FOREST STRUCTURE

IN EASTERN NORTH AMERICA

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1.0 INTRODUCTION

The Ecological Woodlands Restoration project of the Eastern Ontario Model Forest (EOMF) aims to direct the current and future forests of eastern Ontario towards a more natural state. This is important in a region where European settlement and land clearance for agriculture had a profound effect on the distribution and condition of forested land. By 1880, 32 townships in the area had <30% forest cover. Although, by 1992, only 17 townships still had less than 30% forest cover, the forests that remain are generally fragmented and mature forests are rare.

In establishing forest restoration guidelines for a site, it is important to obtain knowledge on site characteristics (including site history), historical tree cover on the site and of the general area (Keddy 1993), and structural characteristics of forests of the area. This document provides information on the structural components of forests in a natural state. These data can be used to derive targets for the development of forest structure against which structural conditions of a particular forest stand can be compared. This comparison would form the basis of a structural restoration prescription for the stand.

Based on a review of the literature on the structure of forests of eastern North America (approximately 700 articles, including Nowacki and Trianosky 1993), those articles most relevant to the forests of the EOMF region were synthesized to derive values for several structural components. Each of the structural components covered is discussed in general in section 3.0. Data from the literature for these components, specific to the three major forest cover types (deciduous, mixed, coniferous), are summarized in sections 4.0, 5.0 and 6.0, respectively. The use of this information for forest management is discussed in section 7.0. Suggestions for further work required to enhance the utility of this structural information for forest management in the EOMF region are made in section 8.0. The literature cited is listed in section 9.0. An appendix is provided for each cover type which contains tables of original structural data used to prepare structural summaries.

2.0 FOREST COVER

2.1 North American Perspective

Eastern Ontario lies near the northern edge of the deciduous forest region (Barnes 1991, Braun 1950; Fig. 1), in the hemlock-white pine-northern hardwoods zone. Typically, the most common species in a mature stand of upland forest would be sugar maple and beech followed by basswood, red maple, yellow birch, hemlock and white ash (Rowe 1972). Others found in lesser abundance would include red oak, bur oak, bitternut hickory, and butternut.

2.2 Forest Cover Types of Eastern Ontario

The forest cover of Site Region 6E (Hills 1959), in which the EOMF lies, has been described in terms of cover types by Boysen (1994). Each cover type meets the following criteria:

1) the dominant cover is trees and tree crowns cover at least 25% of area

2) the cover type occupies a fairly large area, not necessarily in large continuous stands

3) the forest cover type is defined entirely on biological considerations.

Based on these criteria, 25 natural forest cover types were described for the region. Additional anthropogenic forest cover types (e.g., plantations) were identified but not described. Each cover type is described in terms of dominant trees (constituting a major percentage of the canopy), common associated tree species and less common associates. The microclimate, soil moisture regime and soil texture associated with each cover type is also provided. Examples of stand composition are given for each cover type to illustrate representative and characteristic species compositions.

Because forest cover types are natural associations of vegetation that have responded to growing conditions on specific landforms and sites, a knowledge of cover types can provide guidance for forest restoration. It would be ideal to relate the cover types described by Boysen (1994) to forest structure parameters to guide restoration of each type. Unfortunately, there is a paucity of data on forest structure in eastern Ontario and, in eastern North America, for most cover types when considered at this scale.

figure 1.The eastern deciduous forest region of North America (shaded region location of EOMF)

these reasons, the literature on forest structure has been summarized by three gross cover types (deciduous= <30% coniferous, coniferous= <30% deciduous, mixed= ≥30% deciduous/coniferous). While little variation may occur among gross cover types or within gross cover types for some parameters, others may differ depending upon cover type (Table 2 and Appendices A, B, C). Thus it is important to examine these values against cover type in the EOMF prior to deriving structural guidelines.

