapling and small tree species composition of the stands. All uncut, fire-disturbed stands are naturally grouped together in a separate cluster (Fig. 9a). TWINSpan analysis of the data shows a less clear age gradient.

Shrubs

Multivariate analysis of stand shrub density further revealed that age was not the only factor controlling the plant species composition of the forest stands; clustering and TWINSpan analyses showed that non age-related stands were similar. Other factors affecting shrub density

were probably the disturbance intensity (Carleton and MacLellan 1994) and predisturbance vegetative composition of the stands. A clear separation of harvested and uncut stands was not seen. The 5-year-old (5-2) stand was not similar to any other stand and had the highest density of shrubs. This point is also demonstrated in Figure 3d. Two of the uncut stands were similar to the 12-, 13-, and 18-year-old stands, and the remaining uncut stands were similar to the 8- and to the 20- to 26-year-old stands. Clearly, shrub abundance can vary in uncut stands. Since shrubs survive harvest, the number that are left behind to proliferate in the nonlimited resource environment of recently cut stands is highly variable. For instance, some stands may quickly become shrub dominated, yet others may not. Both the disturbance type and the predisturbance vegetative composition would have significant effects on the postdisturbance shrub species composition of the stands. This study suggests that a preharvest assessment of the shrub composition of the stands is essential if one desires to predict the postharvest vegetation of boreal mixedwood stands.

Plant species composition of the forest canopy layers and understory

A clear height gradient was obvious in the plant species composition data, when all height layers were entered as separate variables. There is some evidence of an age gradient within height strata. Separate analyses for each strata further revealed somewhat of an age gradient. In general, strata greater than 25 cm and less than 20 m showed evidence of an age gradient along the second ordination axis. Once again, these data suggest, like the tree and shrub density data, that multiple factors are likely causing the trends in postdisturbance plant species composition.

Effects of residual vegetation on tree regeneration after the disturbance

Data trends and multivariate analyses suggest that neither age nor residual tree abundance alone is controlling the postdisturbance tree regeneration of the stands. The authors therefore conducted linear regression analyses of the data at the level of groups of tree size classes in order to test for these trends. At this level, there was no clear relationship between conifer regeneration and residual conifer density. In the 18 mixedwood stands of this study, the amount of postharvest residual conifer left behind does not control conifer regeneration in harvested stands as one might expect if conifer regeneration was to develop entirely from seed after harvest. Clearly, another factor or a set of factors (possibly including this one) is controlling postdisturbance tree regeneration. One crucial factor is the preharvest tree composition of the stands. As already pointed out, black spruce regeneration is present in the

stands at the time of harvest. This indicates that black spruce regeneration is a consequence of both pre- and postharvest conditions (Fig. 5). The data in this study suggest that there is very little balsam fir regeneration in the stands at the time of harvest, or that smaller balsam fir were damaged during harvest. Therefore, balsam fir saplings in slightly older harvested stands may have seeded in from residual balsam fir left behind after harvest, or they may be the result of balsam fir seedlings that initially had slow growth rates.

Similarly, a significant effect of shrub density on the density of conifer regeneration was not found. Conifer regeneration can be significantly and negatively impacted by shrub development via above- and belowground competition for light/space and nutrients/water, respectively. In this study, regression analyses indicated that there was no clear relationship between shrub development and the amount of conifer regeneration in the stands after a disturbance. As Robertson (1996) pointed out, boreal communities may be explainable using univariate gradients such as residual vegetation, shrub growth age, etc., but the results of harvesting may be confounded by complex environmental gradients (Robertson 1996). This could also be the case for wildfire-generated stands.

Multiple regression analyses further indicated that shrub development, residual tree abundance, and age are insufficient for explaining the variation in postdisturbance tree regeneration. It is therefore thought that predisturbance tree composition and intensity of disturbance likely play a large role in the distribution and abundance of postdisturbance tree regeneration and other plant composition of the stands. As previously mentioned, detailed information about these two factors is missing, as is the case for the majority of plant succession studies. These results strongly suggest that predisturbance vegetation composition of the plant communities and detailed information about the nature of disturbance in a stand, be it fire or harvesting, is essential to explain postdisturbance regeneration patterns in mixedwood forests.

Diversity of postdisturbance forest stands

No linear relationships were found between stand age and the species richness or diversity of the forest stands when all height layers were treated as separate samples. Examination of the data revealed that the relationship between measures of diversity and age were probably not linear and therefore the use of linear techniques was not appropriate. Previous studies have shown that relationships between measures of diversity and environmental variables or along environmental gradients tend to be unimodal (Shafi and Yarranton 1973, Grime 1979).

CONCLUSIONS

In general, the mixedwood stands of this study show patterns that support forest successional trends. The younger stands are dominated by deciduous shrubs and trees (mainly aspen and white birch), and the older stands are dominated by conifers (mainly balsam fir and black spruce). These trends are apparent when looking at tree and shrub density, cover data from 15 height strata, and quadrat life-form cover data. More specifically, the study leads to four main conclusions.

(1) Conifer regeneration is not closely linked to the amount of conifer growth left behind after a disturbance.

One interesting pattern in the data is a bimodal density distribution trend for conifer saplings that is not evident for larger trees. The fact that this trend is unique to saplings suggests that conifer regeneration may be independent from the amount of conifer growth left behind after a disturbance for mixedwood stands.

(2) Harvesting is resulting in little or no conifer regeneration.

Low conifer sapling and small tree densities in the older harvested stands further indicate that harvesting is probably leading to little or no conifer regeneration as the harvested stands age. Harvesting of these stands appears to be leading to a shift from mixedwood stands toward shrub/deciduous dominated forest stands.

(3) Age, disturbance type, and residual conifer abundance alone are not controlling postdisturbance vegetative composition.

Multivariate and regression analyses indicate that there is evidence of an age gradient in the vegetation data of these mixedwood stands. There is also some evidence that vegetation of the forest stands is somewhat controlled by whether it was a fire-originated stand or a harvested stand. Furthermore, regression analyses did not provide evidence of a relationship between the density of conifers left behind and conifer regeneration after harvest. Clearly, none of these three main factors alone control the postdisturbance vegetative composition of these mixedwood stands. The authors propose that another factor or set of factors (possibly including age, disturbance type, and intensity) is controlling the composition of the forest stands after a major disturbance.

- Finegan, B. 1984. Forest succession. *Nature* 312: 109–114.
- Fowells, H.A. 1985. *Silvics of forest trees of the United States*. U.S. Department of Agriculture, Washington, DC. Agricultural Handbook No. 271. 762 p.
- Freedman, B.; Woodley, S.; Loo, J. 1994. Forestry practices and biodiversity with particular reference to the Maritime Provinces of eastern Canada. *Environmental Reviews* 2:33–77.
- Frelich, L.E.; Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs* 65:325–346.
- Gleason, H.A. 1952. *The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada*. Hafner Press, New York, NY. 3 v.
- Glenn-Lewin, D.C.; Peet, R.K.; Veblen, T.T. 1992. *Plant succession. Theory and prediction*. Chapman and Hall, London, United Kingdom. 352 p.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester, NY. 222 p.
- Harvey, B.D.; Bergeron, Y. 1989. Site patterns of natural regeneration following clear cutting in northwestern Quebec. *Canadian Journal of Forest Research* 19:1458–1469.
- Hill, M.O. 1979. TWINSPAN: A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. *Ecology and Systematics*, Cornell University, Ithica, NY.
- Hills, G.A. 1951. *A read reference to the description of the land of Ontario and its productivity: A compendium of maps, charts, tables and brief comments*. Department of Lands and Forests, Research Branch, Maple, ON. 142 p.
- Horn, H.S. 1981. Succession. p. 253–271 in R. M. May, ed. *Theoretical Ecology*. 2nd ed. Blackwell Scientific Publications, Oxford, England. 489 p.
- International Bird Census Committee 1970. Recommendations for an international standard for a mapping method in bird census work. *Audubon Field Notes* 24:727–736.
- Laycock, W.A.; Batcheler, C.L. 1975. Comparison of distance-measurement techniques for sampling tussock grassland species in New Zealand. *Journal of Range Management* 28:235–239.
- Lietti, H.; Whittaker, eds. 1975. *Primary production of the biosphere*. Springer-Verlag, New York, NY. 339 p.
- Magurran, A.E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ. 179 p.
- McKenney, D.W.; Sims, R.A.; Soule, M.E.; Mackey, B.G.; Campbell, K.L., eds. 1994. *Towards a set of biodiversity indicators for Canadian forests: Proceedings of a Forest Biodiversity Indicators Workshop*. 29 November–1 December 1993, Sault Ste. Marie, Ontario. Nat. Resour. Can., Canadian Forest Service–Ontario, Sault Ste. Marie, ON. 133 p.
- Matthews, J.A. 1992. *The ecology of recently deglaciated terrain: A geoecological approach to glacier forelands and primary succession*. Cambridge University Press, New York, NY. 386 p.
- Newton, M.; Cole, E.; White, D.E.; MacCormack, M.L. 1992. Young spruce-fir forests released by herbicides II. Conifer response to residual hardwoods and overstocking. *Northern Journal of Applied Forestry* 9:130–135.
- Noble, I.O.; Slatyer, R.O. 1980. The use of vital attributes to predict successional change in plant communities subject to recurrent disturbances. *Vegetation* 43:5–21.
- Noble, M.G.; DeBoer, L.K.; Johnson, K.L.; Coffin, B.A.; Fellows, L.G.; Christensen, N.A. 1977. Quantitative relationships among some *Pinus banksiana*–*Picea mariana* forests subjected to wildfire and postlogging treatments. *Canadian Journal of Forestry Research* 7:368–377.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164:262–270.
- Ontario Forest Policy Panel. 1993. *Diversity: Forests, people and communities. A comprehensive forest policy framework for Ontario*. Ont. Min. Nat. Resour., Toronto, ON. 147 p.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. p. 144–168 in H.H. Shugart, R. Leemans and G.B. Bonan, eds. *A Systems Analysis of the Global Boreal Forest*. Cambridge University Press, New York, NY. 565 p.
- Pielou, E.C. 1975. *Ecological diversity*. John Wiley and Sons, New York, NY. 165 p.
- Robertson, S.L. 1994. Effect of harvesting methods on the phytosociology of a boreal mixedwood forest community. M.Sc. Thesis, Lakehead University, Thunder Bay, ON. 334 p.
- Robertson, S.L. 1996. Long-term effects of harvest methods on a boreal mixedwoods plant community. p. 158–162 in C.R. Smith and G.W. Crook, comps. *Advancing Boreal Mixedwood Management in Ontario*. 17–19 October 1995, Sault Ste. Marie, Ontario. Nat. Resour. Can., Canadian Forest Service–Sault Ste. Marie, Sault Ste. Marie, ON. 239 p.

- Rohlf, F.J. 1992. NTSYS-pc Numerical Taxonomy and Multivariate Analysis System. Version 1.70. Applied Biostatistics Inc., Setauket, NY.
- Samoil, J.K., ed. 1988. Management and utilization of northern mixedwood. Proceedings of a Symposium. 11–14 April 1988, Edmonton, Alberta. Canadian Forestry Service, Edmonton, AB. Inf. Rep. NOR-X-296. 163 p.
- Shafi, M.I.; Yarranton, G.A. 1973. Diversity, floristic richness, and species evenness during a secondary (post-fire) succession. *Ecology* 54:897–902.
- Shugart, H.H. 1984. A theory of forest dynamics: The ecological implications of forest succession models. Springer-Verlag, New York, NY. 228 p.
- Shugart, H.H.; Leemans, R.; Bonan, G.B., eds. 1992. A systems analysis of the global boreal forest. Cambridge University Press, New York, NY. 565 p.
- Sims, R.A.; Towill, W.L.; Baldwin, K.A.; Wickware, G.M. 1989. Forest ecosystem classification for northwestern Ontario. Ont. Min. Nat. Resour., Thunder Bay, ON.
- ter Braak, C.J.F. 1988. CANOCO—A FORTRAN program for cononical community ordination. Microcomputer Power, Ithaca, NY. 90 p. + appendix.
- Thompson, I.D.; Welsh, D.A. 1993. Integrated resource management in boreal forest ecosystems—impediments and solutions. *For. Chron.* 69:32–39.
- Ward, P.C.; Tithecott, G.A. 1993. The impact of fire management on the boreal landscape of Ontario. Ont. Min. Nat. Resour., Aviation, Flood and Fire Management Branch, Sault Ste. Marie, ON. Publication 305. 12 p.
- Wein, R. W.; El-bayoumi, A. 1982. Limitations to predictability of plant succession in northern ecosystems. p. 214–225 in R.W. Wein, R.A. Riewe and I.R. Methven, eds. Resources and Dynamics of the Boreal Zone. Proc. Conf. August 1982, Thunder Bay, Ontario. Assoc. Of Canadian Universities for Northern Studies, Ottawa, ON. 544 p.
- Welsh, D.A. 1977. Point distance nearest neighbour program in written Fortran IV with advice from C.L. Batcheler. Program recompiled to Watfor and into P.C. version by B. Collins and revised by R. Thompson in 1994.
- Welsh, D.A. 1983. Use of the mapping method to study the effects of forest cutting on boreal bird populations. p. 2–12 in F.J. Porroy, ed. Bird Census and Mediterranean Landscape. Leon, France.
- Welsh, D.A. 1987. The influence of forest harvesting on mixed coniferous-deciduous boreal bird communities in Ontario, Canada. *Acta Oecologica* 8:247–252.
- Welsh, D.A.; Fillman, D.R. 1980. The impact of forest cutting on boreal bird populations. *American Birds* 34:84–94.
- Whitaker, R.H. 1975. Communities and ecosystems. The MacMillan Company, Toronto, ON. 385 p.
- Wickware, G.M.; Rubec, C.D.A. 1989. Terrestrial ecoregions and ecodistricts of Ontario. Env. Can., Sustainable Development Branch, Conservation and Protection, Ottawa, ON.

Appendix A(1). Species present in the 15 strata layers of the mixedwood forest stands of this study. Nomenclature according to Gleason (1952), unless otherwise specified. Also included are species codes and common names used throughout the text, tables, and figures of this report.

Life-form	Latin nomenclature	Common nomenclature	Species code
Conifer tree			
	<i>Abies balsamea</i> (L.) Mill.	Balsam fir	ABIE BAL
	<i>Picea glauca</i> (Moench) Voss.	White spruce	PICE GLA
	<i>Picea mariana</i> (Mill.) BSP.	Black spruce	PICE MAR
	<i>Pinus banksiana</i> Lamb.	Jack pine	PINU BAN
	<i>Thuja occidentalis</i> L.	Eastern white cedar	THUJ OCC
Deciduous tree			
	<i>Betula papyrifera</i> Marsh	White birch	BETU PAP
	<i>Fraxinus nigra</i> Marsh.	Black ash	FRAX NIG
	<i>Larix laricina</i> (Du Roi) K. Koch.	Tamarack	LARI LAR
	<i>Populus balsamifera</i> L.	Balsam poplar	POPU BAL
	<i>Populus tremuloides</i> Michx	Trembling aspen	POPU TRE
Shrub			
	<i>Acer spicatum</i> Lam.	Mountain maple	ACER SPI
	<i>Alnus crispa</i> (Ait.) Pursh.	Green alder	ALNU CRI
	<i>Alnus rugosa</i> (Du Roi) Spreng.	Speckled alder	ALNU RUG
	<i>Amelanchier</i> spp.	Juneberry/Serviceberry spp.	AMEL SP
	<i>Aralia hispida</i> Vent.	Bristly sarsaparilla	ARAL HIS
	<i>Aralia nudicaulis</i> L.	Wild sarsaparilla	ARAL NUD
	<i>Cornus canadensis</i> L.	Bunchberry	CORN CAN
	<i>Cornus stolonifera</i> Michx.	Red-osier dogwood	CORN STO
	<i>Corylus cornuta</i> Marsh.	Beaked hazel	CORY COR
	<i>Diervilla lonicera</i> Mill.	Bush honeysuckle	DIER LON
	<i>Epigaea repens</i> L.	Trailing arbutus	EPIG REP
	<i>Gaultheria hispida</i> (L.) Muhl.	Creeping snowberry	GAUL HIS
	<i>Ledum groenlandicum</i> Oeder.	Labrador tea	LEDU GRO
	<i>Lonicera</i> spp.	Honeysuckle spp.	LONI SP
	<i>Potentilla fruticosa</i> L.	Shrubby cinquefoil	POTE FRU
	<i>Prunus pennsylvanica</i> L.f.	Pincherry	PRUN PEN
	<i>Prunus virginiana</i> L.	Choke cherry	PRUN VIR
	<i>Rhamnus alnifolia</i> L'H r.	Buckthorn	RHAM ALN
	<i>Ribes</i> spp.	Current/Gooseberry sp	RIBE SP
	<i>Ribes glandulosum</i> Grauer.	Skunk current	RIBE GLA
	<i>Ribes hirtellum</i> Michx.	Smooth gooseberry	RIBE HIR
	<i>Rosa acicularis</i> Lindl.	Prickly rose	ROSA ACI
	<i>Rosa blanda</i> Ait.	Meadow/Pasture rose	ROSA BLA
	<i>Rubus pubescens</i> Raf.	Red raspberry	RUBU PUB
	<i>Rubus strigosus</i> Michx.	Dwarf raspberry	RUBU STR
	<i>Salix</i> spp.	Willow spp.	SALI SP
	<i>Sambucus pubens</i> Michx.	Red-berried elder	SAMB PUB
	<i>Sorbus</i> spp.	Mountain-ash spp.	SORB SP
	<i>Vaccinium angustifolium</i> Ait.	Lowbush blueberry	VACC ANG
	<i>Vaccinium myrtilloides</i> Michx.	Velvet-leaved blueberry	VACC MYR
	<i>Viburnum edule</i> (Michx.) Raf.	Squashberry	VIBU EDU

Herbaceous flowering plants

<i>Achillea millefolium</i> L.	Yarrow	ACHI MIL
<i>Anaphalis margaritacea</i> (L.) Benth. & Hook.	Pearly everlasting	ANAP MAR
<i>Anemone quinquefolia</i> L.	Wood anemone	ANEM QUI
<i>Aster</i> spp.	Aster spp.	ASTE SP
<i>Aster macrophyllus</i> L.	Large-leaved aster	ASTE MAC
<i>Calamagrostis canadensis</i> (Michx.) Beauv.	Canada bluejoint	CALA CAN
<i>Caltha palustris</i> L.	Marsh marigold	CALT PAL
<i>Clintonia borealis</i> (Ait.) Raf.	Bluebead lily	CLIN BOR
<i>Coptis trifolia</i> (L.) Salisb.	Goldthread	COPT TRI
<i>Epilobium angustifolium</i> L.	Fireweed	EPIL ANG
<i>Fragaria vesca</i> L.	Woodland strawberry	FRAG VES
<i>Fragaria virginiana</i> Duchesne.	Wild strawberry	FRAG VIR
<i>Galium triflorum</i> Michx.	Fragrant bedstraw	GALI TRI
Graminoid	Grass spp.	GRAM SP*
<i>Linnaea borealis</i> L.	Twinflower	LINN BOR
<i>Maianthemum canadense</i> Desf.	Canada mayflower	MAIA CAN
<i>Mertensia paniculata</i> (Ait.) G. Don.	Bluebell/Lungwort	MERT PAN
<i>Mitella nuda</i> L.	Naked mitrewort	MITE NUD
<i>Petasites frigidus</i> (L.) Fries.	Sweet coltsfoot	PETA FRI
<i>Sanicula marilandica</i> L.	Black snakeroot	SANI MAR
<i>Smilacina trifolia</i> (L.) Desf.	Three-leaved false solomon's-seal	SMIL TRI
<i>Solidago canadensis</i> L.	Canada goldenrod	SOLI CAN
<i>Streptopus roseus</i> Michx.	Rose twisted-stalk	STRE ROS
<i>Taraxacum</i> spp.	Dandelion spp.	TARA SP
<i>Trientalis borealis</i> Raf.	Starflower	TRIE BOR
<i>Viola</i> spp.	Violet spp.	VIOL SP
<i>Waldsteinia fragarioides</i> (Michx.) Tratt.	Barren strawberry	WALD FRA

Ferns and fern allies

<i>Athyrium filix-femina</i> (L.) Roth.	Lady fern	ATHY FIL
<i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs**	Spinulose wood fern	DRYO CAR
<i>Equisetum</i> spp.	Horsetail spp.	EQUI SP
<i>Gymnocarpium dryopteris</i> (L.) Newm.	Oak fern	GYMN DRY
<i>Lycopodium</i> spp.	Clubmoss spp.	LYCO SP
<i>Osmunda claytoniana</i> L.	Interrupted fern	OSMU CLA
<i>Pteridium aquilinum</i> (L.) Kuhn.	Bracken fern	PTER AQU

Bryophytes

amphibious moss		AMPH MOS*
feather moss		FEAT MOS*
<i>Marchantia</i> spp.	Aquatic liverwort	MARC SP
<i>Polytrichum</i> spp.	Hair-cap moss spp.	POLY SP
<i>Sphagnum</i> spp.	Peat moss spp.	SPHA SP

Lichens

<i>Cladonia</i> spp.	Bushy lichen spp.	CLAD SP
lichen spp.	Lichen spp.	LICH SP*

* Used in percent cover vegetation calculations only.

** Nomenclature according to Cody and Britton (1989).

Appendix A(2). Calculation of the density of tree species in multiple size classes.

Density was calculated only for vegetation classes overall and by species. Therefore, further division into separate categories, such as diameter, required a proportion calculation. For example, the density of large trees was estimated for all tree species together and for individual species using the point distance nearest neighbor program. The occurrence by diameter class could only be known proportionally, so estimated size class densities required the following calculation:

$$d2 = d1 * (n2/n1)$$

where: d2 is the estimated density of stems in any size class per plot (in stems/hectare);

d1 is the calculated density of all stems in a plot (in stems/hectare);

n2 is the number of stems in the size class per plot; and

n1 is the total number of stems in the plot.

For example, the density of balsam fir between 10 and 15 cm DBH would be calculated as follows:

If the density of all balsam fir in a plot = 100 stems/hectare and ten of the 80 stems sampled in the plot are between 10 and 15 cm DBH, it follows that the density of balsam fir stems between 10 and 15 cm DBH is:

$$\begin{aligned} & 100 \times (10/80) \\ & = 13 \text{ stems/hectare.} \end{aligned}$$

Appendix B(1). Density of 17 size classes of small and large trees in all stands. Bars correspond to total density for each size class.

Figure B(1).1. 0-year-old stands.