3.0 FOREST STRUCTURE COMPONENTS

For the purposes of this review, structure covers species composition (e.g., number of species, physical characteristics (e.g., size (age), health, decomposition) and spatial arrangement (e.g., density, canopy gaps) of the trees in the forest and composition and density of the groundflora (shrubs, herbs). This section provides general information on forest structure components which is derived largely from deciduous and mixed forests for which there is more information than for coniferous forests. The discussions centre on structural conditions in old-growth stands (characterized by Martin 1992) because these are the closest one can get to "control" stands against which conditions in managed forests can be evaluated. Where information is available, trends over time are discussed which may assist in putting particular forest stands in perspective. In the next three sections (4.0, 5.0, 6.0), data are provided on most of the structural components discussed below for three main cover types: deciduous, mixed, coniferous.

The structure of a forest is a synthesis of many characteristics, including those discussed below. No one characteristic should be used to characterize forest structure. Management prescriptions will be most appropriate when they are based on many structural variables.

3.1 Canopy Composition

The number of species dominating the canopy of mature forests is typically lower than that for disturbed forests (Doyle 1980). With this in mind, this study examines two indicators of canopy composition- the number of tree species making up the majority (defined as 70%) of the canopy and the number of species that contribute a substantial proportion (defined as 15%) of the total number of stems. When comparing numbers of species in forests over a broad geographical area, it is also important to take into account the latitudinal variation in species diversity.

As deciduous forests mature, the proportion of shade-tolerant species composing the canopy will increase. While natural disturbance will maintain some shade-intolerant (early successional) species (Runkle 1985), they will make up a smaller proportion of an old-growth forest canopy than a canopy of a early successional forest. The general relationship between forest age and species successional stage for forests is shown in Figure 2. Wang and Nyland (1993) suggest that prior to human settlement, shade-intolerant species made up 2-10% of the canopy tree stem density. As a result of disturbance, the proportion of shade-intolerant and semi-tolerant species in the upper canopy will increase.

3.2 Age Class Structure

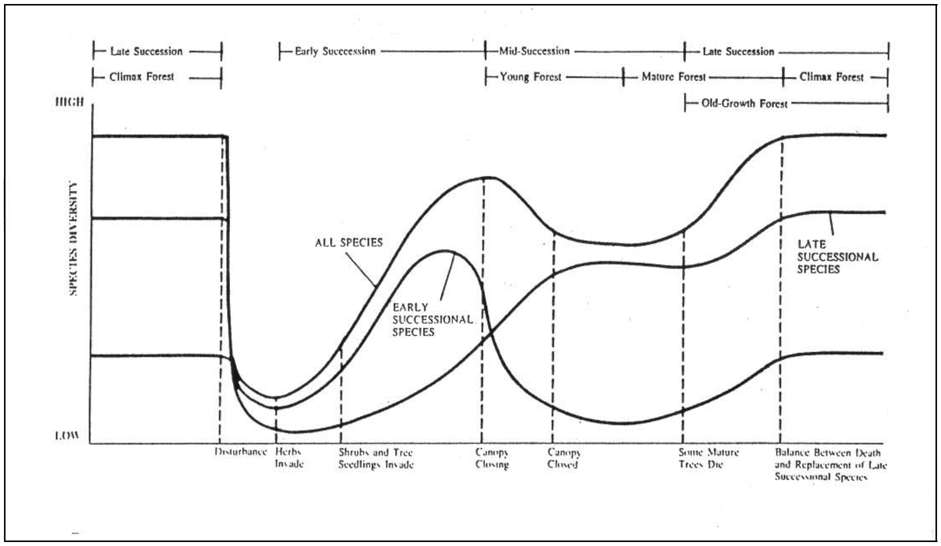
Old-growth deciduous forests are typically uneven-aged (all-aged) because of the nature of the predominating natural disturbance regime (see 3.7) and the variation in longevity and stress-tolerance of canopy trees (Jones 1945). Leopold *et al*. (1988) provide data on age for individuals of dominant canopy tree species in old-growth forests in the Adirondacks and show that these trees averaged 240 years old.

Martin (1992) suggests, for mesophytic old-growth forests, that many species groups and canopy trees in general will have an inverse J-shaped DBH (stem diameter at breast height) frequency distribution from small to large diameter classes (Fig. 3). Lorimer and Frelich (1994), however, found in Michigan that only about 20% of the old-growth stands approached this shape of curve and many other shapes were observed. As well, the inverse-J curve is not unique to old-growth forests, but may occur in other kinds of forests, depending upon management history.