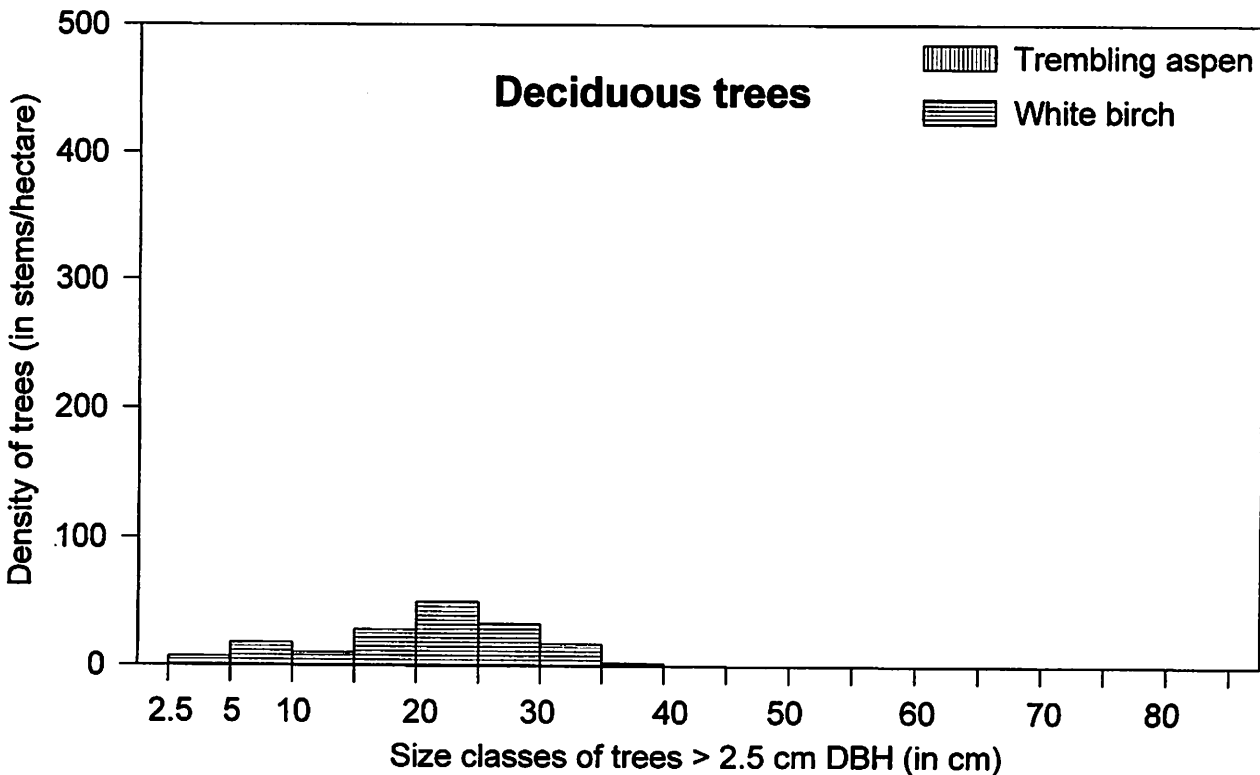
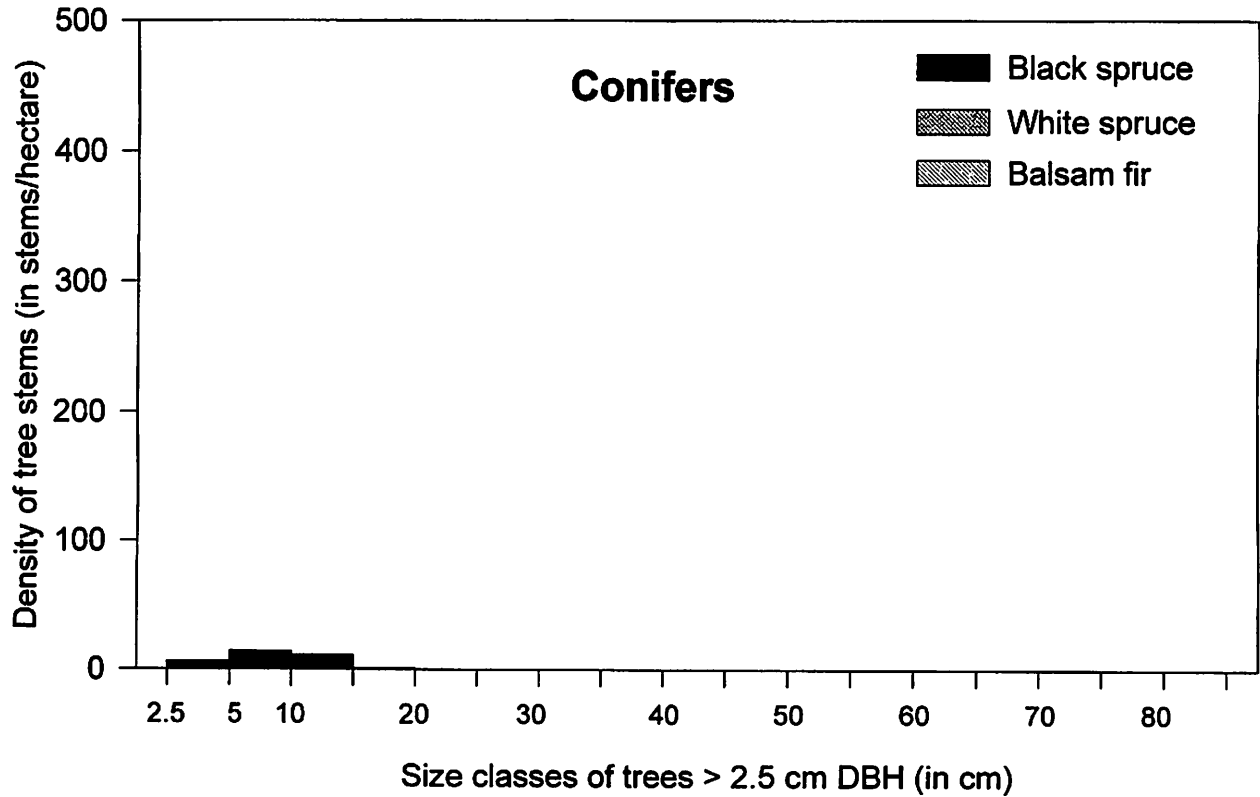


Figure B(1).2. 3-year-old stand.

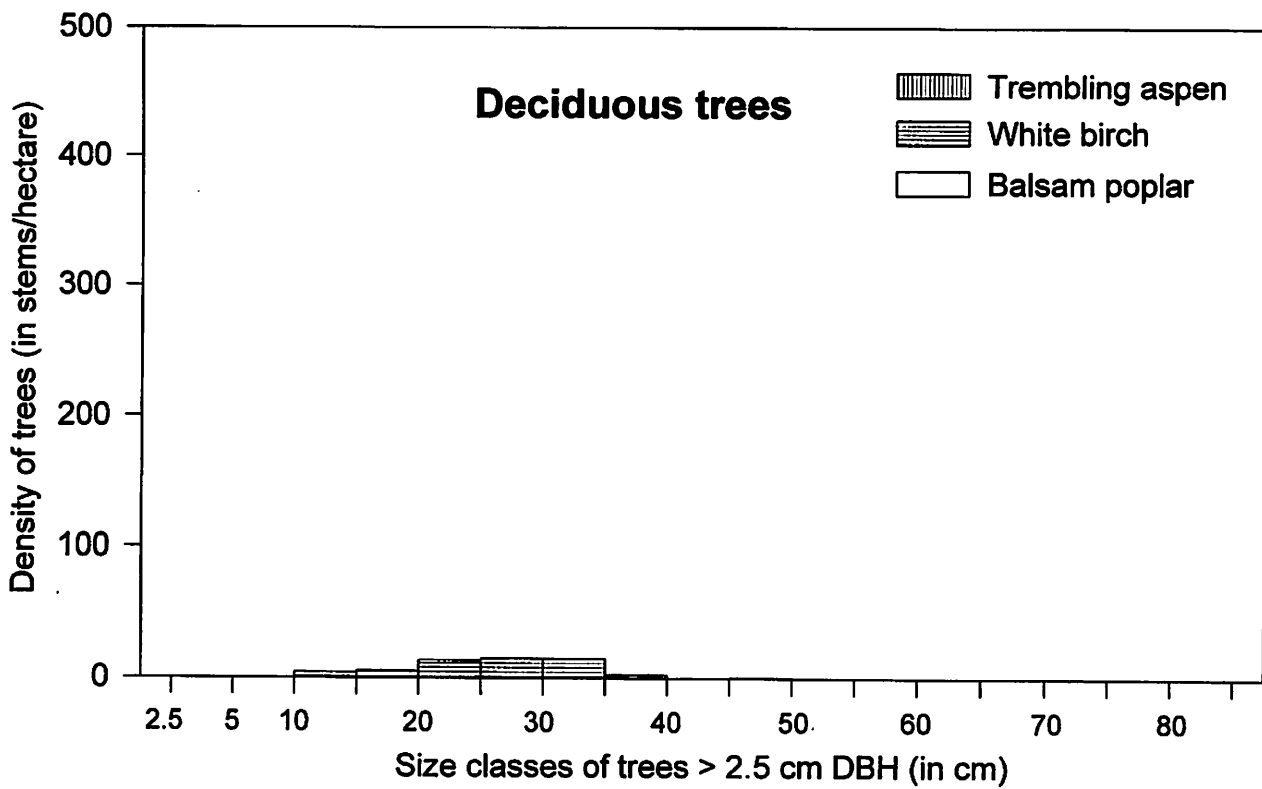
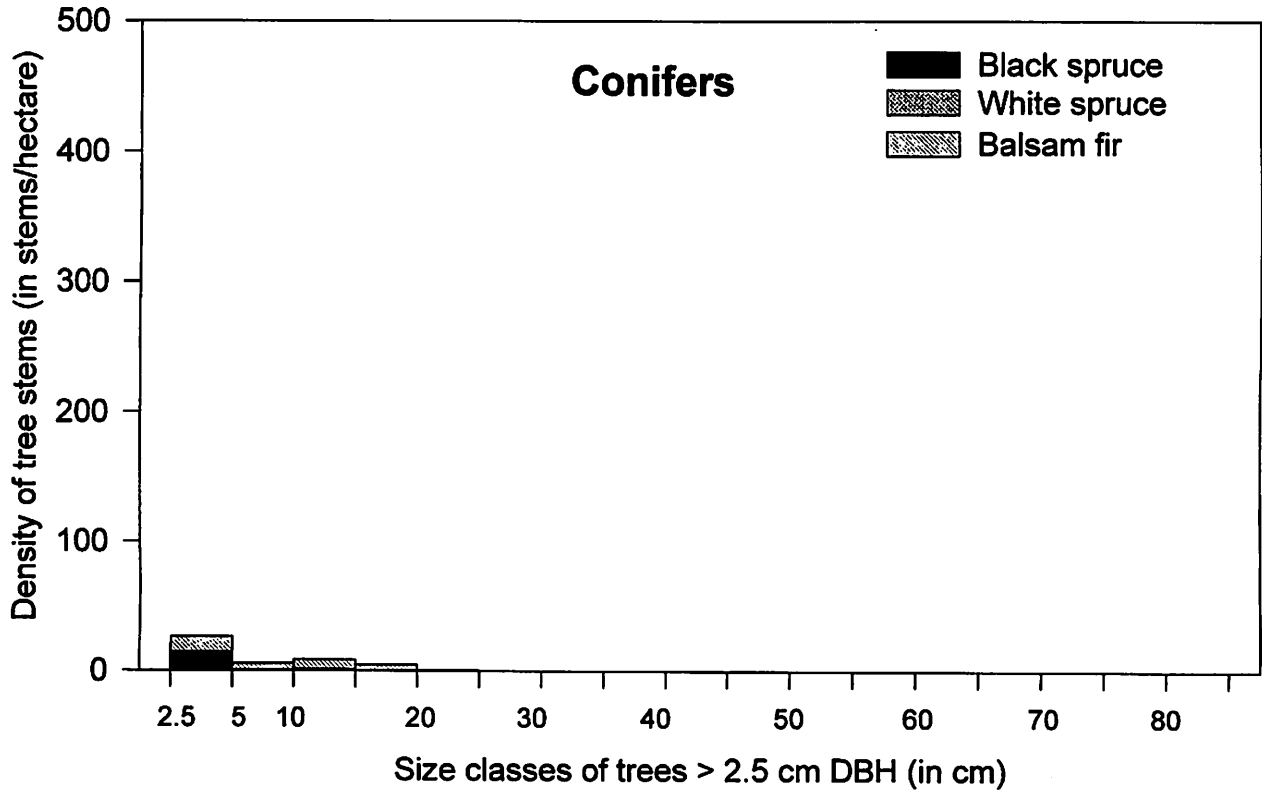


Figure B(1).3. 5-year-old stand (5-1).

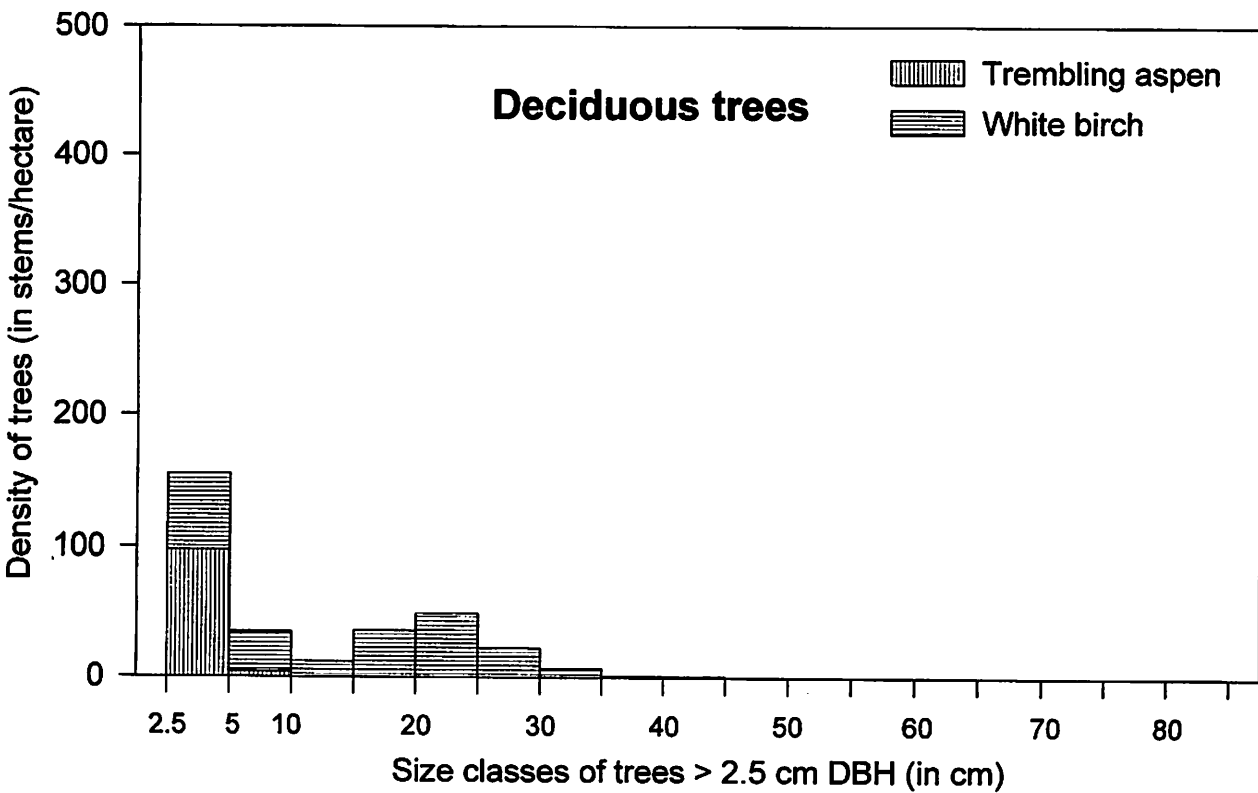
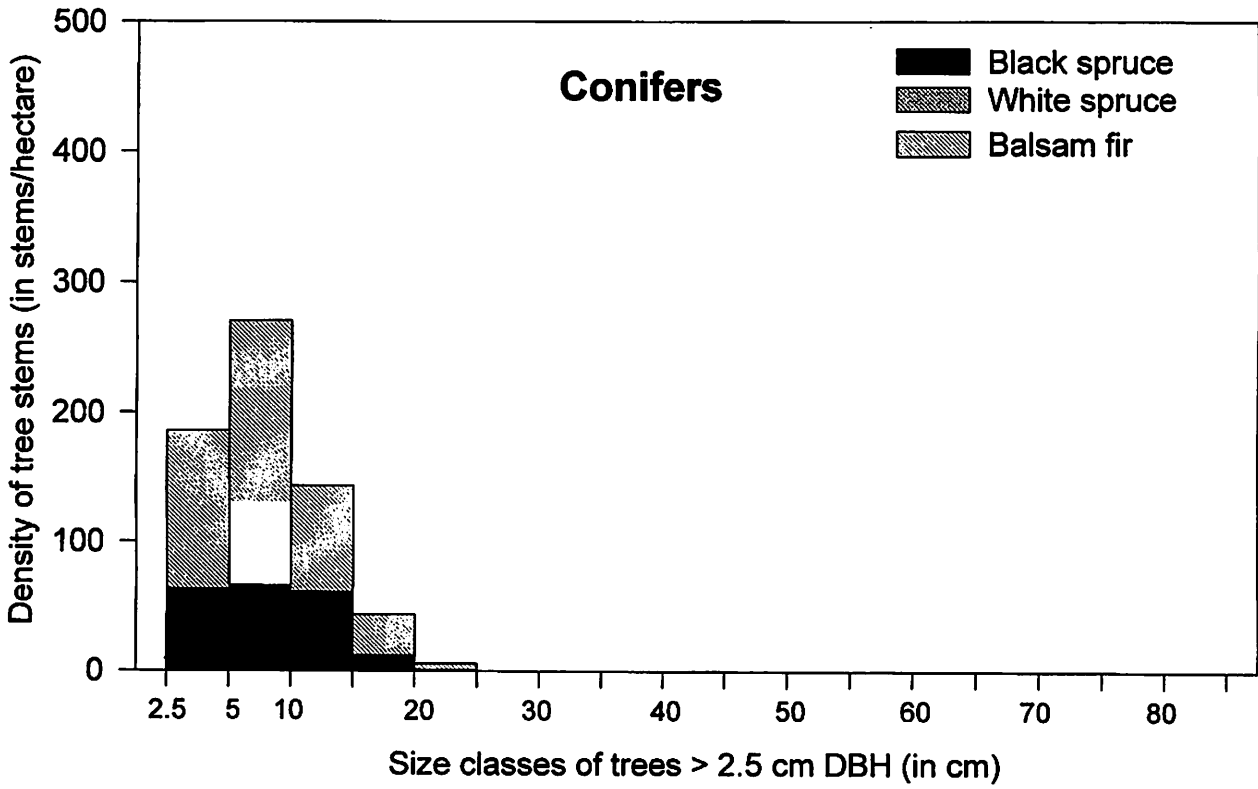


Figure B(1).4. 5-year-old stand (5-2).

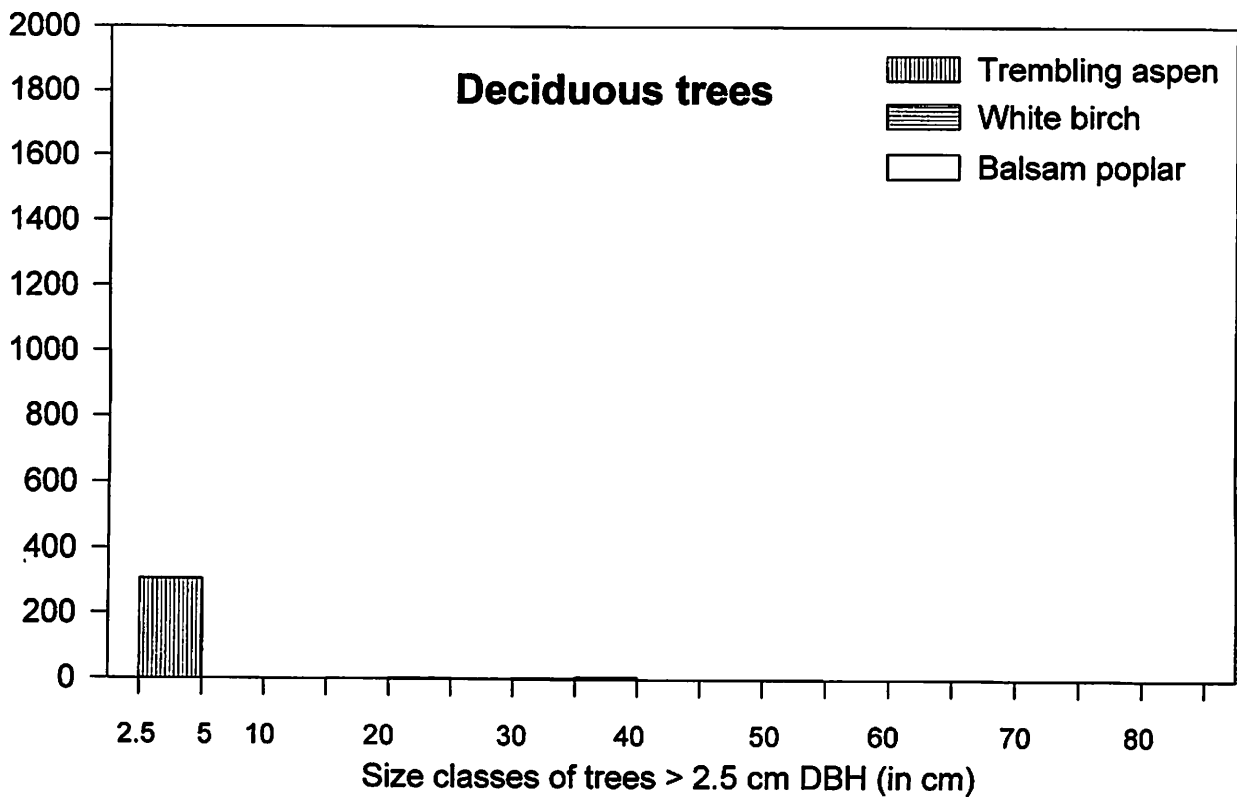
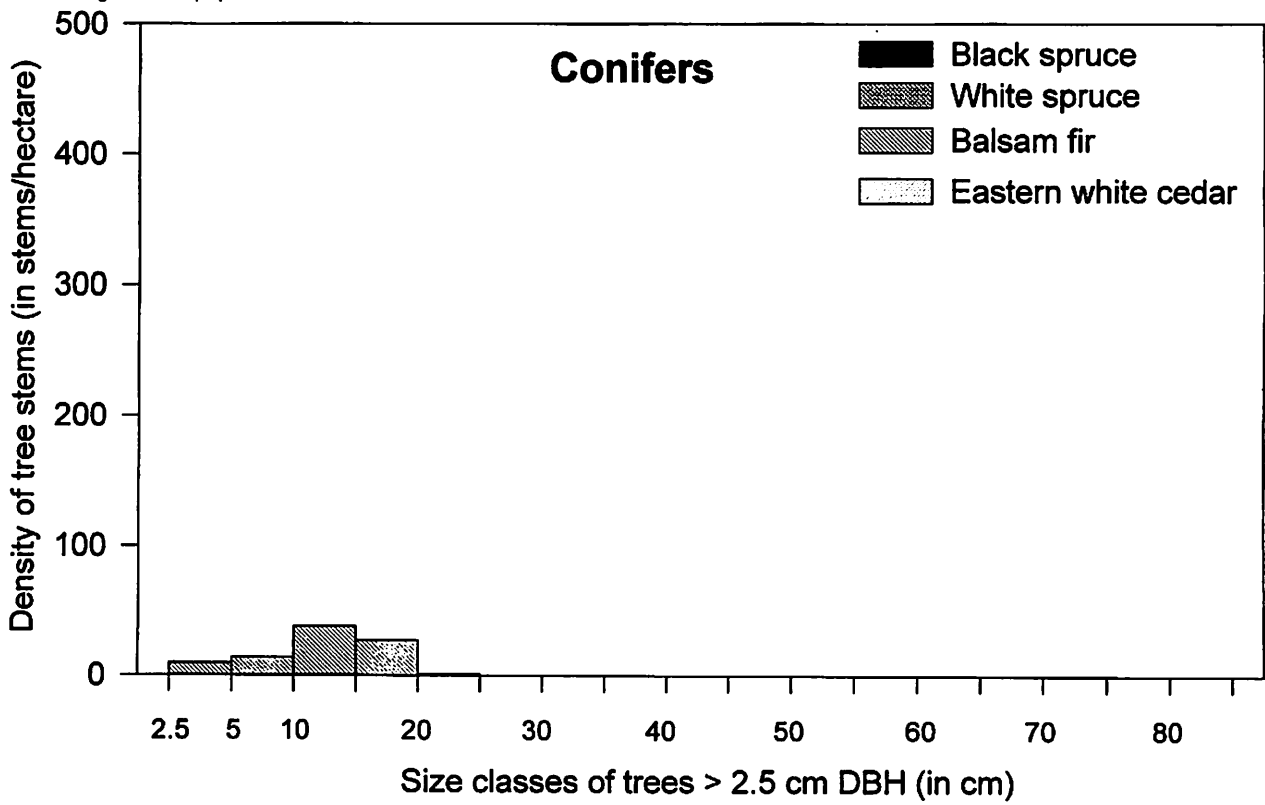


Figure B(1).5. 8-year-old stand.