3.3 Tree Size

Tree size determines in part the diversity of wildlife a forest can support. Large trees provide habitat for species that require big cavities for nesting and denning. Susceptibility to windthrow, which is related to soil moisture and thickness, will reduce the potential for large trees.

There are several measures that can provide structural information related to tree size including basal area (cross sectional area of tree stem at stem base) of all trees/ha or average basal area/tree, tree diameter (DBH) of the largest tree or average diameter of canopy trees, tree density (tree size is inversely related to density) figure 2: Changes in plant species diversity during succession in an ideal forest (from Barnes, 1989)



and the relationship between size (DBH or basal area/tree) and stem frequency (stems/ha). The latter provides the most comprehensive information on tree size.

The general relationship between size (DBH) and stem density is illustrated in Figure 3. With age the number of stems in higher diameter classes increases and the distribution of trees over all age classes exhibits a typical pattern that is distinguishable from younger forests. Insufficient information was available in the literature to examine the contribution to total basal area of trees of various diameter classes. Generally, one would expect the basal area contributed by trees of larger diameters to increase as forests progress toward old-growth.

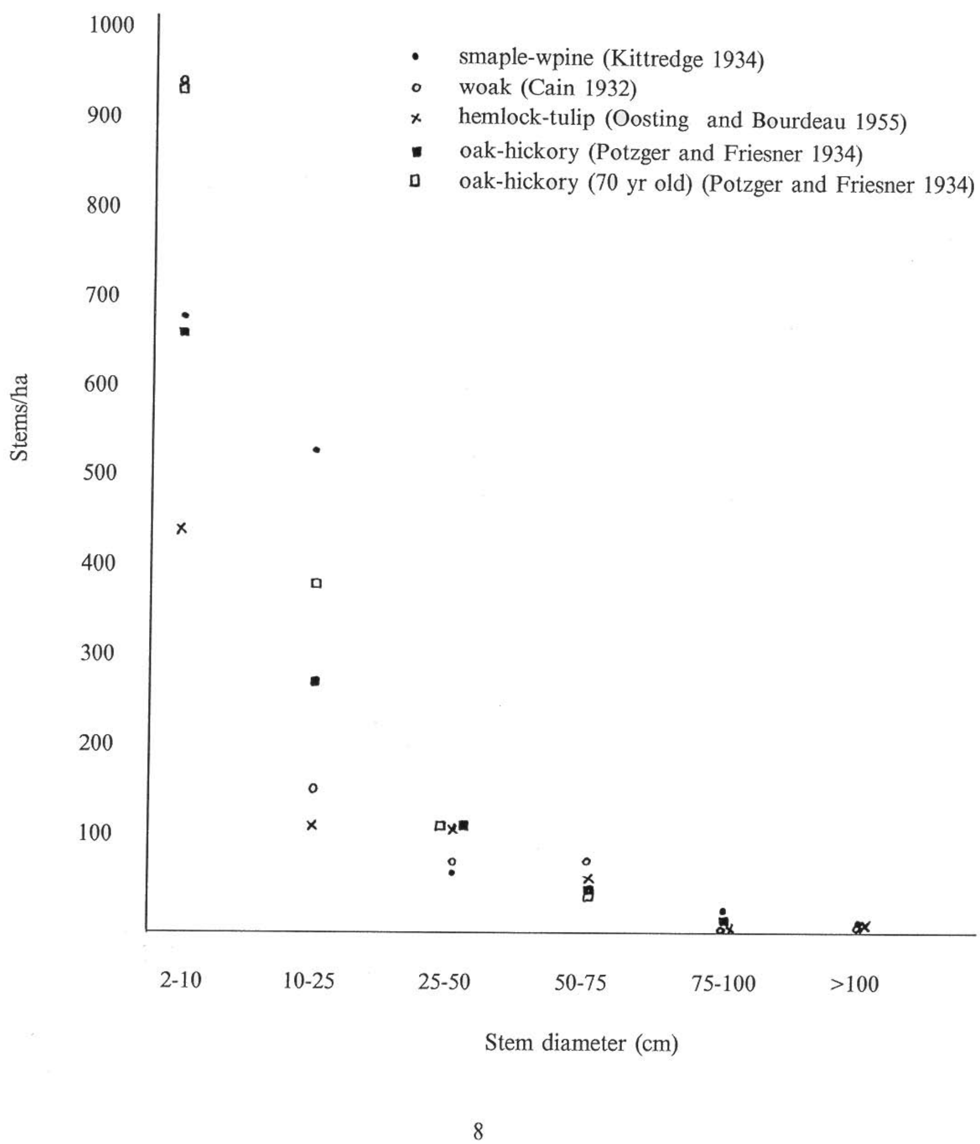
Martin (1992) suggests typical eastern mesophytic mixed old-growth forests would contain several large canopy trees (e.g., 7 trees/ha ≥75 cm DBH), but the majority of the canopy trees would fall into diameter classes from 12.5 to 60 cm DBH. Leopold *et al*. (1988) reported for the Adirondacks maximum canopy tree sizes ranging from 28.2 cm (balsam fir) to 109.2 cm (white pine) DBH, and varying from 23.2 m (red spruce) to 47.9 m (white pine) in height.