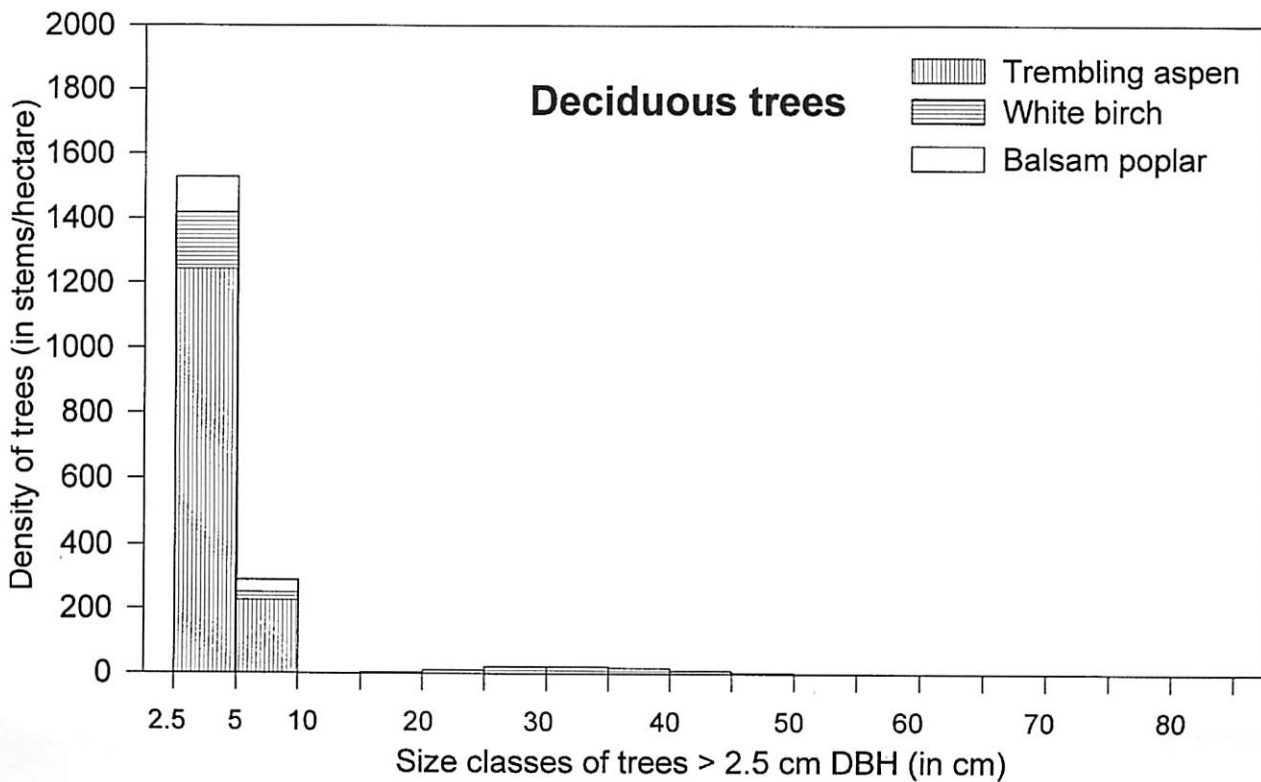
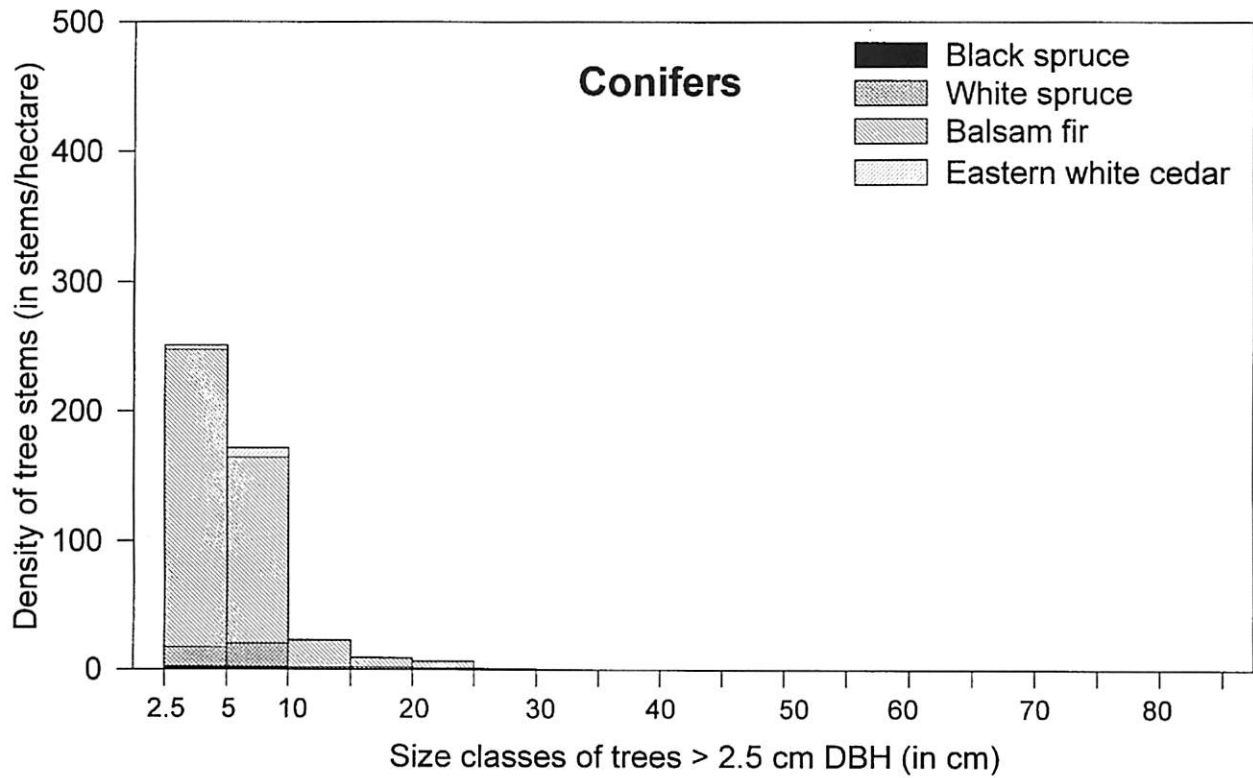


Figure B(1).6. 12-year-old stand.

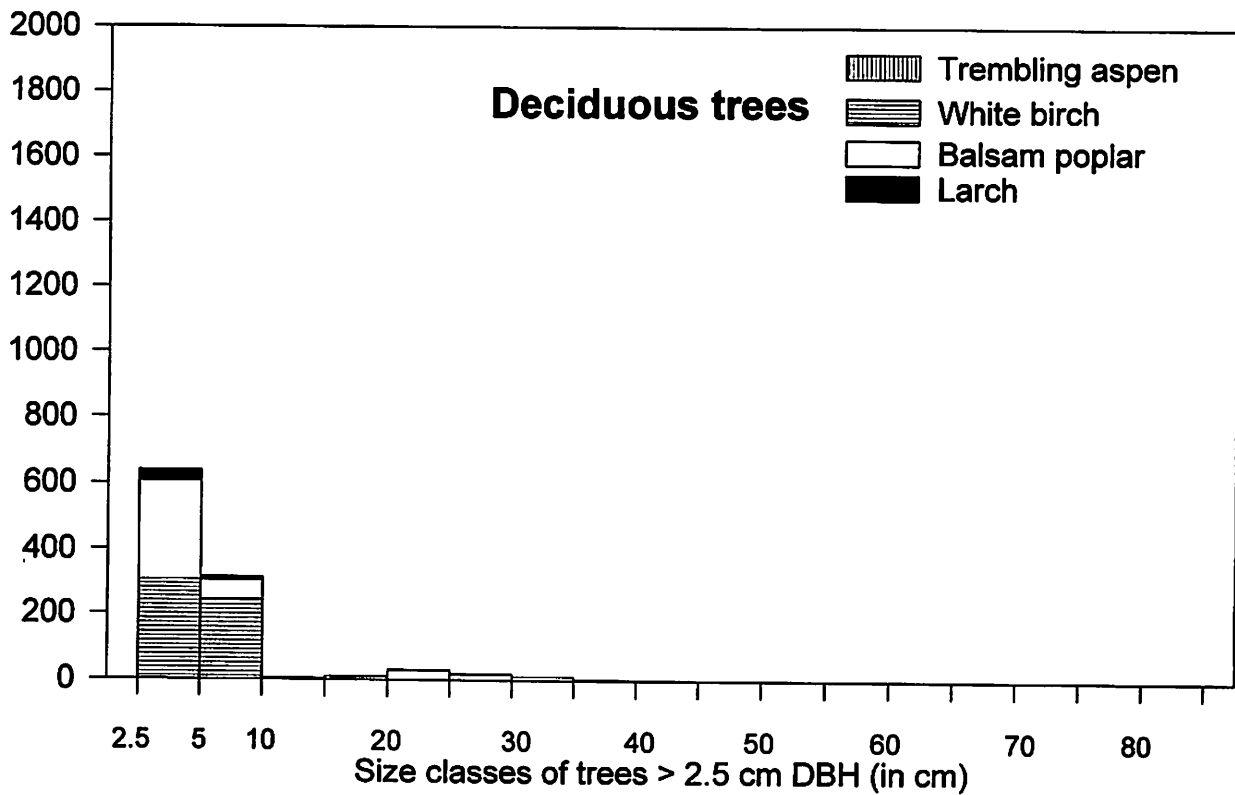
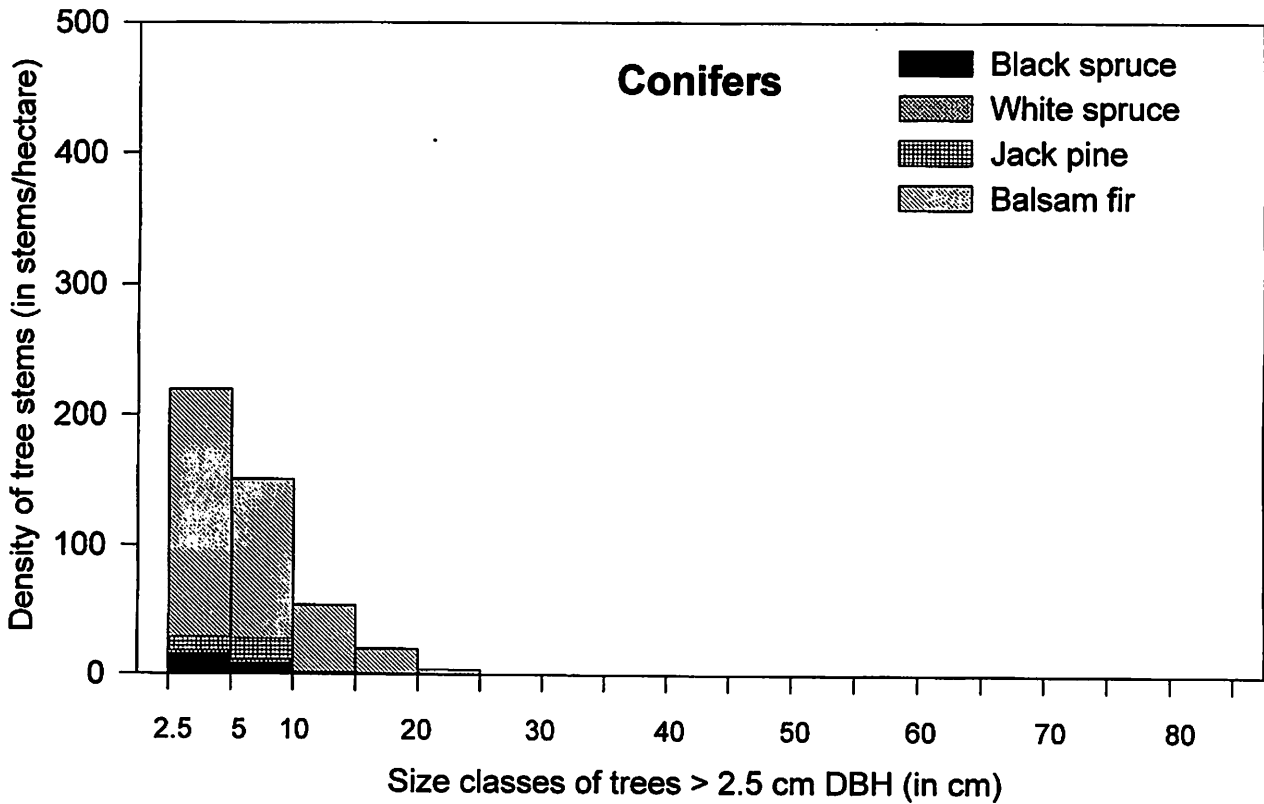


Figure B(1).7. 13-year-old stand.

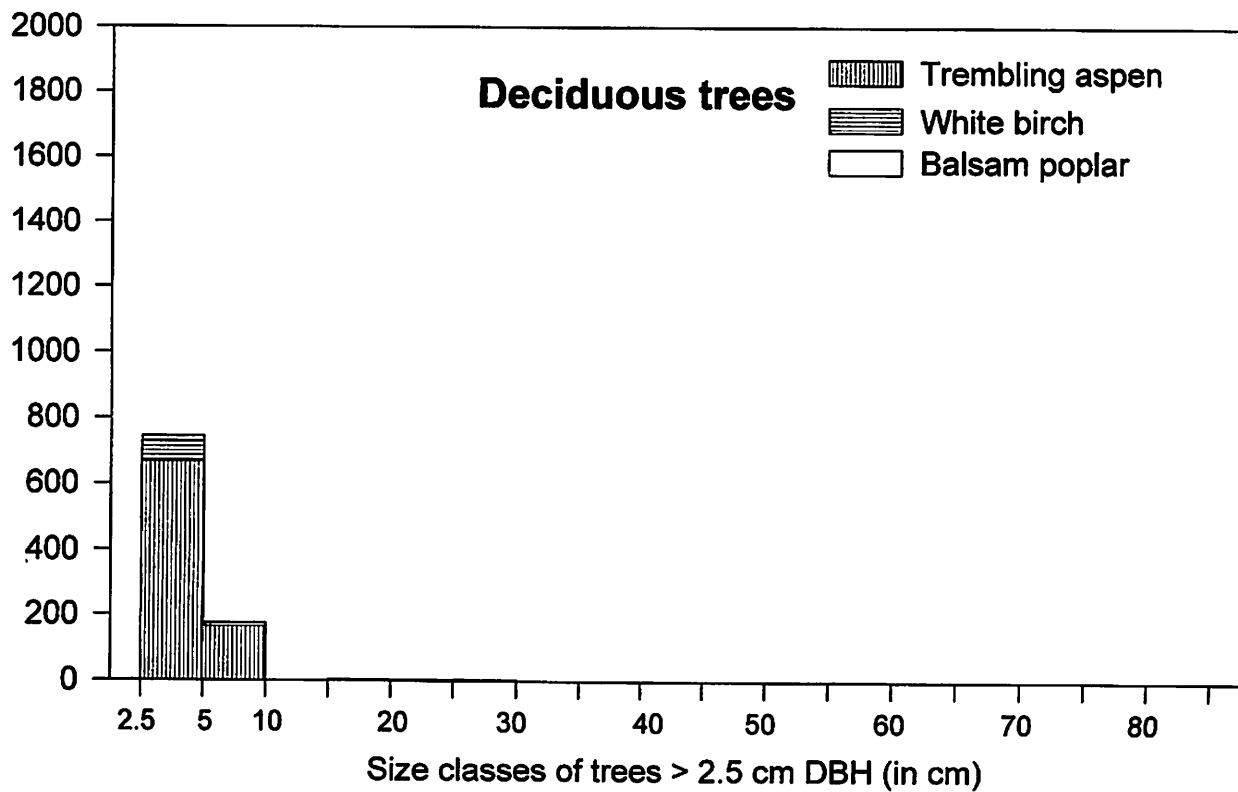
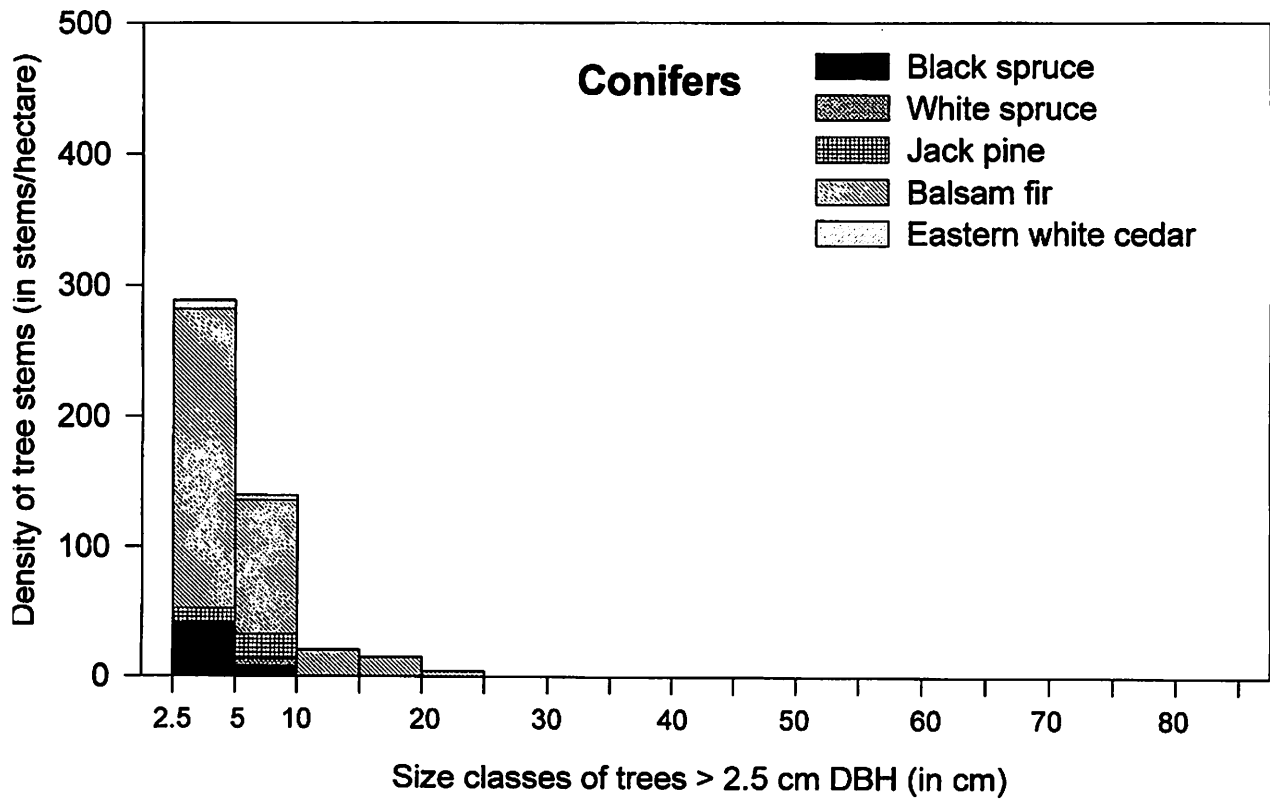


Figure B(1).8. 18-year-old stand.