DBH data are relatively scarce in the literature and less often reported than basal area. Often when DBH data are presented, each DBH class covers a large range of diameters and the limits of diameter classes vary considerably among studies making accurate calculation of a mean impossible. As well, tedious calculations using the raw tabulated data are required to obtain means.

Tree size in this study is assessed in terms of canopy tree basal area/ha which is the most common expression of size reported in the literature. Basal areas for undisturbed mesophytic old-growth forests have been found to be very similar (Keddy and Drummond 1994, Held and Winstead 1975). Martin (1992) suggests the use of basal area as one of his 12 structural criteria for characterizing old-growth forests. Basal area generally is lower in disturbed forests than old-growth forests, but basal area differences could also be due to variations in soil moisture, aspect, latitude and species composition.

Martin (1992) also uses stem density to characterize old-growth forest. Density is one of the most commonly measured structural variables in field investigations. As with basal area, density is influenced by a variety of factors such as disturbance history, site conditions and species composition. Density is an objective measure that can be used with basal area to compare structure. For forests of similar composition growing under similar conditions, one would generally expect the basal area contributed by larger trees to be increase with maturity.

Figure 3: The relationship between stem diameter and frequency of four old-growth deciduous and mixed forests and one young deciduous forest



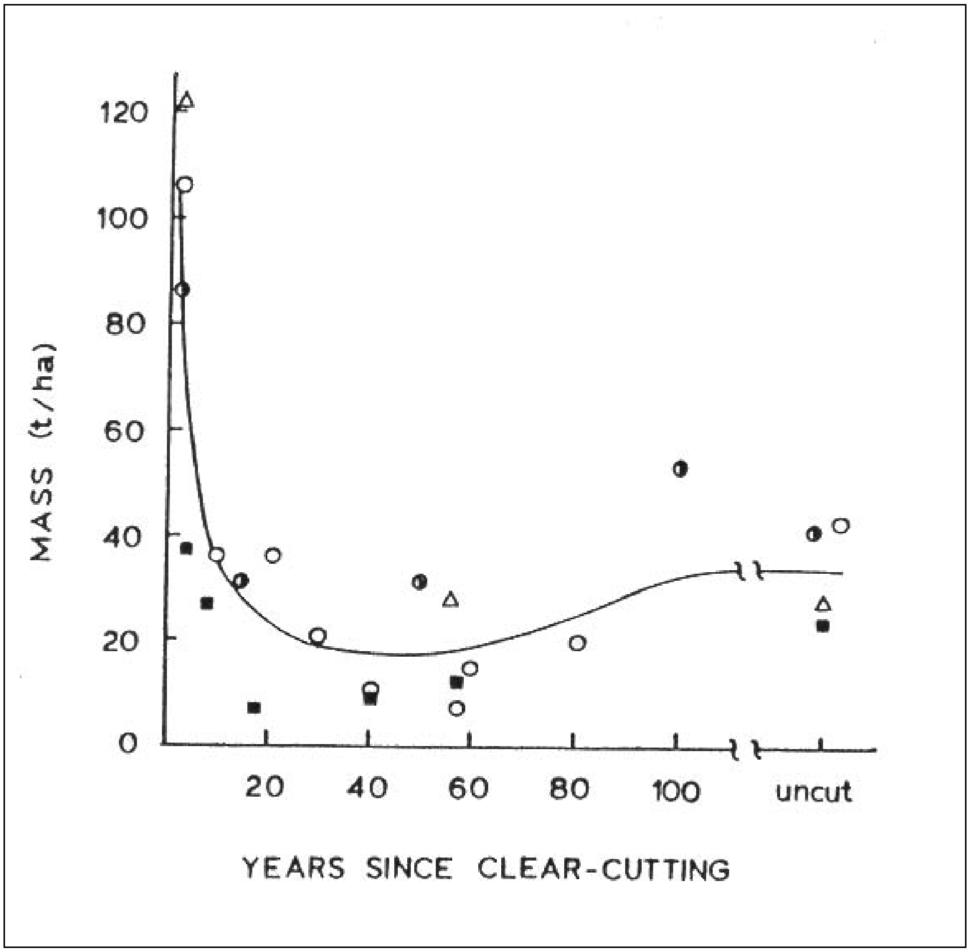
Values of both basal area and density will vary depending upon the lower limit of tree size used for calculation. For example, basal area or density figures calculated using trees >20 cm DBH would differ from the those calculated using trees >10 cm DBH. There are an infinite number of arbitrary lower limits for tree size that could be chosen for calculating density or basal area. A minimum diameter of 10 cm DBH was chosen for calculating stem density in this document since this is the most common lower limit reported in the literature. Occasionally the results of additional studies with lower minimal DBH limits were used to supplement these data. The merits of selecting other size limits and particular values for the evaluation of forest structure requires further discussion and calibration for forest types and variable growing conditions of the EOMF region. In any event, neither density nor basal area values alone are good indicators of old-growth forest structure. Both values must be examined as an indicator of tree size.

3.4 Logs and Snags

Snags are standing dead trees. Logs are dead boles on the ground resulting from natural causes of tree fall (e.g., windthrow, decay). The presence and condition of large logs and snags are two of the most important components of old-growth forest structure. Logs and snags provide microhabitat for many forest organisms including birds, mammals, herptiles, invertebrate decomposers, bryophytes, fungi and tree seedlings (McComb and Muller 1983, Harmon *et al*. 1986). The abundance of logs and snags depends on disturbance history and successional stage (Harmon *et al*. 1986, Keddy and Drummond 1994). The relationship between age and mass of logs is shown in Figure 4. A young forest may have high numbers of logs attributable to a severe disturbance (e.g., slash from clearcutting, windstorms), but examination of log diameter would separate this situation from that in an old-growth forest (Gore and Patterson 1986). The presence of logs will also depend on rates of decay, which are higher in warmer, moister, southern climates (MacMillan 1981). Old-growth forests will have logs of varying ages and decay classes. Particularly, they will have large, heavily decayed logs (i.e., >40 cm diameter, having no bark, twigs or branches remaining, having at least 50% bryophytic cover, and being oval in shape) (MacMillan 1981).

Old-growth forests have lower numbers of snags/ha than younger forests (MacDonald 1992, Carey 1983, McComb and Muller 1983). Proportionally, old-growth forests have more large diameter snags (supporting the greatest number of snag-dependent species) than young forests.

Figure 4: Estimates of mass of logs from four studies of northern hardwoods in central New Hampshire (curve fit by eye by Gore and Patterson, 1986).



3.5 Shrubs

Shrub species, like tree species, may be shade-tolerant or shade-intolerant. As forest succession progresses, those tolerant of shade will form a larger proportion. These shrubs have the ability to maintain themselves and reproduce. A smaller number of species less tolerant to shade will persist under natural openings in the canopy, dispersing to new openings as they are created (3.7). In deciduous forests, Vankat and Snyder (1991) have shown that the percentage of woody species (vs. herbaceous species) in the groundflora increases with stand age.