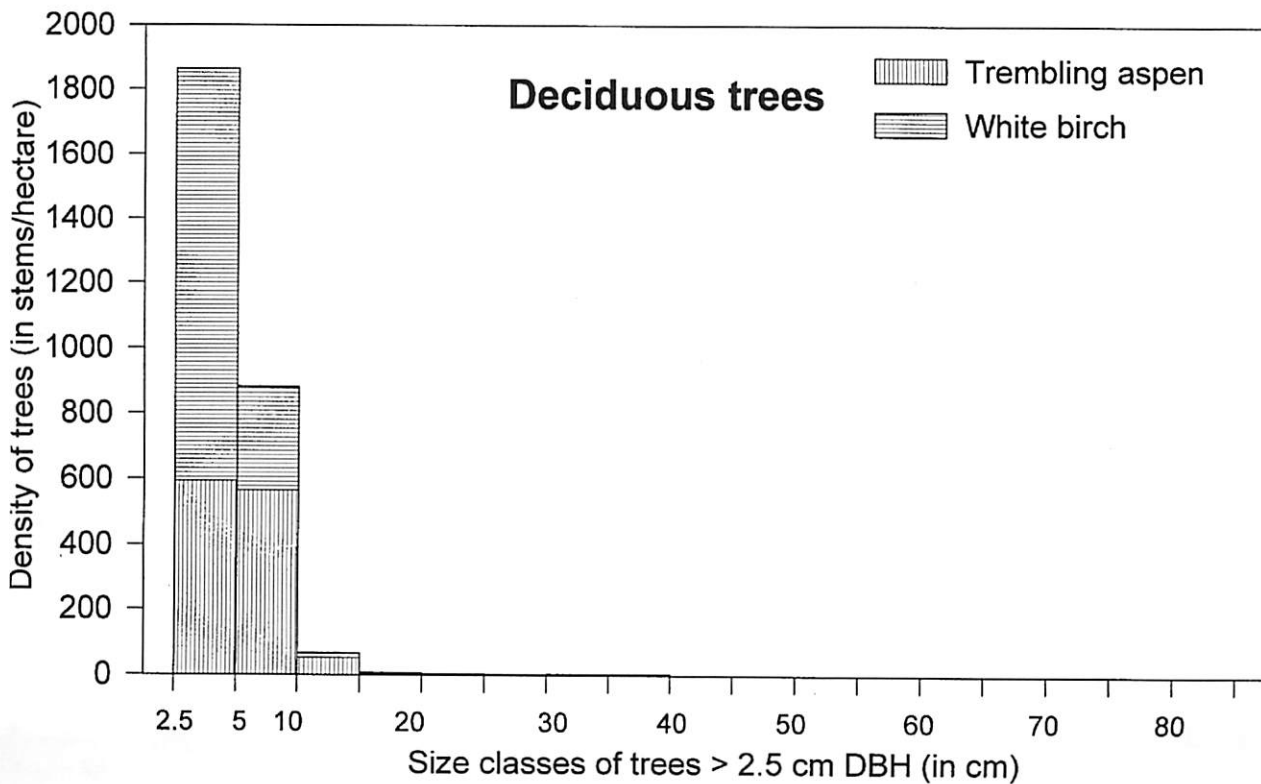
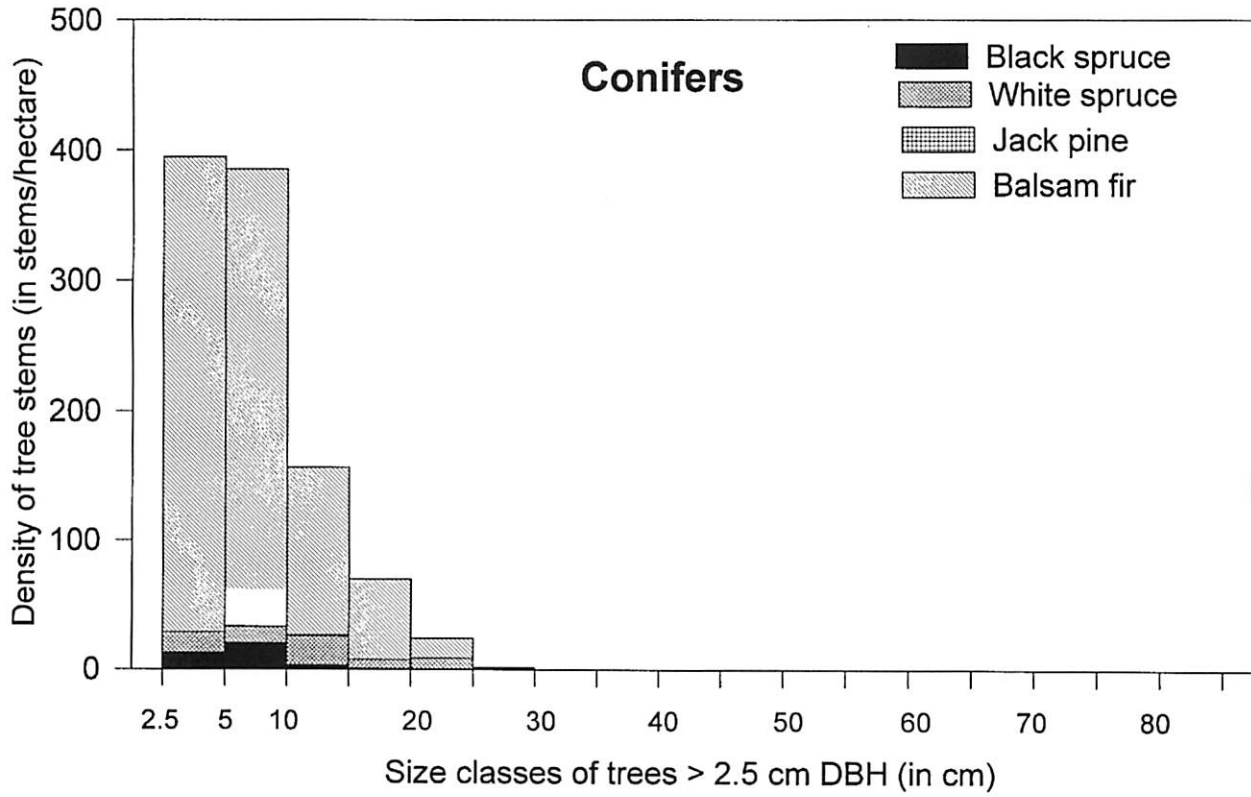


Figure B(1).9. 20-year-old stand.

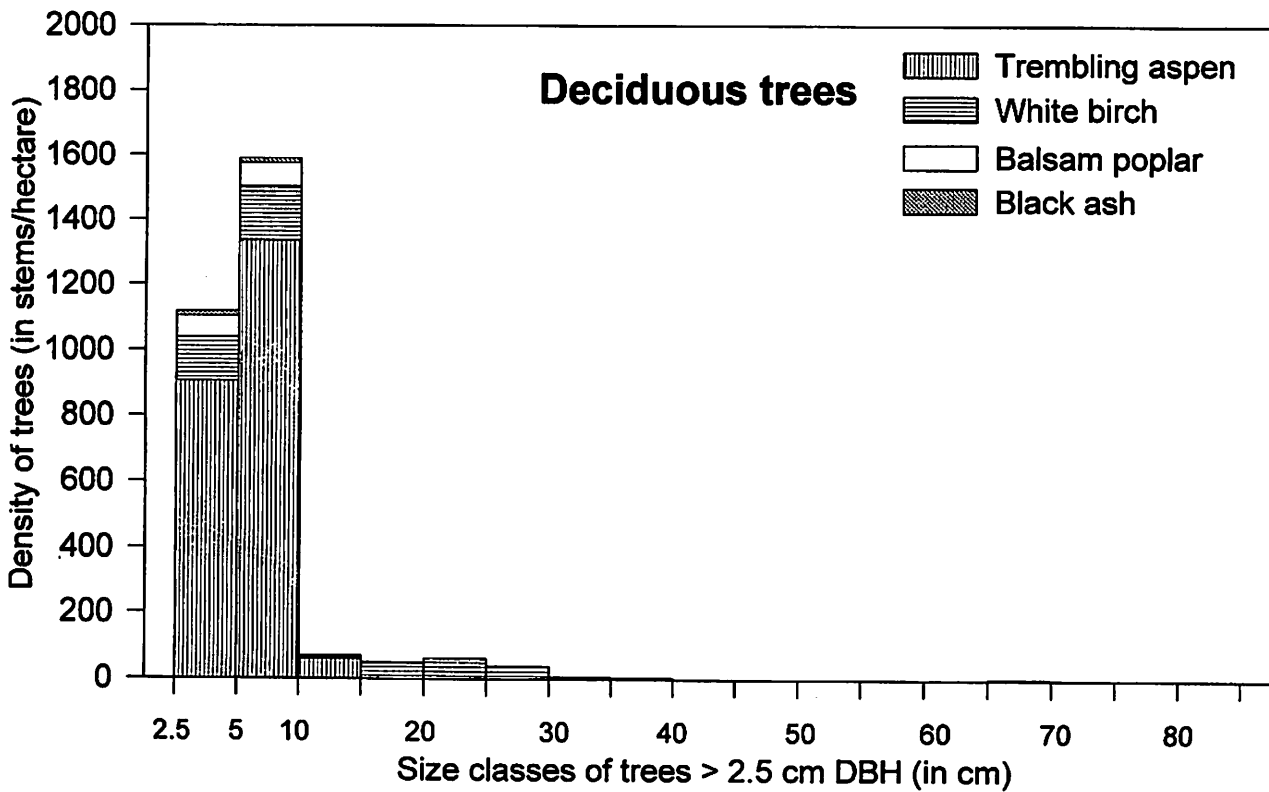
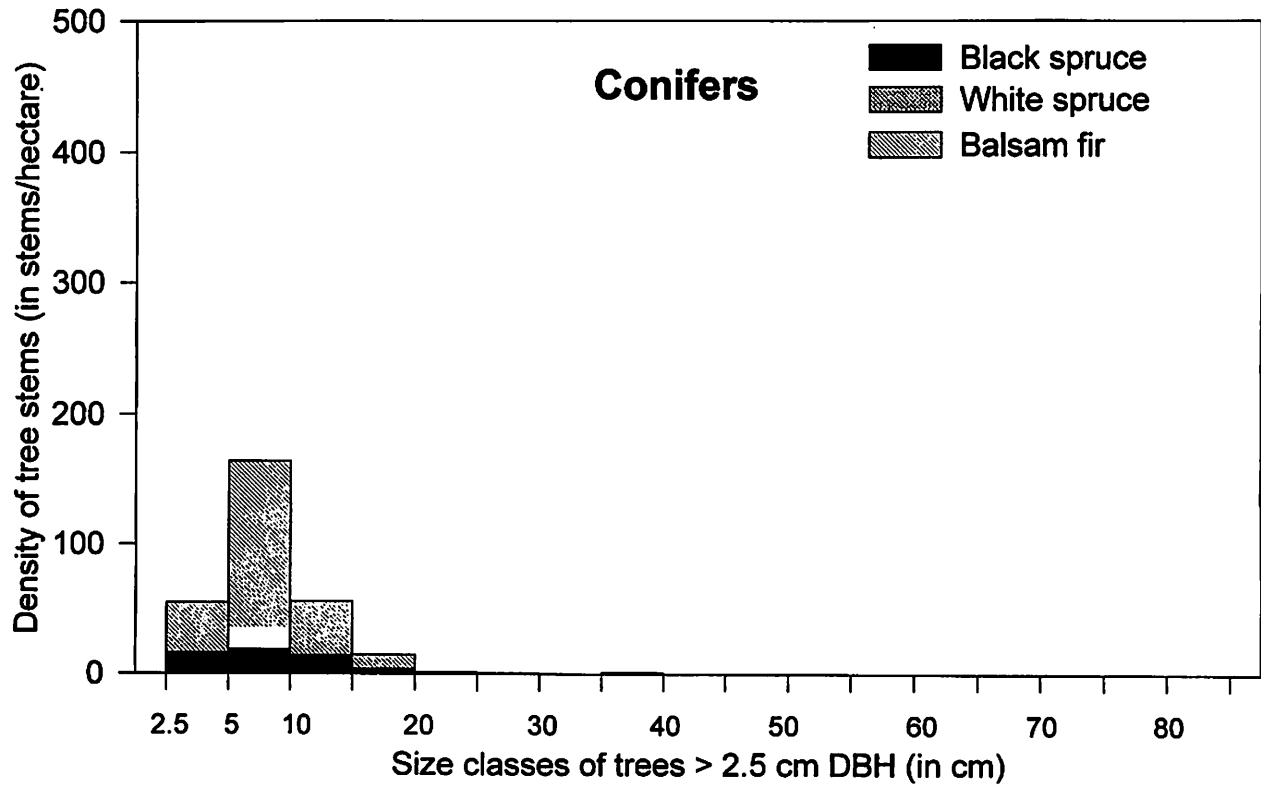


Figure B(1).10. 23-year-old stand.

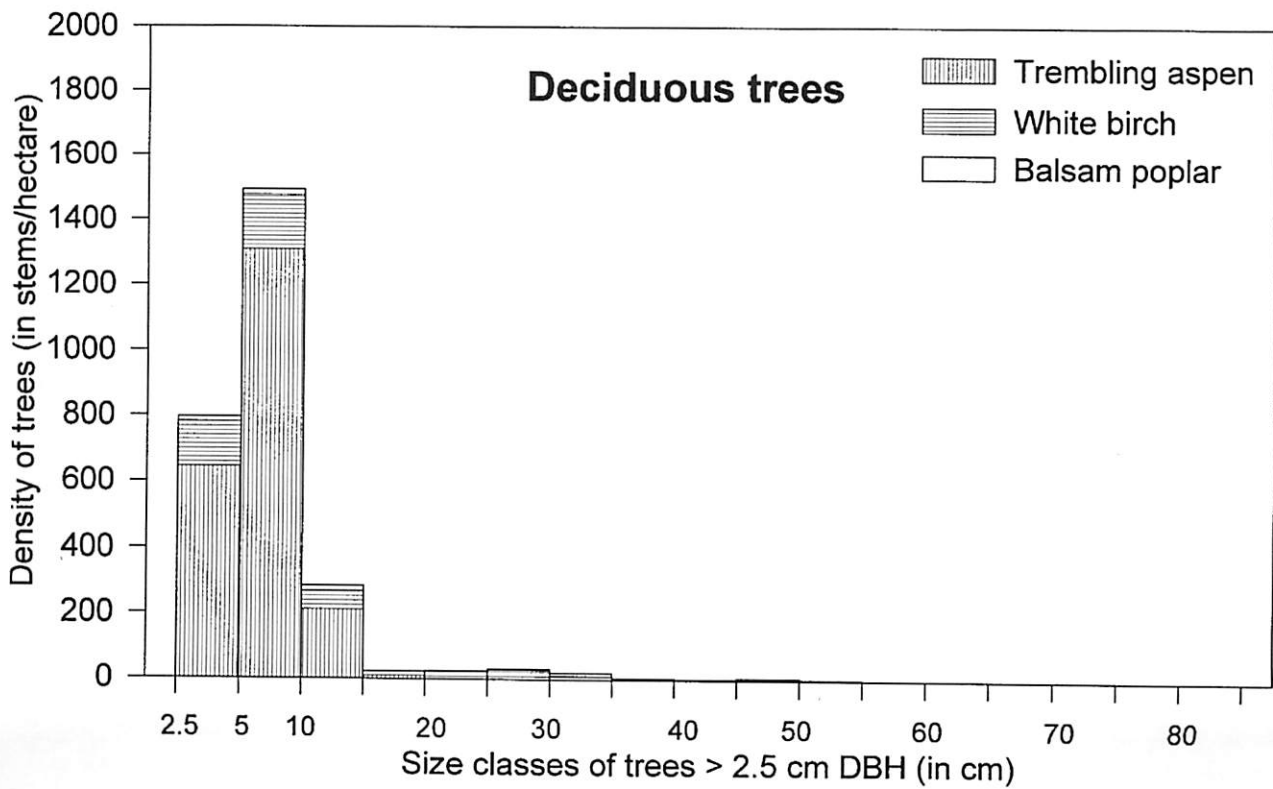
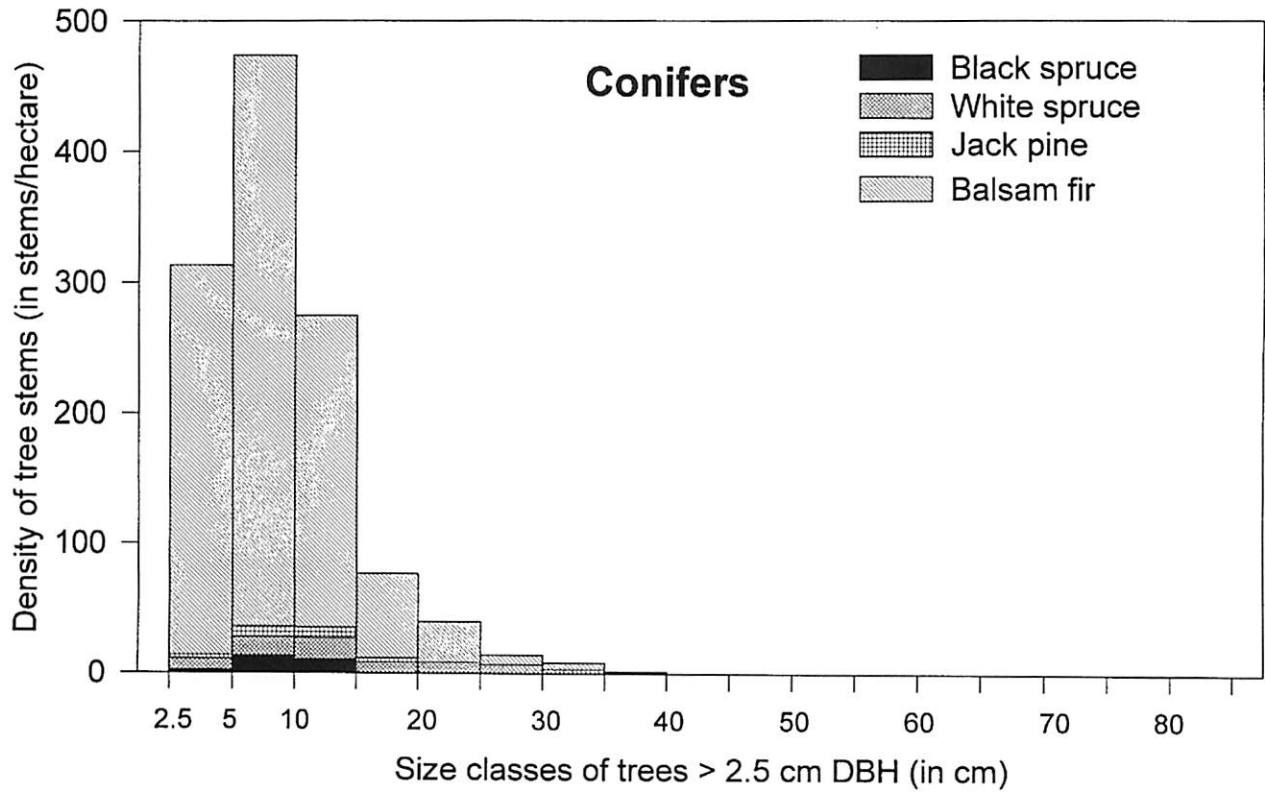


Figure B(1).11. 26-year-old stand.

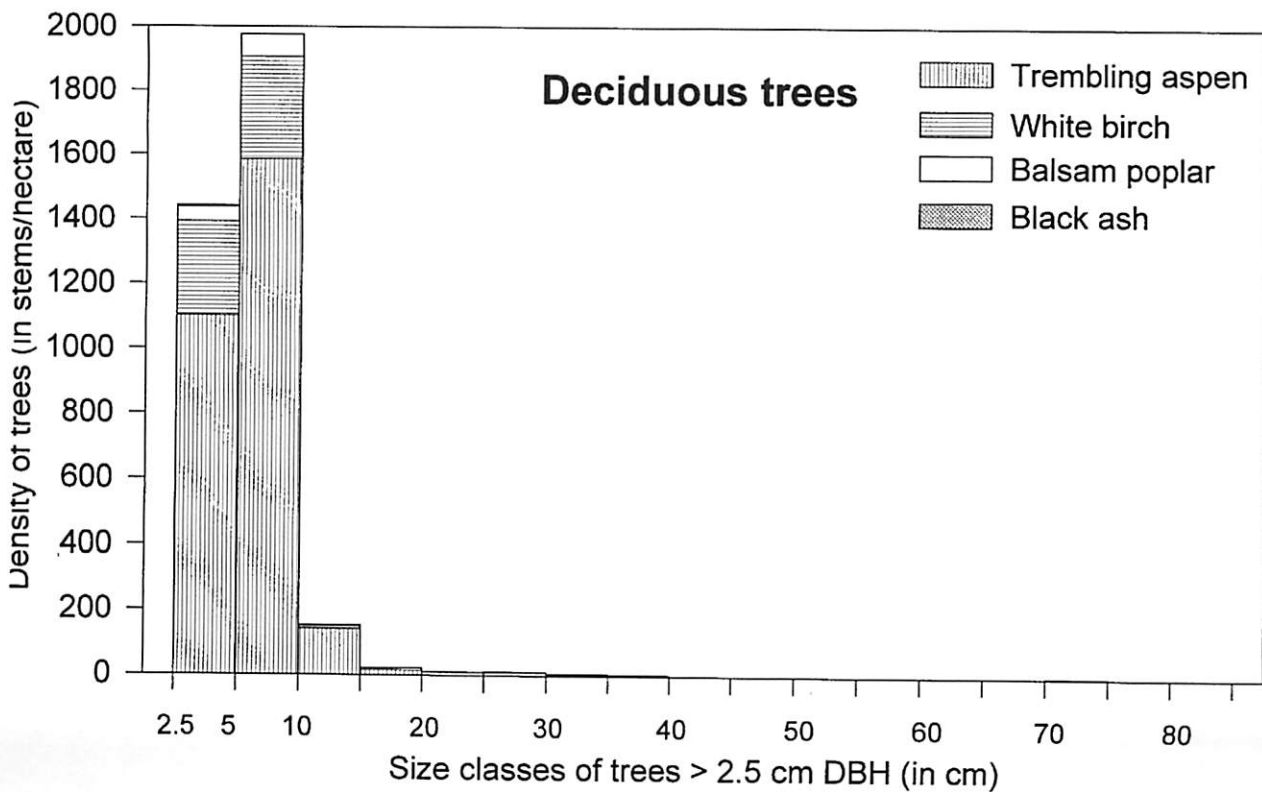
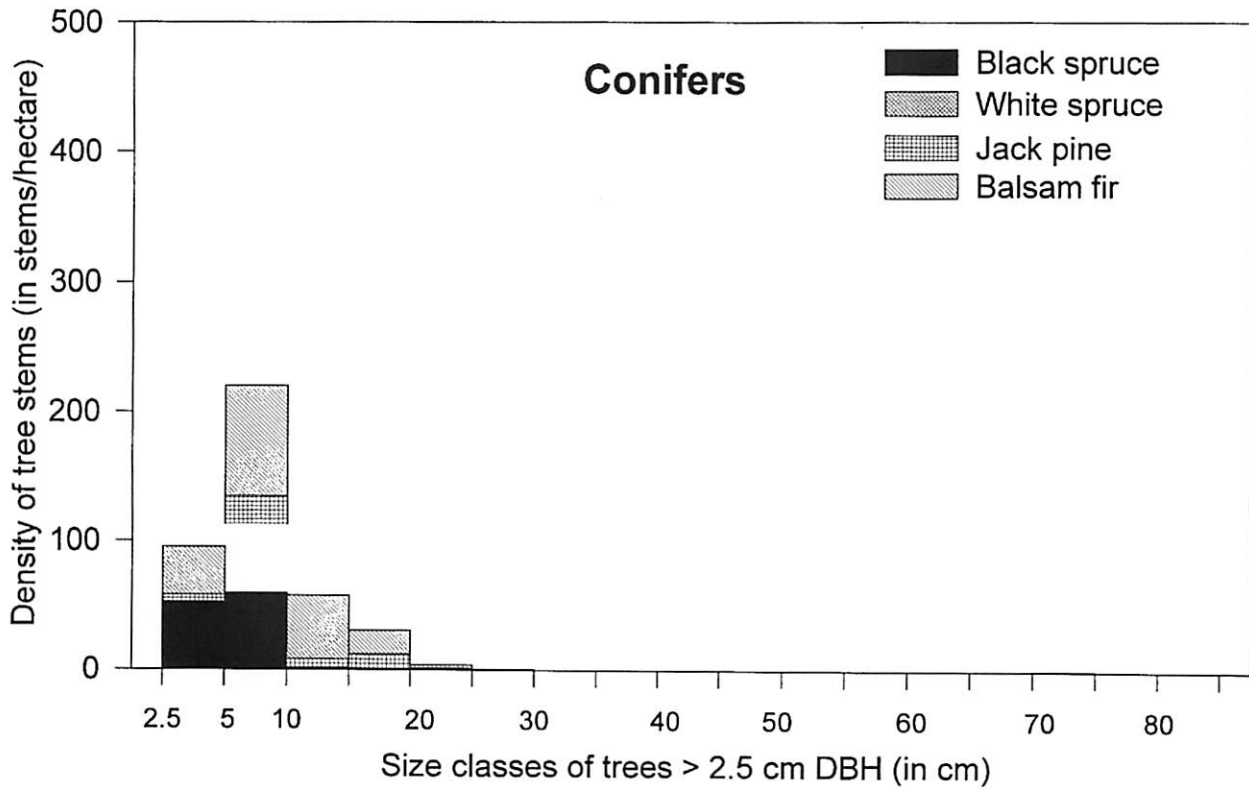


Figure B(1).12. 33-year-old stand.