3.6 Herbs

The species present and their distributions within and among forests are mainly a result of variations in microclimatic conditions, seed production rates and colonizing abilities. In deciduous forests, a significant decrease in annual and biennial herb species and the predominance of perennial herbs occurs as the forest stand ages (Vankat and Snyder 1991). This successional sequence is also reflected in the proportions of seeds found in the seed banks of forests of varying ages (Roberts and Vankat 1991).

A New England study showed that there were significant differences in the understorey flora between old-growth and secondary (50-60 yr old, regenerating from old field) forests for both coniferous and deciduous forests (Whitney and Foster 1988). There is also evidence from mixed forests that herb patches may play a major role in determining the density and distribution of seedlings of dominant trees species and that the distribution of herb patches is significantly affected by other herb patches as well as tree canopy foliage (Maguire and Forman 1983).

Herbaceous species that emerge and photosynthesize primarily before tree leaf expansion (spring ephemerals) are a typical component of the ground flora of undisturbed deciduous forests. Their distribution, abundance and diversity may provide some indication of forest history (Lutz 1930, Steinbrenner 1951). While the herbaceous flora may be relatively insensitive to selective logging (Reader 1987) when it mimics natural gap formation, it is sensitive to grazing. Native species diversity is dramatically reduced in heavily grazed woodlots (C. Keddy pers. obs.).

3.7 Gaps

In the eastern deciduous forest region, small openings created by tree falls play an important role in shaping forest structure (Fig. 5). A single tree may fall, creating the gap, while slightly larger gaps are formed when a falling tree creates a domino effect causing a few other trees in its path to fall with it. The relationship between gap size and relative frequency and gap size and the proportion of the forest occupied is provided in Table 1.

Because frequent gap formation removes many of the large or senescent trees, old-growth stands do not have a uniform, unbroken canopy of large trees. Rather, these stands typically have an irregular, uneven-aged canopy with trees in various stages of development. On a regional basis as well it can be seen that natural disturbance results in 'pristine' habitats of a variety of successional stages. For example, Lorimer and Frelich (1994) found for 56,000 acres of remnant 'pristine' hemlock-hardwood forests in upper Michigan that old-growth occupied 70% while mature stands occupied 21% and pole stands occupied 9%.

Small gaps formed from the downing of a few trees do not greatly affect forest structure for a long period of time. They promote biodiversity in the forest interior by creating additional habitat for animals and providing sites where shade-intolerant species become established as common associates with more shade-tolerant ones. Gaps are sites of renewal and perpetuation in a dynamic ecosystem that ensures a shifting mosaic steady state (Martin 1992).

Large openings of several hectares, which may occur in the forest canopy as a result of catastrophic disturbances due to intense thunderstorms, hurricanes, tornadoes and extensive fires, are generally infrequent in much of the northern hardwood region (Fig. 5, Lorimer and Frelich 1994). The rotation period (time between occurrences) of these disturbances increases exponentially with disturbance intensity. In forests dominated by sugar maple and hemlock in Michigan, heavy disturbances (removing $\geq$ 60% of the canopy), have an estimated rotation period of >1500 years while less intense disturbances (removing 30-50% of the canopy) recur about every 300 years (Frelich and Lorimer 1991a). Disturbances on this scale can significantly affect forest structure and composition (Martin 1992) and in some forest regions (e.g., boreal, montane) dominate the regeneration process (Runkle 1990; Frelich and Lorimer 1991b).

Figure 5: Geography of disturbance for the eastern deciduous forest region (from Runkle, 1990). The numbers refer to the forest regions of Braun (1950). F, f=locations where fire was of major and minor importance, respectively; B, b=locations where big blowdowns were of major and minor importance, respectively; G, g= locations where gaps were of major and minor significance, respectively.