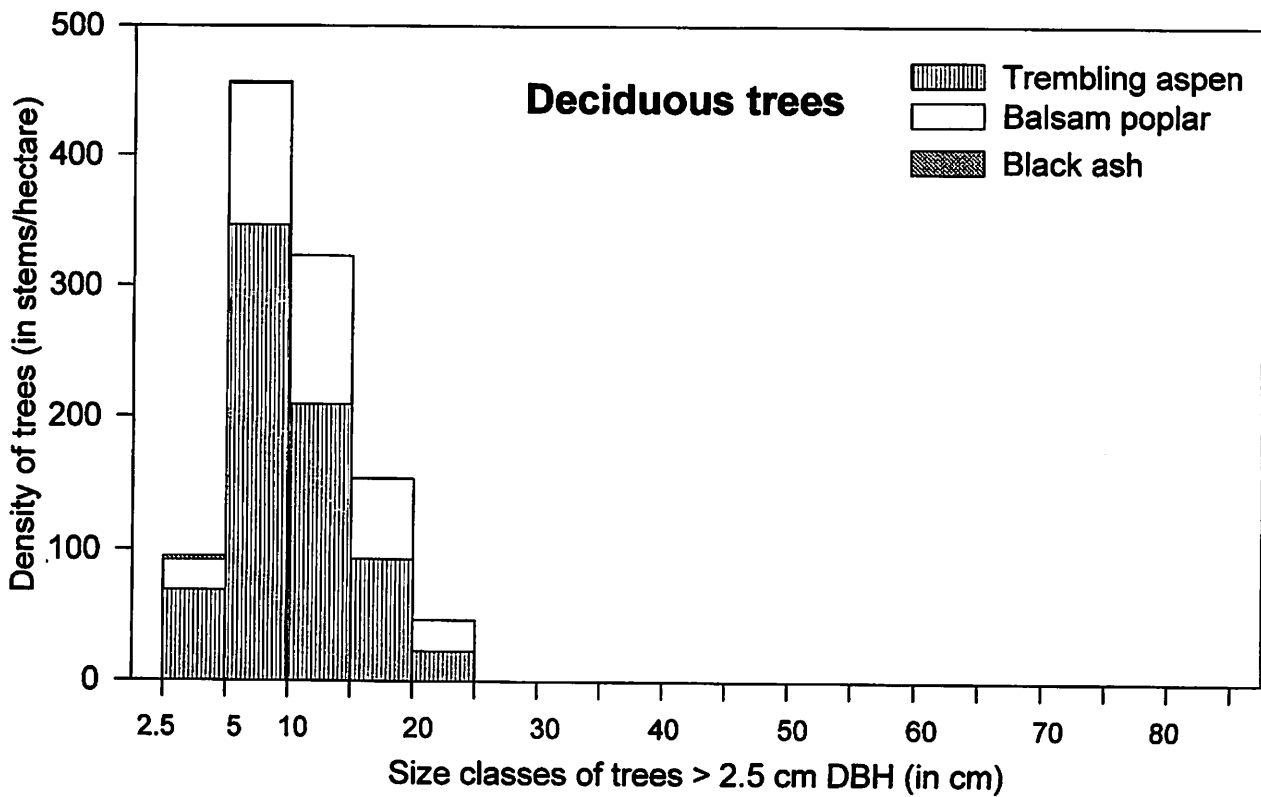
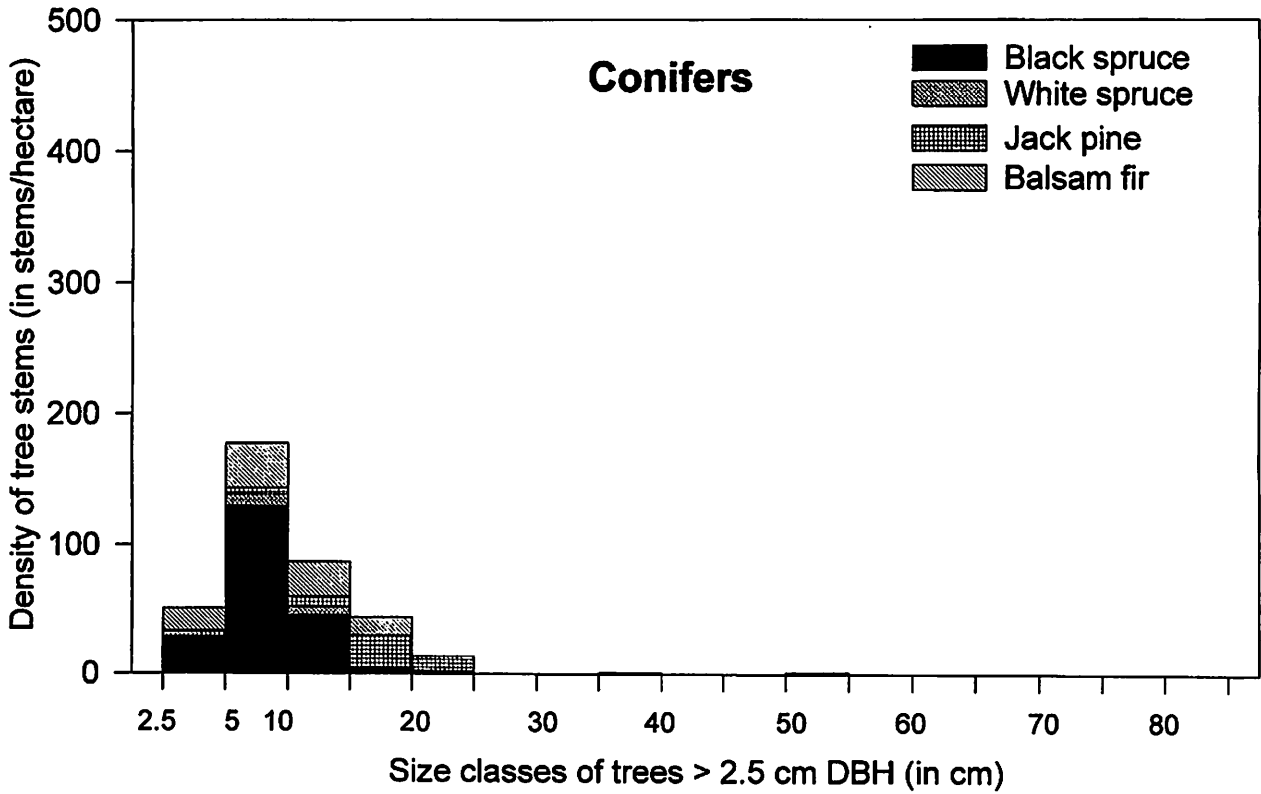


Figure B(1).13. 56-year-old stand.

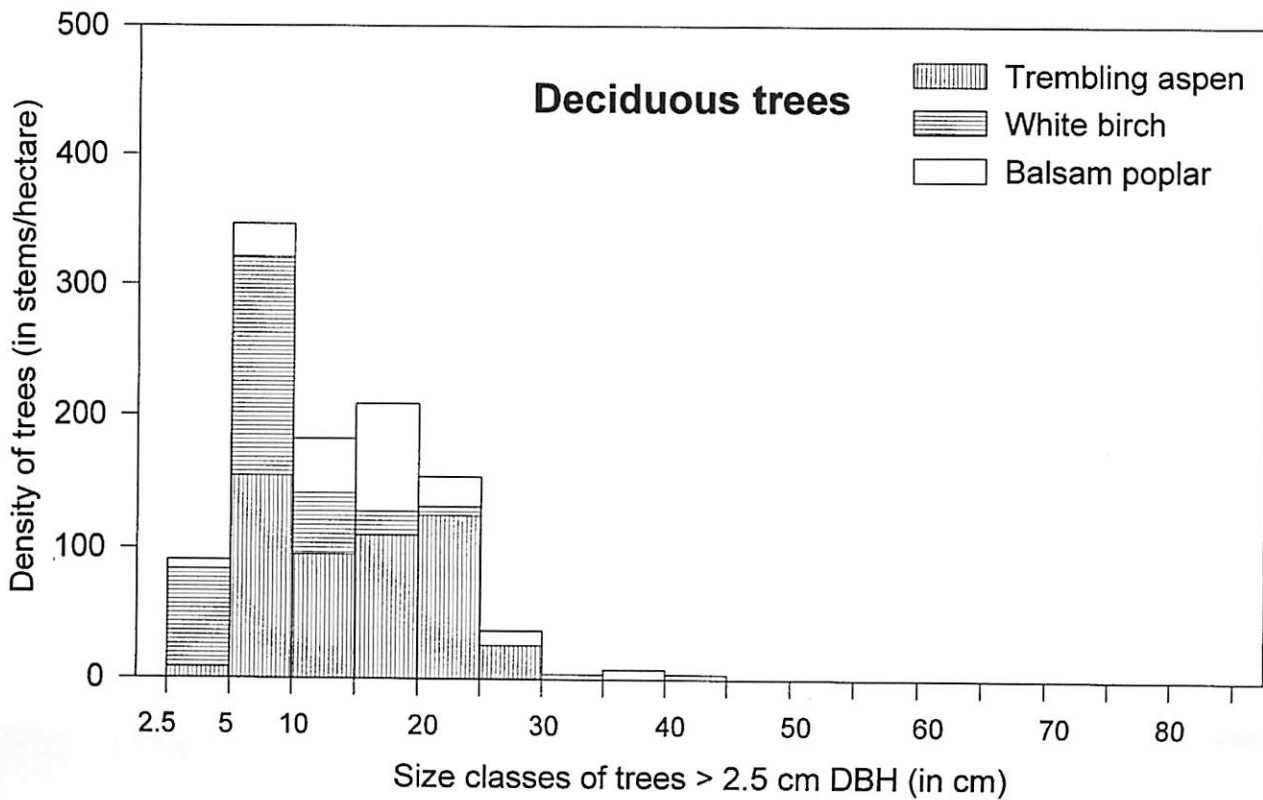
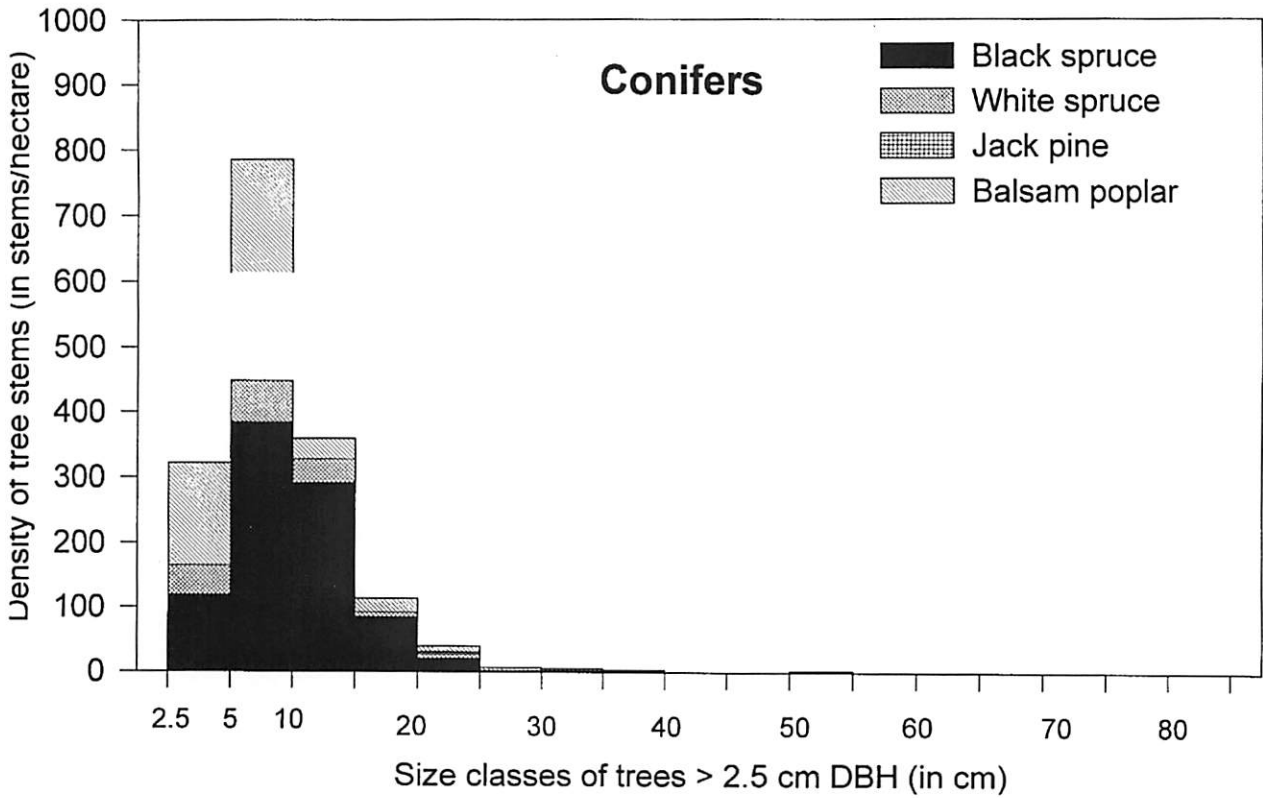


Figure B(1).14. 109-year-old stand.

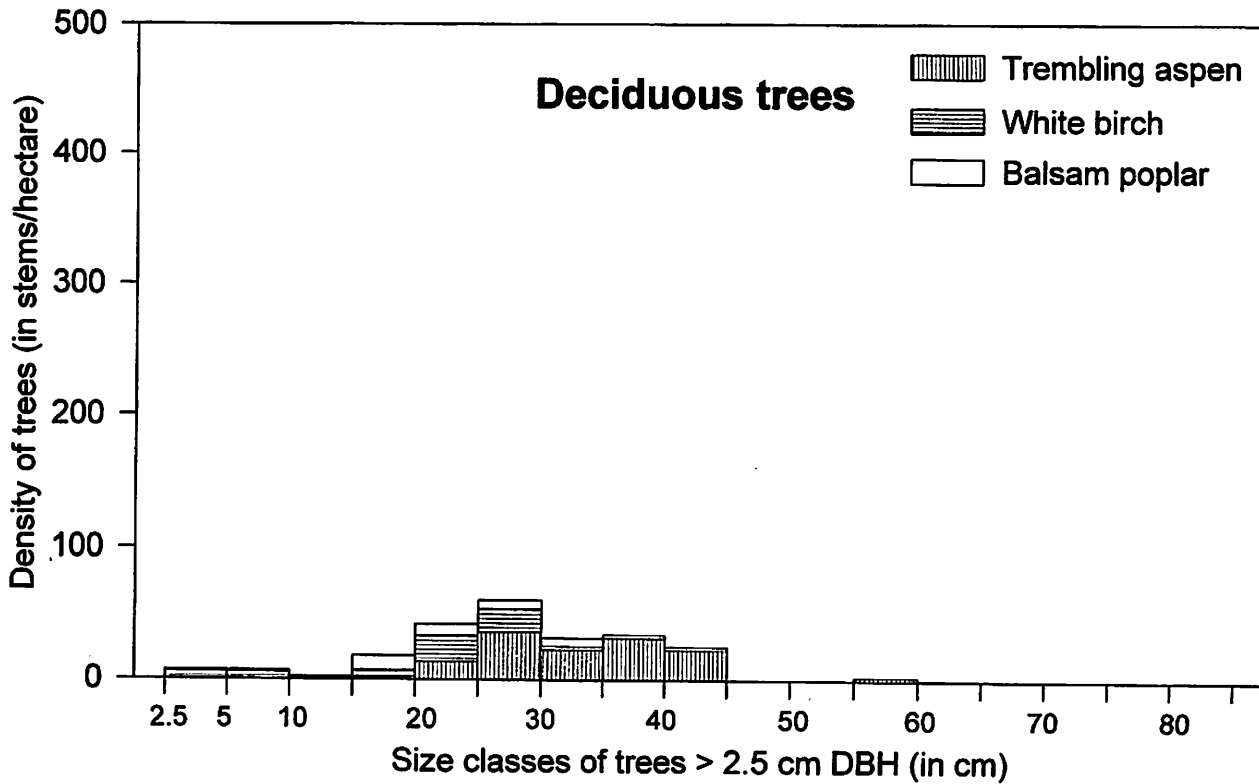
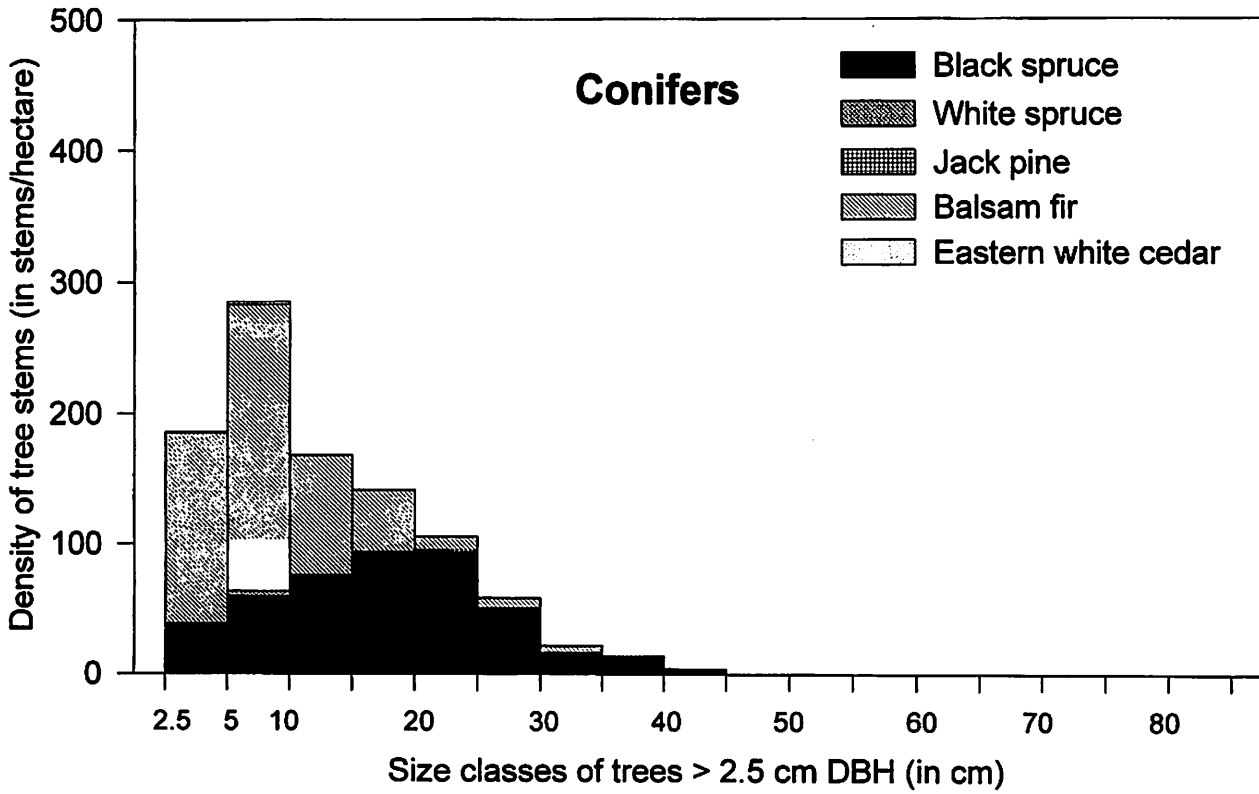


Figure B(1).15. 110-year-old stand.

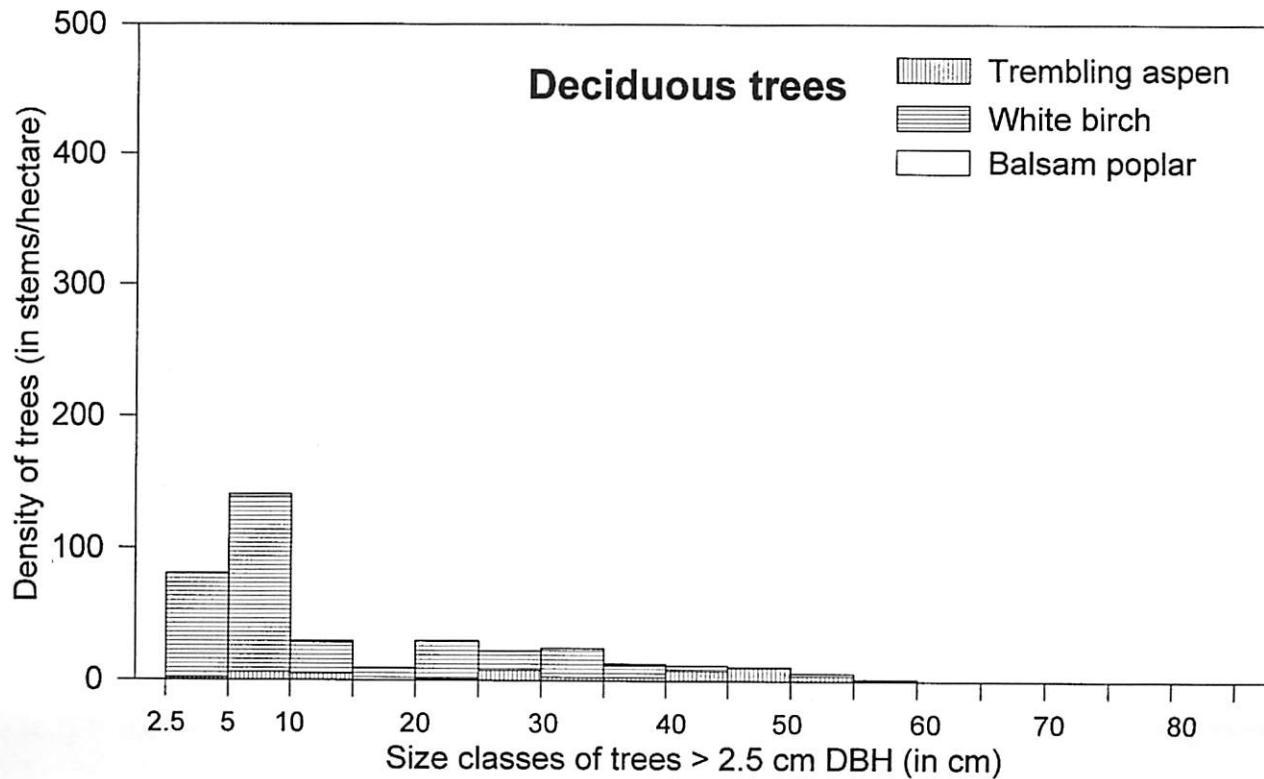
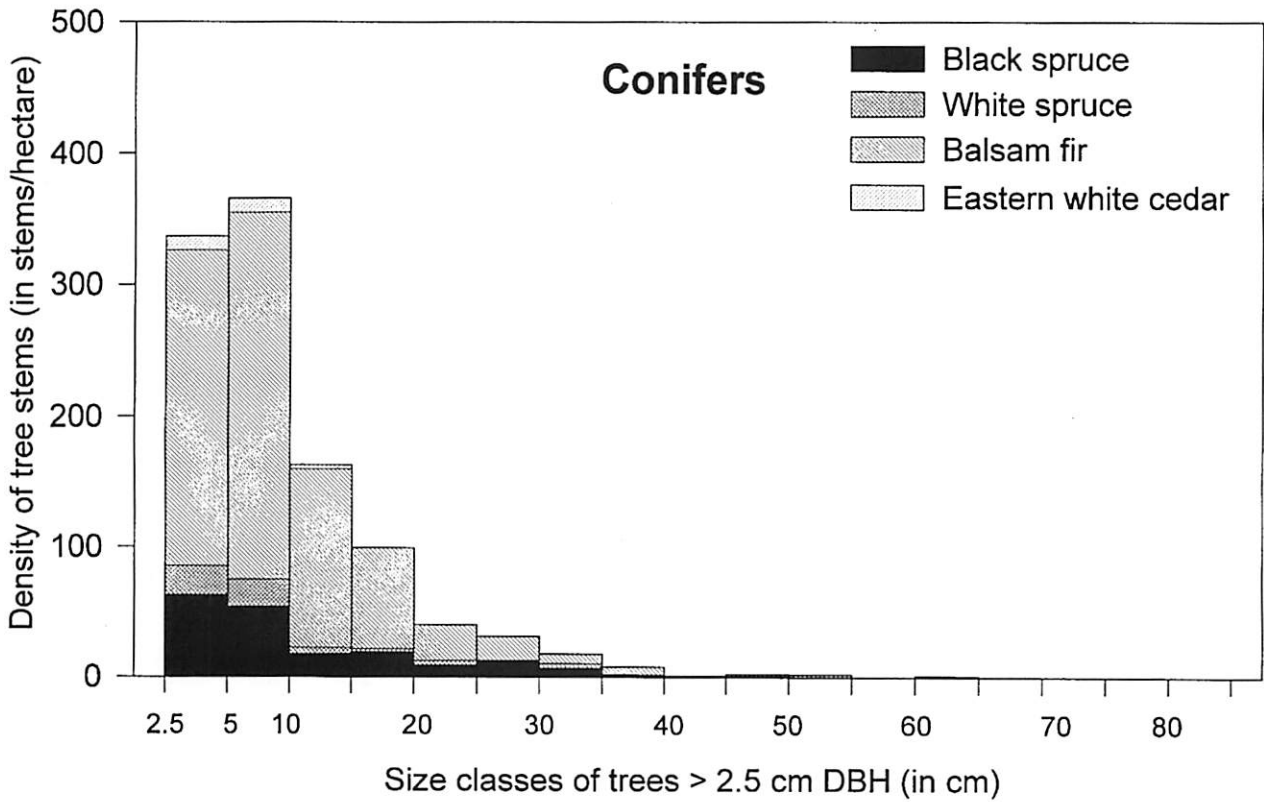


Figure B(1).16. 147-year-old stand (147-1).

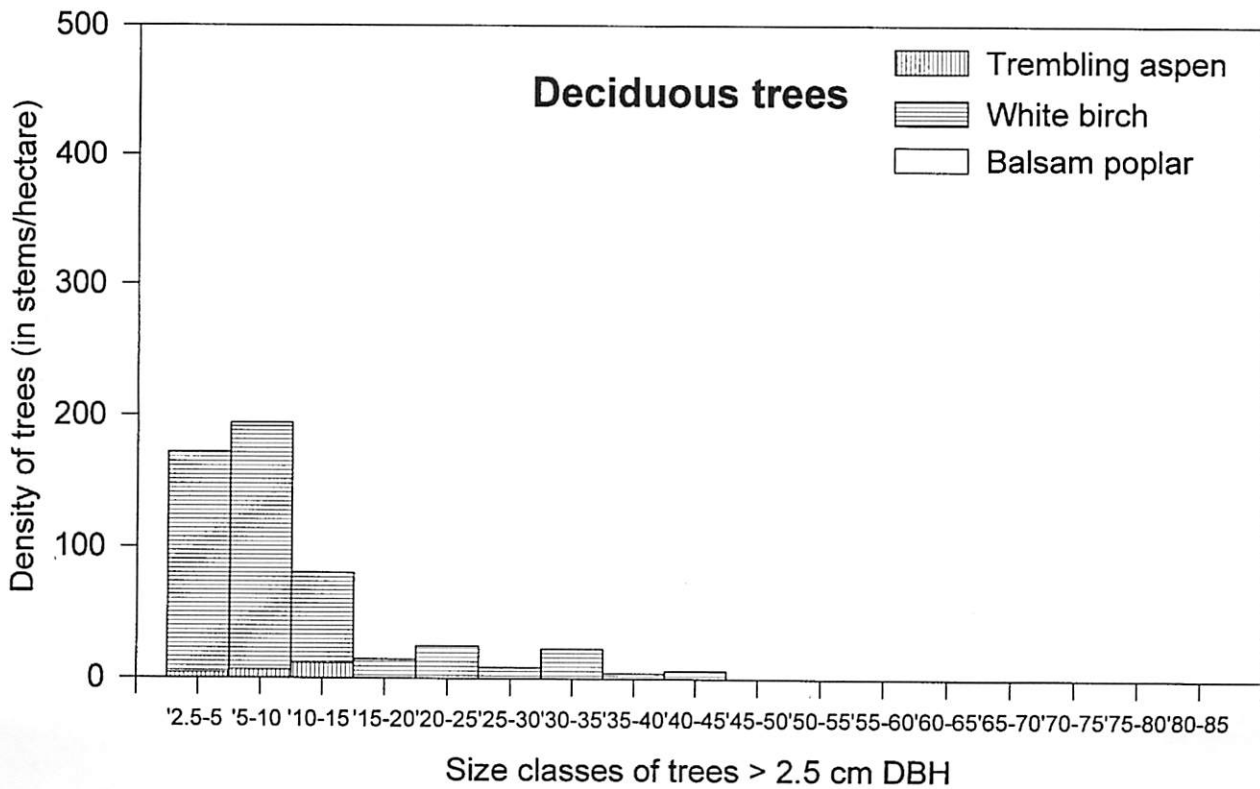
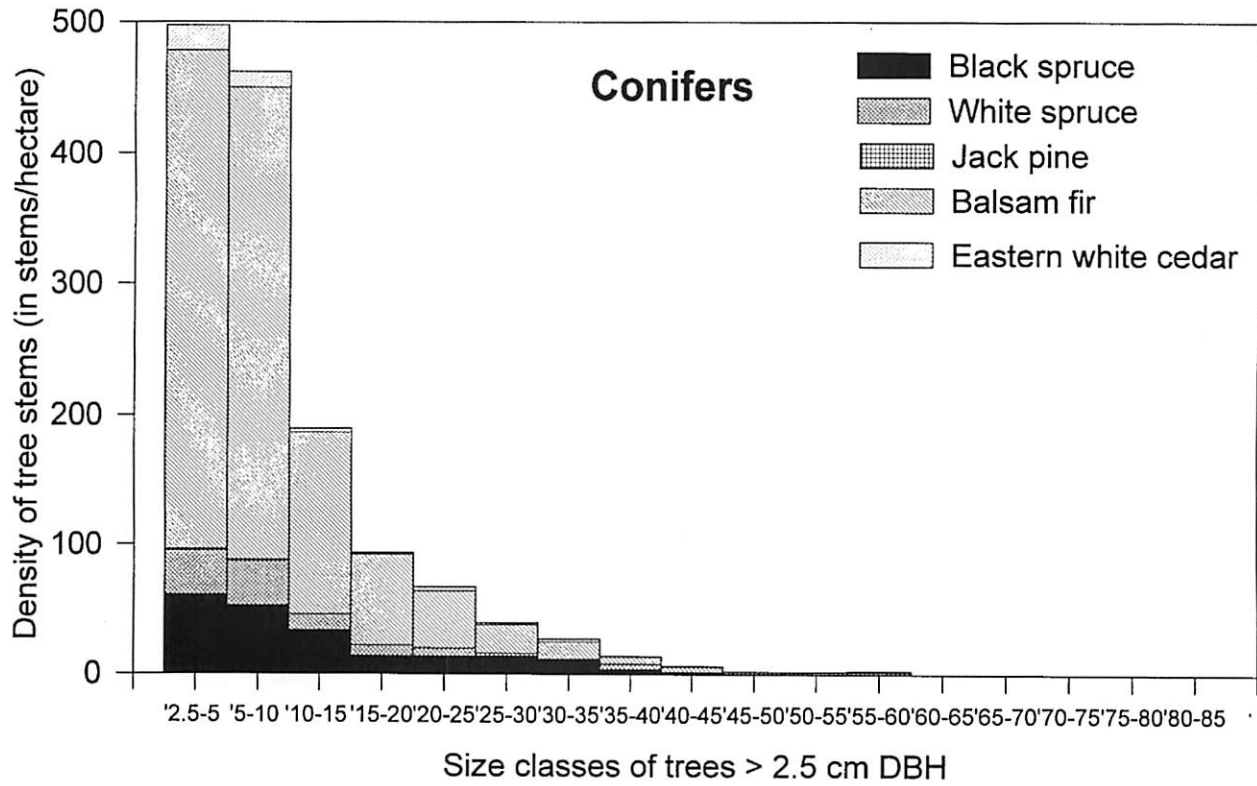
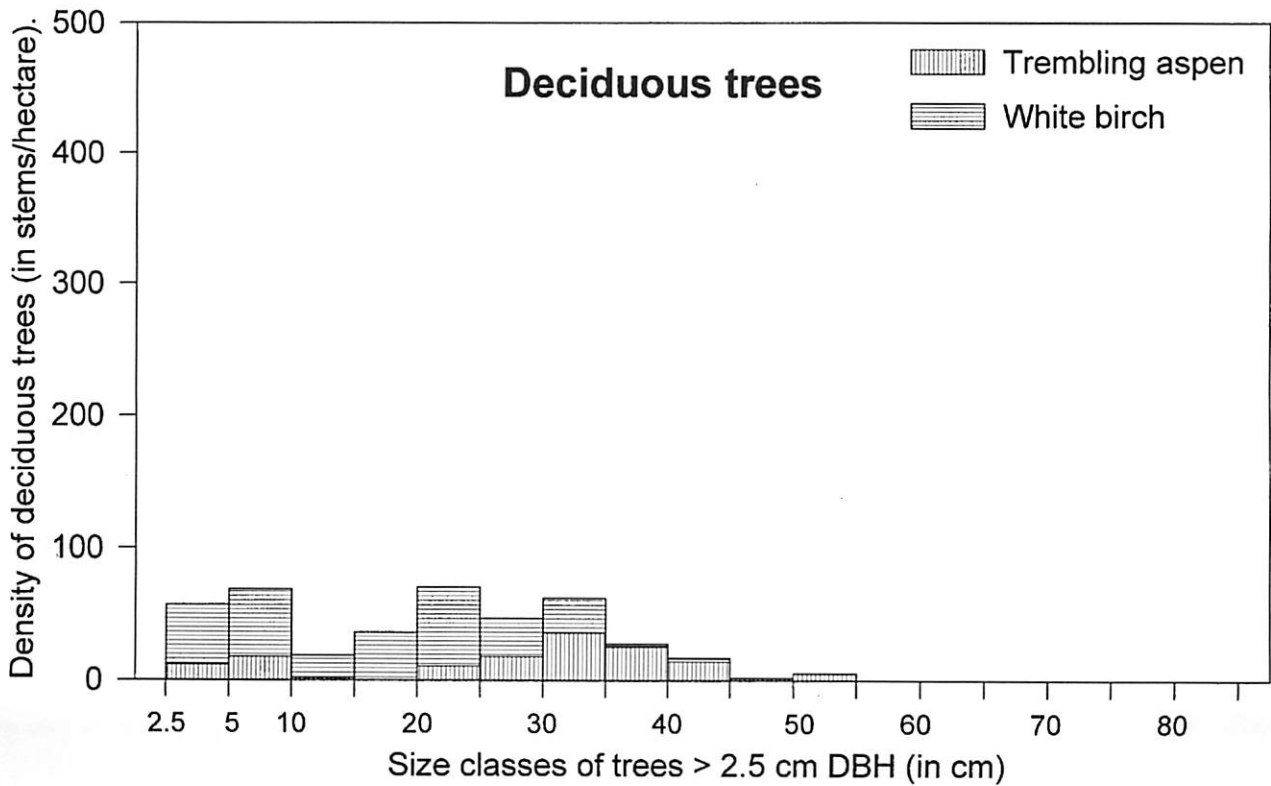
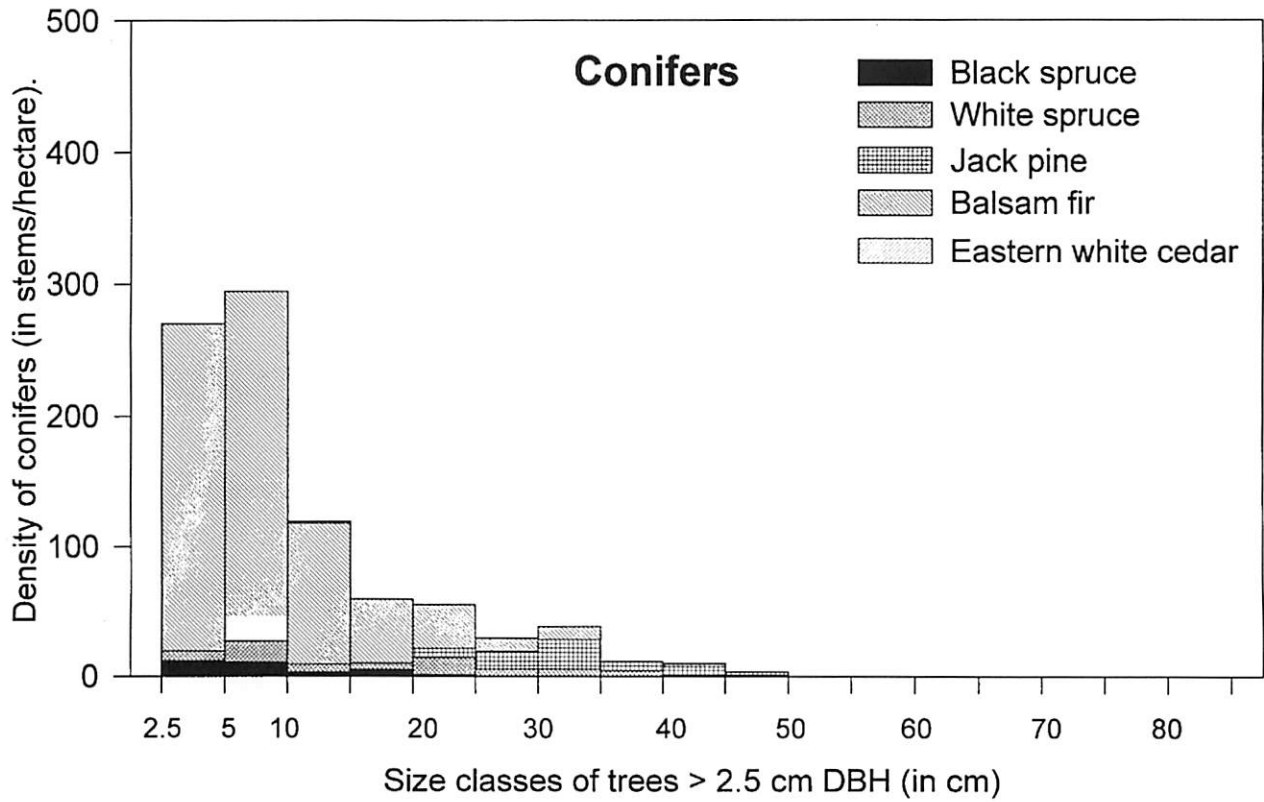
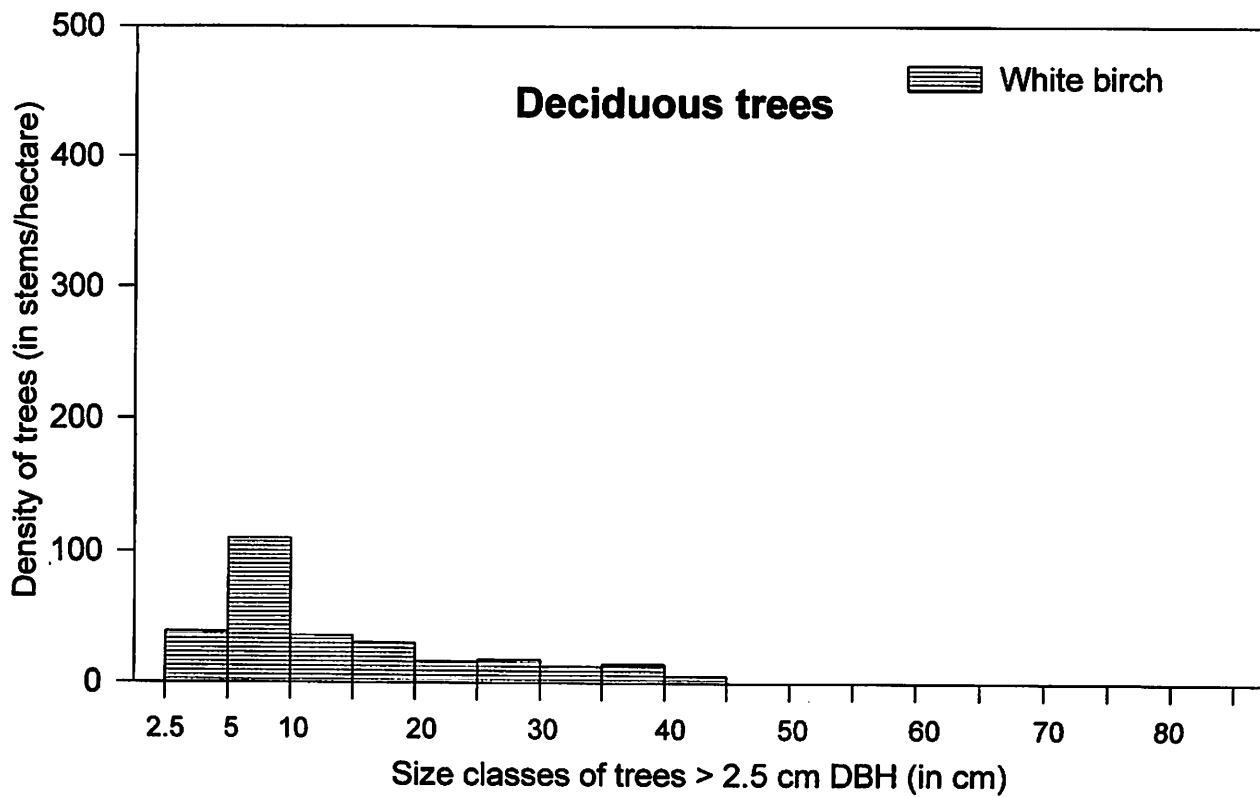
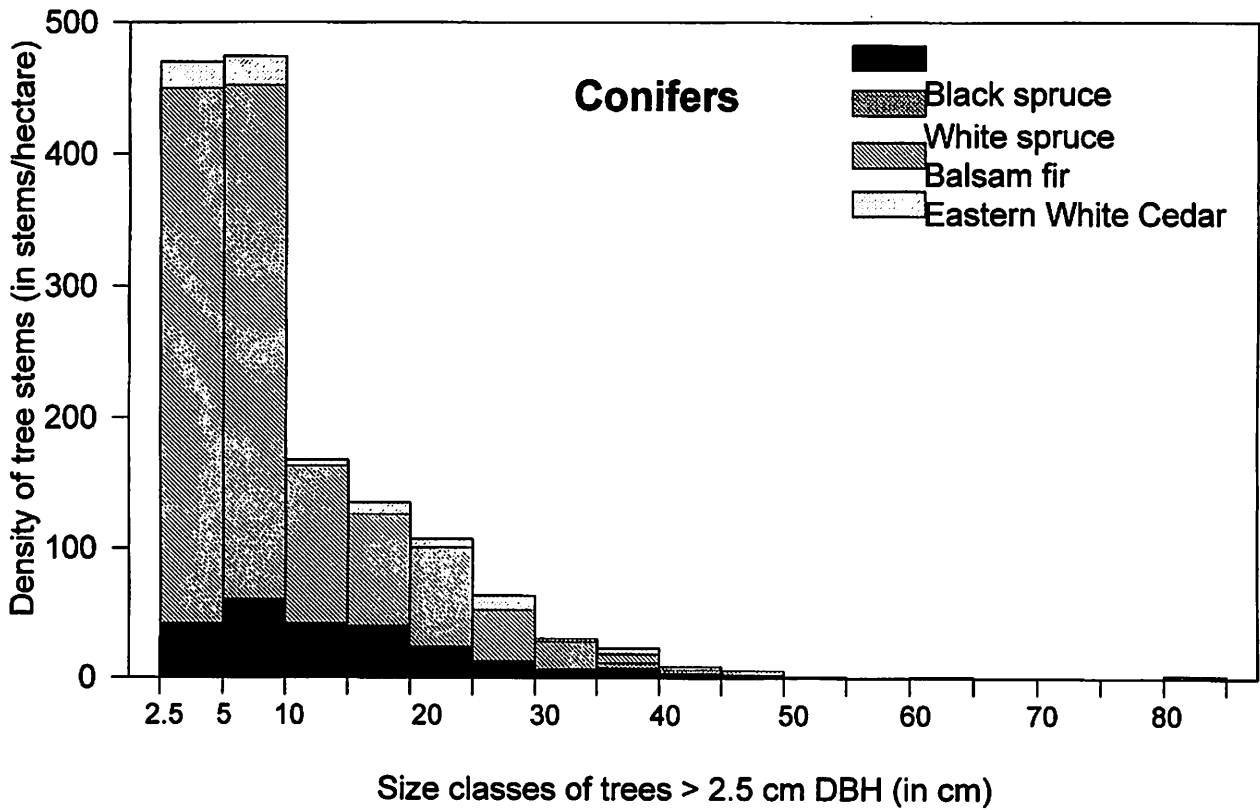


Figure B(1).17. 147-year-old stand (147-2).