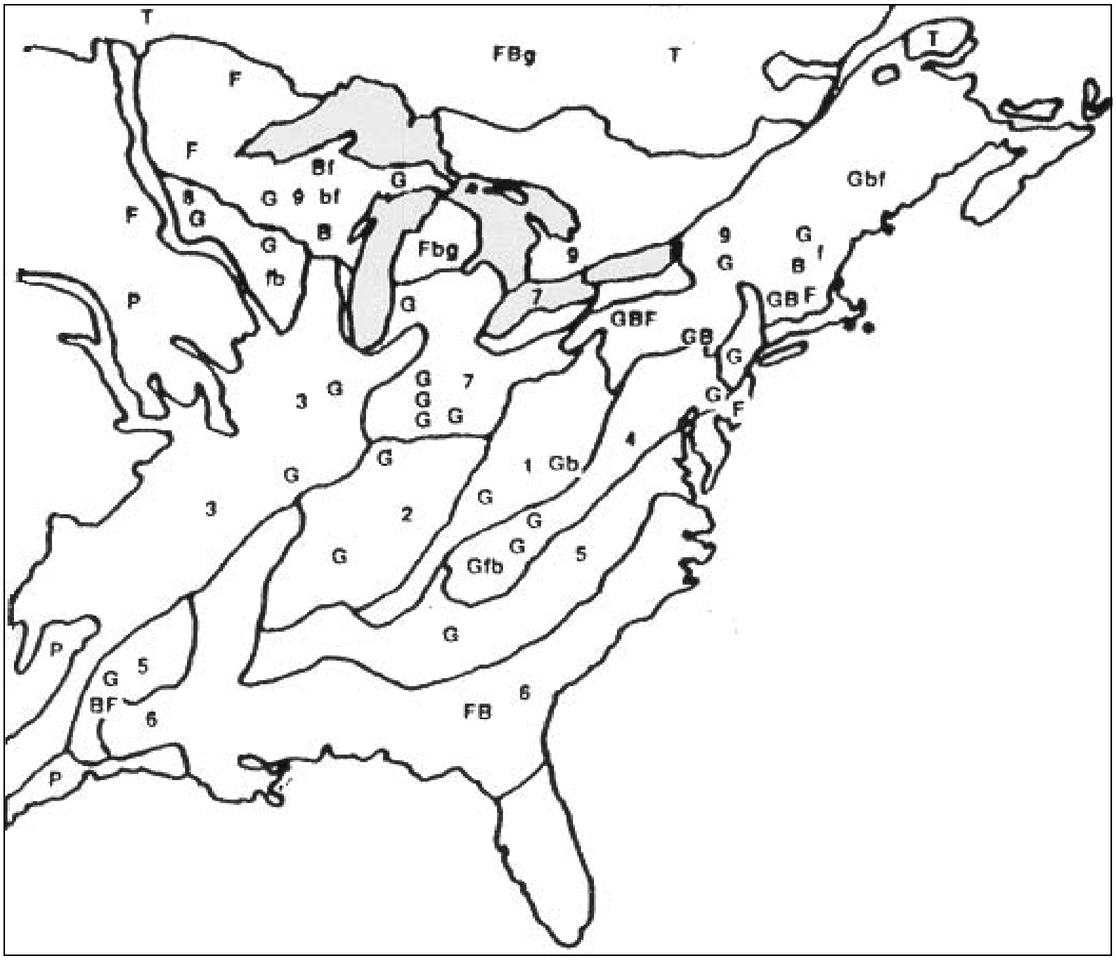


Table 1. Relative frequency (% of total number of gaps) of canopy gaps of various size classes in old growth deciduous forests (numbers in brackets are % of land area in gaps of a given size).