Appendix B(2). Across stand density summary for 17 size classes of small and large trees.

Species	Number of uncut stands species occurs in (/6)	Number of harvested stands species occurs in (/12)	Size group and stand with peak density (size group, age, density)	Notes	Number of size groups that species spans (year-#)
Black spruce	6	12	2.5–5 cm, 56 years, (close to 400 stems/hectare)	Density significantly drops off for stands less than 26 years old	0-4, 3-4, 5-1-5, 5-2-4, 8-4, 12-4, 13-5, 18-4, 20-5, 23-3, 26-2, 33-6, 56-6, 109-9, 110-10, 147-1-9, 147-2-5, 199-10
White spruce	6	12	5–10 cm, 56 years, (close to 70 stems/hectare)	Occurs at densities less than 25 stems/hectare in most	0-3, 3-4, 5-1-2, 5-2-1, 8-5, 12-4, 13-2, 18-5, 20-3, 23-8, 26-2, 33-5, 56-8, 109-3, 110-10, 147-1-11, 147-2-10, 199-8
Jack pine	4	6	30–35 cm, 147-2 year old stand; 15–20 cm, 33-year-old harvested stand (close to 30 stems/hectare)	Minor component	12-2, 13-2, 18-1, 23-4, 26-5, 33-5, 56-1, 109-2, 147-1-2, 147-2-6
Balsam fir	6	12	5–10 cm, 8 years (close to 450 stems/hectare)	Remains an important component in terms of abundance	0-1, 3-5, 5-1-5, 5-2-5, 8-6, 12-5, 13-5, 18-6, 20-5, 23-7, 26-7, 33-5, 56-7, 109-7, 110-8, 147-1-8, 147-2-8, 199-10
Eastern white cedar	5	3	2.5–10 cm, 199-year-old stand and one of the 147-1 year old stands (close to 25 stems/hectare)		5-1, 8-7, 13-6, 109-2, 110-3, 147-1-8, 147-2-1, 199-9
Larch	0	1	Very low density	Incidental	12-2

Appendix B(2) (continued)

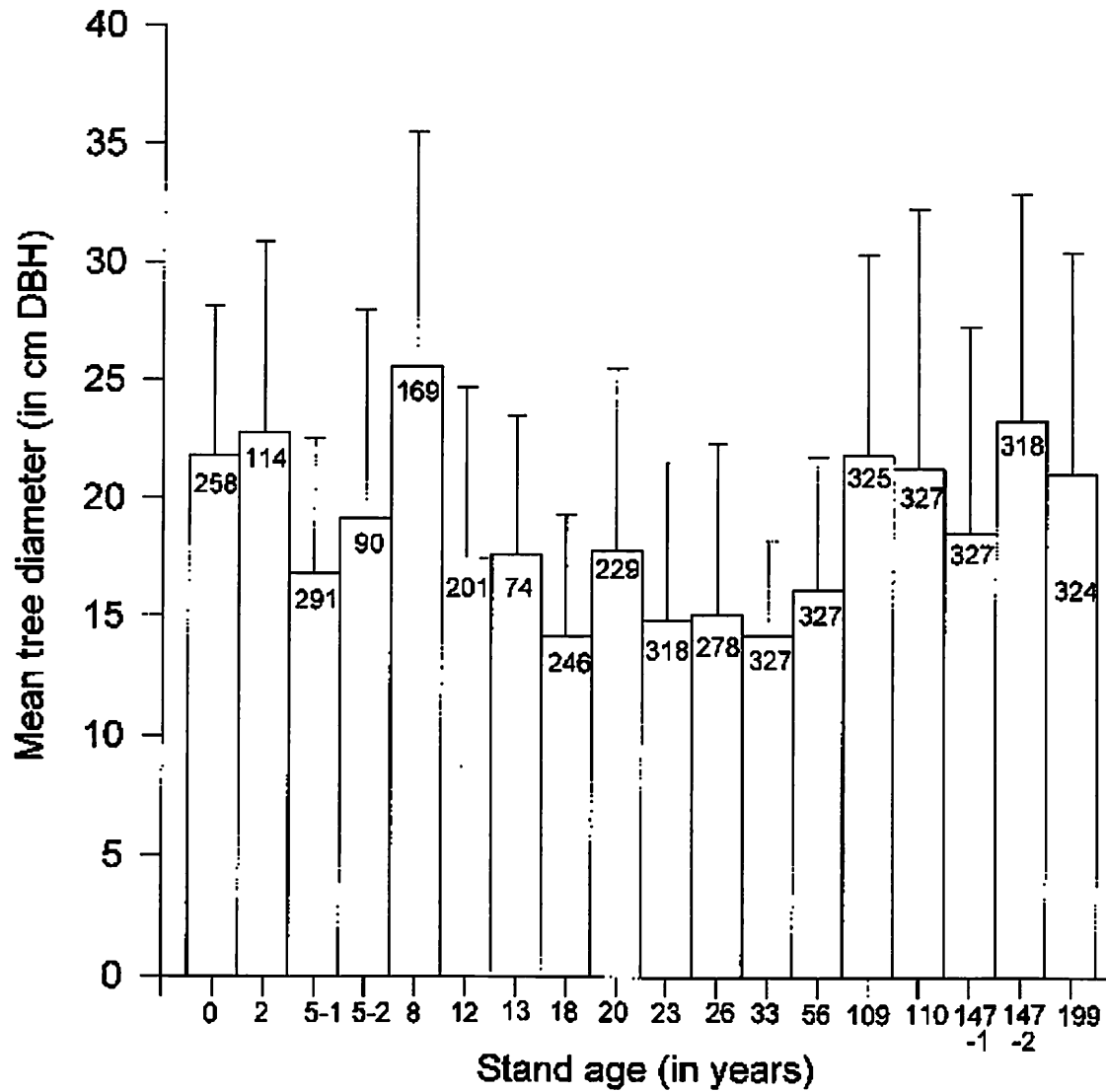
Trembling aspen	4	12	5–10 cm, 26 years, (close to 1600 stems/hectare)	More dense in the uncut stands, increases dramatically between 26- and 33-year-old stands, high throughout harvested stands until a drop in one of the 5-year-old stands (Stand 14), hereafter density in every size class is less than 300 stems/hectare	0-3, 3-1, 5-1-3, 5-2-1, 8-2, 12-2, 13-2, 18-4, 20-4, 23-4, 26-5, 33-6, 56-6, 109-8, 110-11, 147-1-3, 147-2-10
White birch	5	11	2.5–5 cm, 18 years, (close to 1300)	A major deciduous species, no size class density exceeds 200 stems/hectare in uncut stands, tends to be more dense than trembling aspen in the uncut stands, density drops down below 100 stems/hectare for all size classes in uncut stand less than 7 years old	0-9, 3-9, 5-1-9, 5-2-8, 8-11, 12-9, 13-6, 18-9, 20-8, 23-8, 26-9, 56-5, 109-6, 110-10, 147-1-9, 147-2-9, 199-9
Balsam poplar	4	9	10–15 cm, 33 years (close to 125 stems/hectare)	Minor deciduous component, drops off to very low abundance levels in all stands less than 8 years since harvest	3-1, 5-6, 8-4, 12-6, 13-3, 20-7, 23-9, 26-4, 33-5, 56-9, 109-9, 110-3, 147-1
Black ash	0	4	2.5–10 cm, 20-year-old stand (close to 20 stems/hectare)	Minor component of the study area	0-2, 20-3, 26-1, 33-2

Appendix B(3). Across species summary of density of 17 size classes of small and large trees.

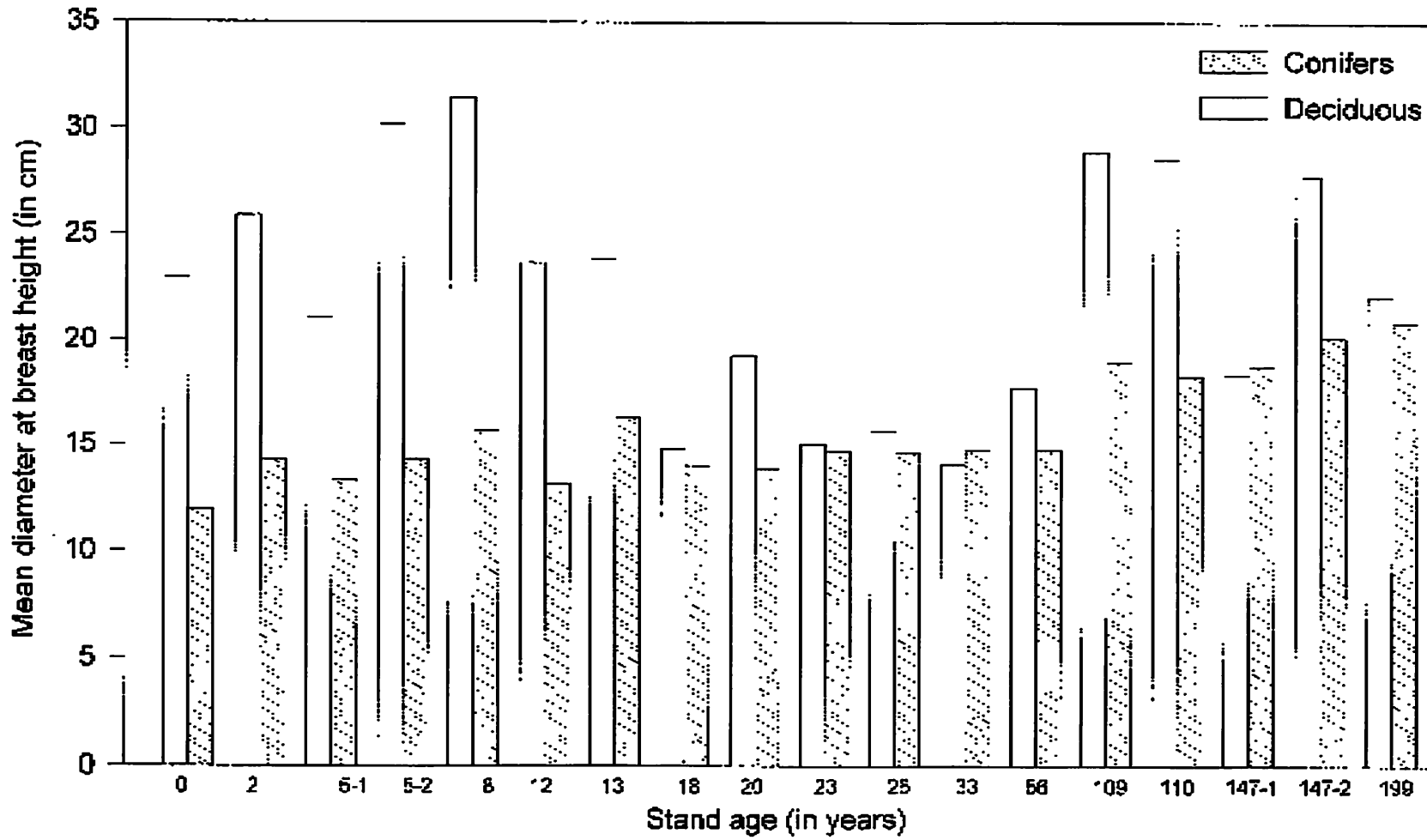
Stand age (years)	Species with highest density in any size class (size class, density)	Species distributed across most size classes (#)	Species present in stand	Species with density above 100 stems/hectare in any size class
0	White birch, 20–25 cm (close to 70 stems/hectare)	White birch (9)	White birch, black spruce, white spruce, balsam fir, trembling aspen, black ash	None
3	White birch, 20–35 cm (close to 25 stems/hectare)	White birch (9)	White birch, balsam fir, black spruce, white spruce, trembling aspen, balsam poplar	None
5-1	Balsam fir, 5–10 cm (close to 150 stems/hectare)	White birch (9)	Balsam fir, white birch, trembling aspen, black spruce, white spruce	Balsam fir
5-2	Trembling aspen, 2.5–5 cm (close to 350 stems/hectare)	White birch (8)	Trembling aspen, black spruce, white spruce, balsam fir, eastern white cedar, white birch, balsam poplar	Trembling aspen
8	Trembling aspen, 2.5–5 cm (close to 1300 stems/hectare)	White birch (11)	Trembling aspen, balsam fir, white birch balsam poplar, black spruce, white spruce, eastern cedar	Trembling aspen, balsam fir, white birch, balsam poplar
12	White birch, trembling aspen 2.5–5 cm (close to 325 stems/hectare)	White birch (9)	White birch, trembling aspen, balsam fir, black spruce, white spruce, jack pine, balsam poplar	White birch, trembling aspen, balsam fir
13	Trembling aspen, 2.5 and 5 cm (close to 700 stems/hectare)	White birch, eastern white cedar (6)	Trembling aspen, white birch, black spruce, white spruce, jack pine, eastern white cedar, balsam poplar	Trembling aspen, balsam fir
18	White birch, 2.5–5 cm (close to 1400 stems/hectare)	White birch (9)	White birch, trembling aspen, balsam fir, black spruce, white spruce, jack pine	White birch, trembling aspen, balsam fir
20	Trembling aspen, 5–10 cm (close to 1400 stems/hectare)	White birch (8)	Trembling aspen, white birch, balsam fir, balsam poplar, black spruce, white spruce, black ash	Trembling aspen, white birch, balsam fir
23	Trembling aspen, 5–10 cm (close to 1400 stems/hectare)	Balsam poplar (9)	Trembling aspen, balsam fir, white birch, black spruce, white spruce, jack pine, balsam poplar	Trembling aspen, balsam fir, white birch
26	Trembling aspen, 5–10 cm (close to 1600 stems/hectare)	White birch (9)	Trembling aspen, white birch, balsam fir, black spruce, white spruce, jack pine, balsam poplar, black ash	Trembling aspen, white birch
33	Trembling aspen, 5–10 cm (close to 350 stems/hectare)	Trembling aspen Black spruce (6)	Trembling aspen, black spruce, balsam poplar, white spruce, jack pine, balsam fir, black ash	Trembling aspen, black spruce, balsam poplar

Appendix B(3). (continued)

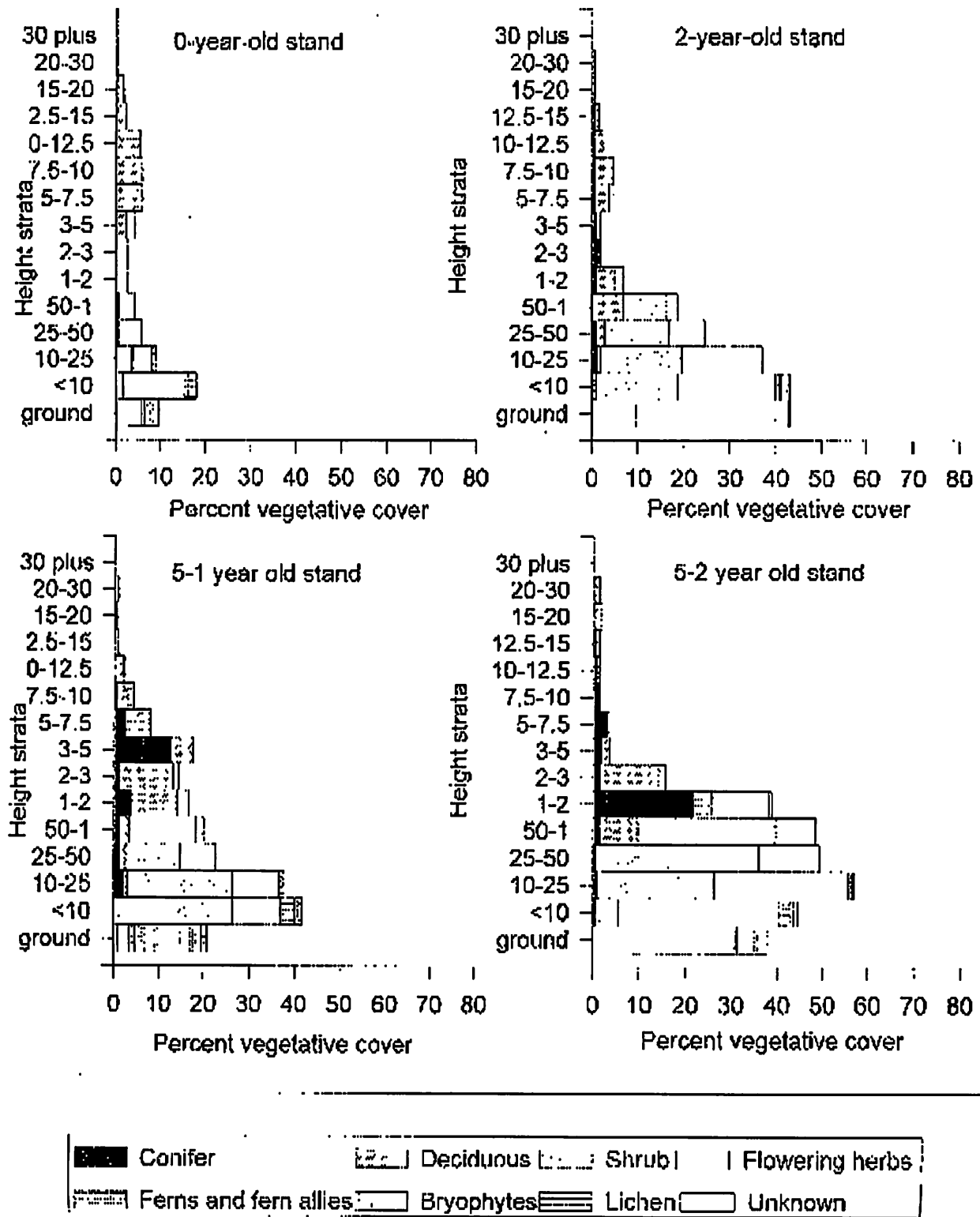
56	Black spruce, 5–10 cm (close to 400 stems/hectare)	Balsam poplar (9)	Black spruce, balsam fir, white birch, trembling aspen, balsam poplar, white spruce, jack pine	Black spruce, balsam fir, white birch, trembling aspen
109	Balsam fir, 5–10 cm (close to 200 stems/hectare)	Black spruce Balsam poplar (9)	Balsam fir, black spruce, white spruce, jack pine, eastern white cedar	Balsam fir
110	Balsam fir, 5–10 cm (300 stems/hectare)	Trembling aspen (11)	Balsam fir, white birch, black spruce, white spruce, eastern white cedar, trembling aspen, balsam poplar	Balsam fir, white birch
147-1	Balsam fir, 2.5–5 cm (close to 400 stems/hectare)	White spruce (11)	Balsam fir, white birch, black spruce, white spruce, jack pine, eastern white cedar, trembling aspen, balsam poplar	Balsam fir, white birch
147-2	Balsam fir 2.5–5 cm (close to 300 stems/hectare)	White spruce Trembling aspen (10)	Balsam fir, white birch, trembling aspen, eastern white cedar, jack pine, white spruce, black spruce	Balsam fir
199	Balsam fir 2.5–5 cm (close to 450 stems/hectare)		Balsam fir, white birch, black spruce, white spruce, eastern white cedar	Balsam fir



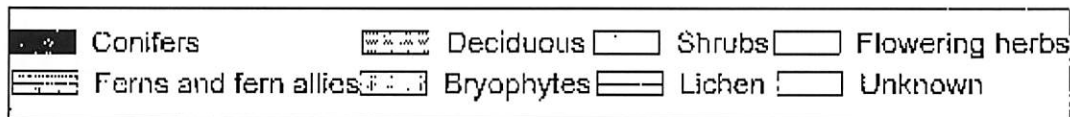
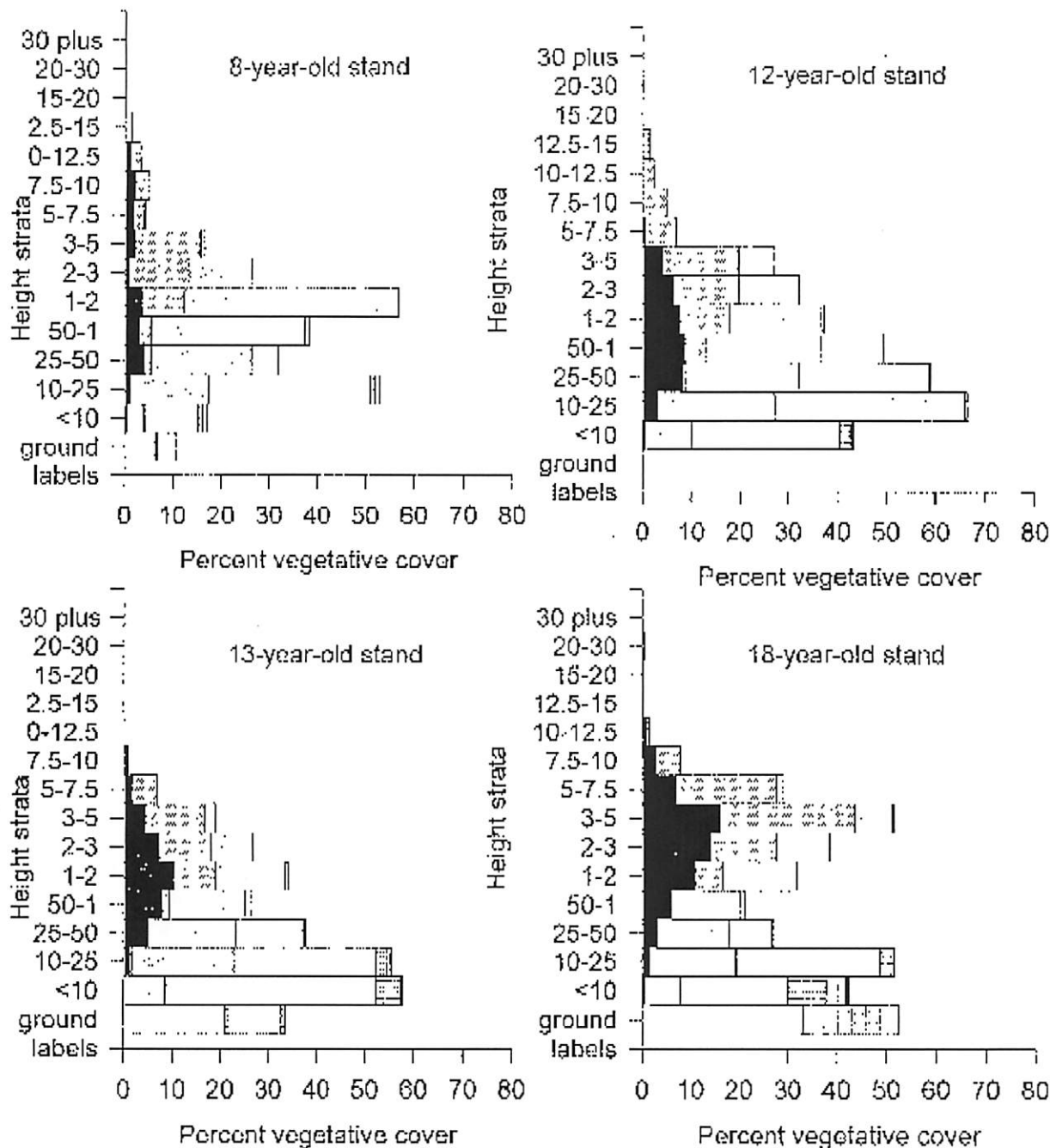
Appendix B(5). Mean diameter of coniferous and deciduous trees > 10 cm DBH.



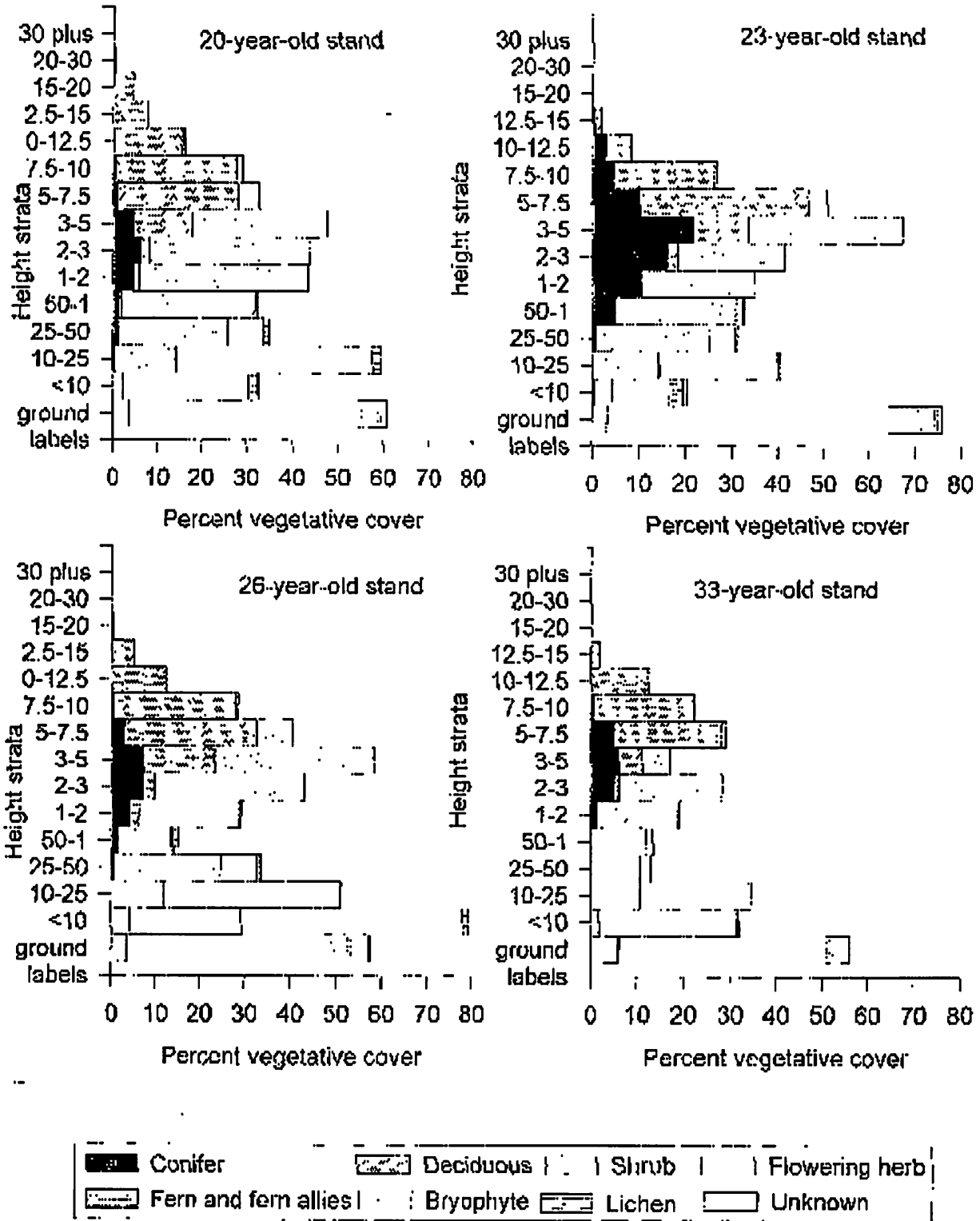
Appendix D(1). Percent cover of vegetation in 18 mixedwood stands of this study. Bars correspond to total percent cover per stratum.



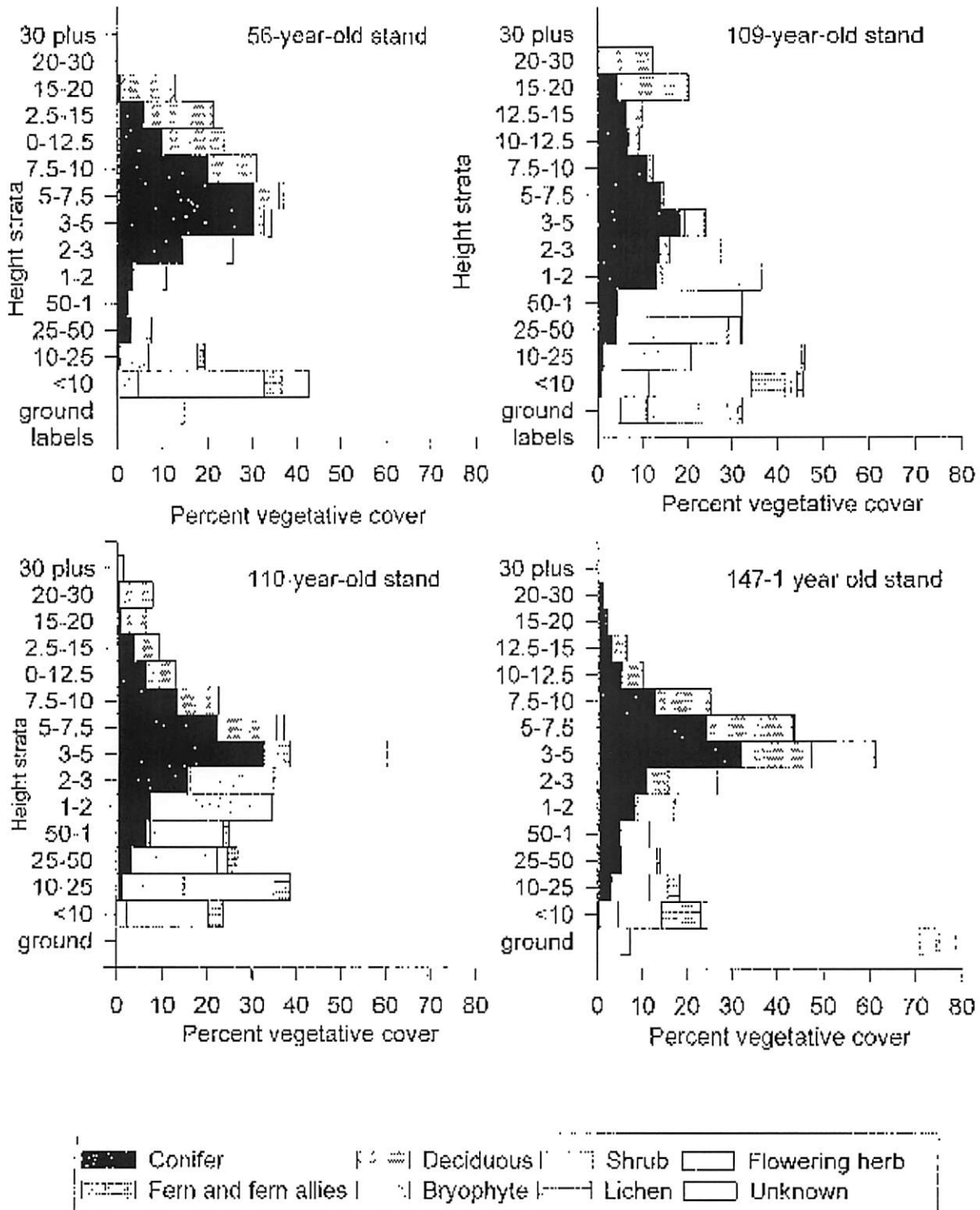
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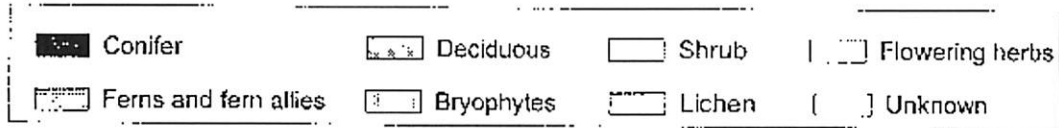
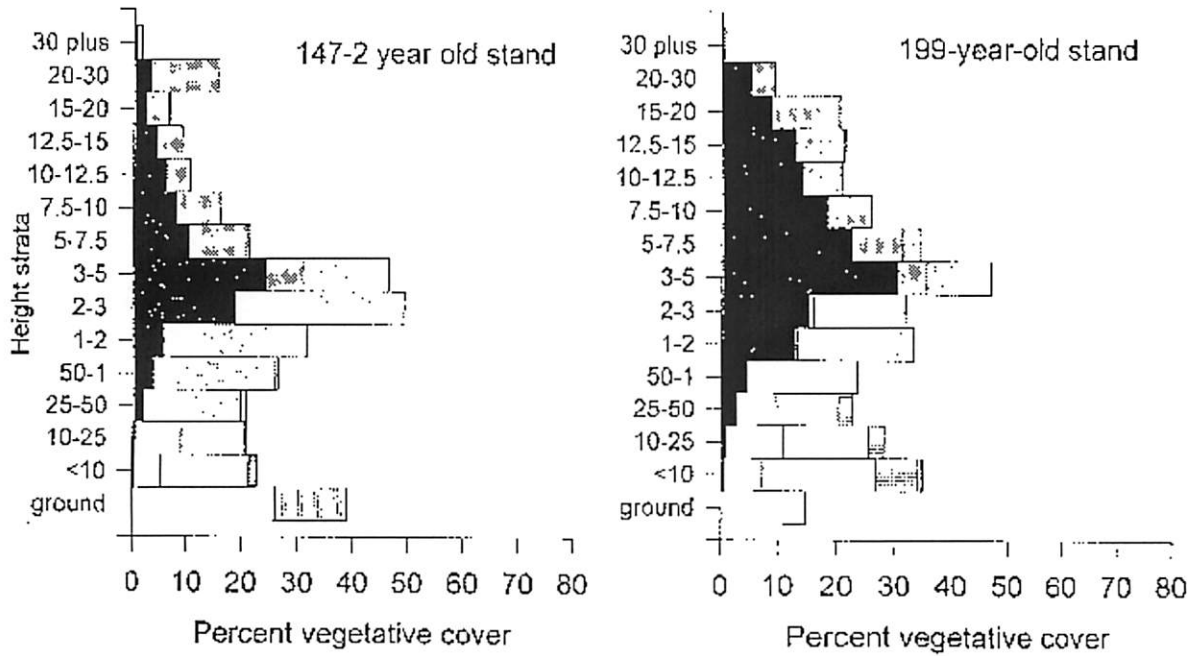
Appendix D(1). continued.



Appendix D(1). continued.



Appendix D(1). continued.



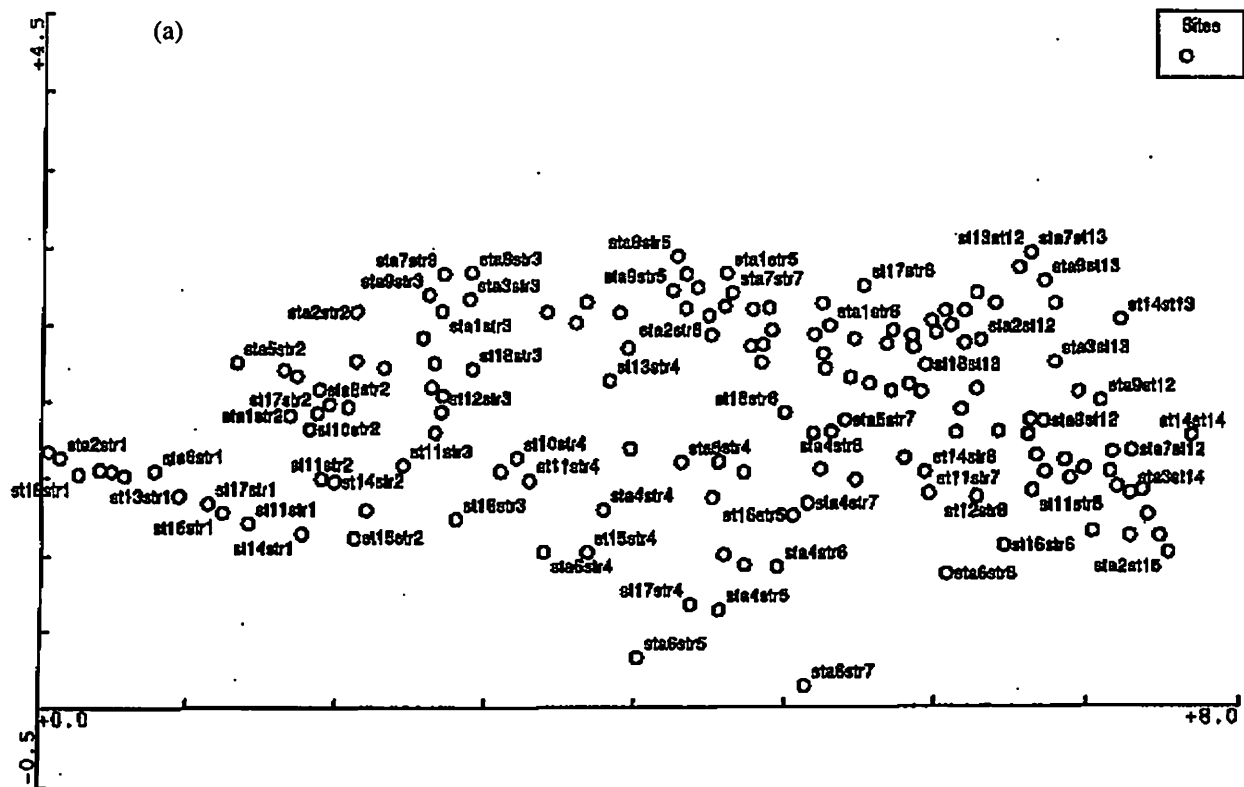
Appendix E. Detrended correspondence analysis of forest strata and understory plant composition data for: (a) all height strata, (b) the 25–50 cm stratum, and (c) the 1–2 m stratum. Data tables are two part; the first half corresponds to the stand number and the second to the strata number. The stand and strata numbers are as follows:

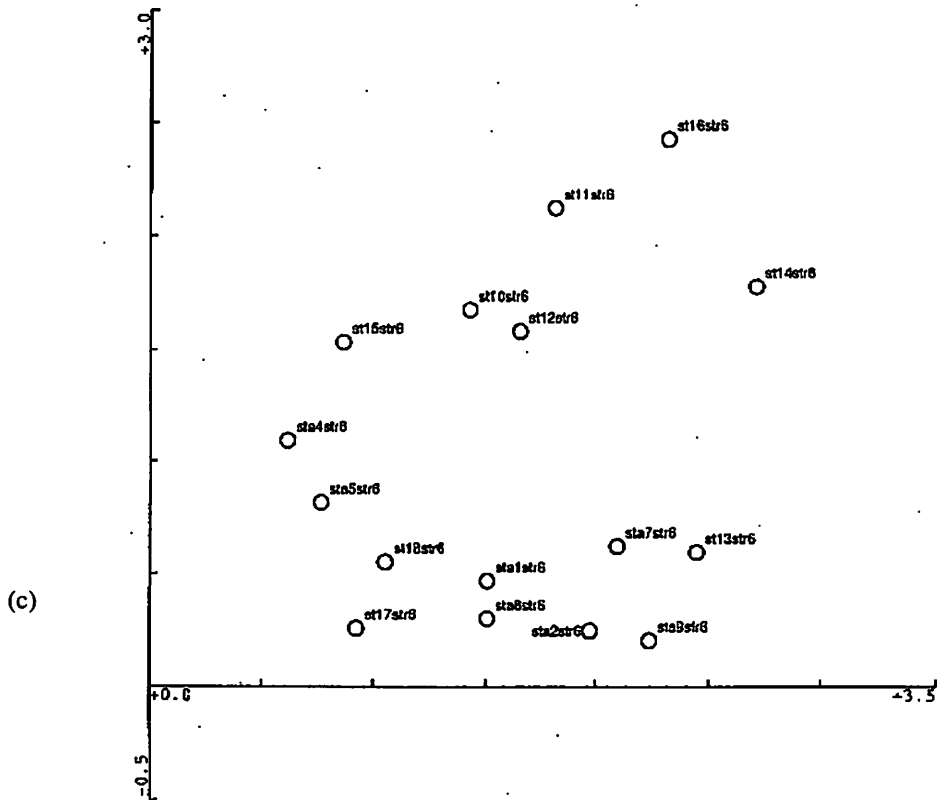
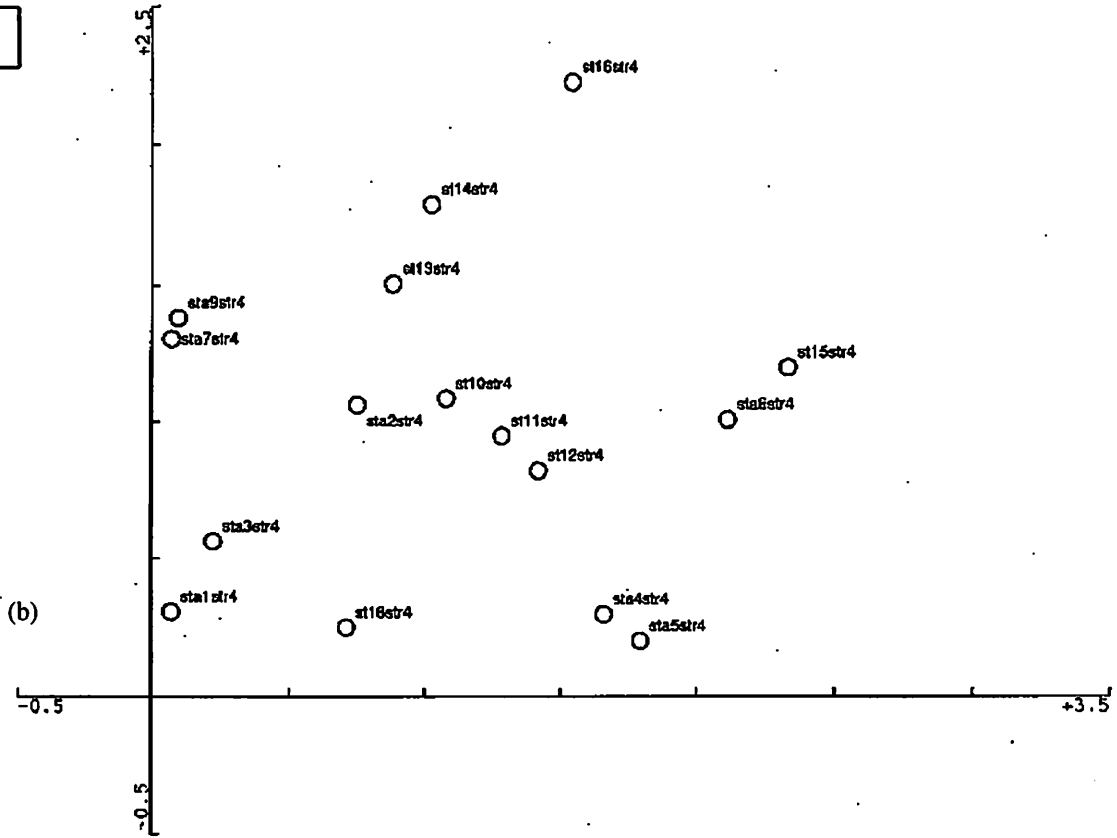
Stand numbers

sta1	199-year-old stand
sta2	147-2 year old stand
sta3	110-year-old stand
sta4	109-year-old stand
sta5	56-year-old stand
sta6	33-year-old stand
sta7	26-year-old stand
sta8	23-year-old stand
sta9	20-year-old stand
st10	18-year-old stand
st11	13-year-old stand
st12	12-year-old stand
st13	8-year-old stand
st14	5-2 year old stand
st15	5-1 year old stand
st16	2-year-old stand
st17	0-year-old stand
st18	147-1 year old stand

Strata numbers

str1	ground
str2	<10 cm
str3	10–25 cm
str4	25–50 cm
str5	50 cm–1m
str6	1–2 m
str7	2–3m
str8	3–5m
str9	5–7.5 m
st10	7.5–10.0 m
st11	10.0–12.5 m
st12	12.5–15.0 m
st13	15.0–20.0 m
st14	20.0–30.0 m
st15	> 30 m





Appendix F. A summary of non-vascular and herbaceous life form cover trends.

This discussion summarizes the trends in non-vascular and herbaceous life forms. There was no clear age trend in lichen cover; lichen occurred at low abundance (< 3 percent) in some younger and older harvested stands and in some uncut stands. Similarly, the peak lichen cover in a range of jack pine–black spruce stands was 3 percent in a 14-year-old logged stand and close to 2 percent in one of the 100-year-old stands described by Noble et al. (1977). Bryophytes were generally more abundant in the uncut stands compared to the harvested stands, although bryophytes formed greater than 10 percent of the cover in one of the 5-year-old stands (5-1), in the 18-year-old stand, and in the 23-year-old stand. This is consistent with previous successional trends that show mosses were generally more abundant in older stands (Noble et al. 1977, Freedman et al. 1994), and more diverse in older stands (Crites and Dale 1995). Ferns and fern ally cover did not reveal a clear age trend, although one would expect a trend because ferns like the bracken fern (*Pteridium aquilinum* [L.] Kuhn) tend to increase with increased disturbance. On the other hand, the rattlesnake fern (*Botrychium virginianum* [L.] Sw.) tends to decrease with increased disturbance. The abundance of this vegetation group was highest in the 18-, 109-, and one of the 147-year-old stands (147-1). Historical information revealed that the 18-year-old stand probably had the highest level of soil disturbance at the time of harvest because part of the plot covers roads and skidways. This same portion of the stand would also have had little or no postharvest residual vegetation. Disturbance in the 18-year-old plot may have been similar in nature to fire and this could explain why it was so similar to two of the old uncut stands in terms of fern and fern ally composition. A clear age gradient was also not evident for flowering herbs. They were most abundant in one of the 5-year-old stands (5-2), and in the 12- and 13-year-old stands, yet they were at low to medium levels of abundance throughout the range. Although abundance levels may have been somewhat higher for harvested stands compared to uncut older stands, the trend was slight.