GAP SIZE (m^2)

LOCATION	<100	100-200	200-300	300-400	400-500	500-600	600-700	700-800	800-900	>900
Ohio (Runkle 1991)	64 (2.4)	30 (3.7)	0	0	3 (.2)	3 (.7)	0	0	0	0
Quebec (Payette *et al*. 1990)	20	41	21	19	0	0	0	0	0	0
Appalachians (Runkle 1991)	65 (6.5)	21 (2.6)	5 (.9)	5 (1.2)	2 (.5)	<1 (.1)	1 (.5)	<1 (.2)	0	1 (.4)

4.0 STRUCTURE OF DECIDUOUS FORESTS

In eastern Ontario, the following deciduous cover types have been described by Boysen (1994):

moist poplar
dry aspen
sugar maple
sugar maple-bitternut hickory-black maple
sugar maple-ironwood
sugar maple-white ash-basswood
sugar maple-basswood
sugar maple-beech
bur oak
red oak
white oak
red maple-ash
silver maple-black ash-red maple
black willow-Manitoba maple
silver maple-ash
rich lowland hardwoods (basswood-hackberry-oak)

Many of these are represented in the literature reviewed, although they are not covered well enough for comparison and contrast on a structural basis. The majority of data published in the literature relate to old-growth forests, limiting the scope for making structural comparisons with younger forests. As well, the literature focused on upland forests, providing fewer studies of wetland and lowland forests.

Data on deciduous forest structure are summarized in Table 2, while the original data are in Appendix A or in the text below. Each of the structural characteristics discussed in section 3.0, for which data specific to deciduous forests are available, will be briefly reviewed. In addition, the results of the review of mosses and fungi by Keddy and Drummond (1994) are presented.

4.1 Canopy Composition

Table 2 shows that few species (4 on average) constituted the majority (70%) of the canopy tree stems in old-growth deciduous forests of eastern North America. On

Table 2. Summary of structural characteristics of deciduous, mixed and coniferous forests in eastern North America. Mean values are provided with ranges in parentheses. Where few data are available, only ranges are provided. A single number indicates one observation. The data from which these figures are derived are provided in Appendices A, B and C (---= no information available, og= old-growth, a= all old growth and mature stands combined, d= disturbed/young, u= upland, l=lowland, DBH= diameter breast height).

STRUCTURAL FEATURE		FOREST TYPE	
Canopy Composition (live trees >10cm DBH)	**Deciduous**	**Mixed**	**Coniferous**
No. species constituting majority (70%) of canopy tree stems	3.8 og (2-6)	2.9 og (2-4)	2.2 og (1-4)
No. species contributing 15% of canopy tree stems	2.1 og (1-3)	2.4 og (1-4)	2.1 og (1-3)
Density (stems/ha)	398 (184-1127) og 496 (184-1127) a	500 (200-1450) og 623 (200-1938) a	556 (189-925) og 721 (189-1267) a
Basal area (m^2/ha)	36 (27-47) og 32 (19-47) a 17 (10-24) d	36 (22-57) og 34 (22-57) a	42 (19-64) ogu 40 (36-47) ogl 34 (19-36) au
Snags (standing dead trees >10cm DBH)*			
Density (trees/ha)	98 (49-245) a 99 (37-164) d	129 (49-487) a 125 (31-219) d	309 (40-574) a
% total density	12 (6-22) a	12 (5-24) a	27 (14-36) a
Basal area (m^2/ha)	4.9 (.78-19.3) a	5.4 (.9-12.0) a	20.5 (4.9-35.0) a
% total basal area	11 (2-34) a	14 (3-35) a	35 (11-58) a
Logs** Weight (tonnes/ha)	32 (16-54) og	42 og	---
Density (logs/ha)	58 (50-70) og	---	---

STRUCTURAL FEATURE	FOREST TYPE		
Logs**	**Deciduous**	**Mixed**	**Coniferous**
Large log density (>60cm DBH/ha)	>3 og	---	---
Surface area (m^2/ha)	164 og	300 og	---
Log decay state (% logs in classes 4+5)	63-70 og		
Shrubs			
Species/m^2	.014 (.001-.025) og	.015 (.002-.042) og	---
Species/stand	12 (5-19) og	6 (4-10) og	---
Herbs			
Species/m^2	.271 (.005-.350) og	.320 (.020-.783) og	---
Species/stand	48 (19-48) og	42 (11-54) og	---
Spring ephemerals/stand	8 (6-11)* og	---	---
Canopy Gaps***			
Canopy gap area (m^2)	107 (9-385) og	---	38 (9-147) og
% area in canopy gaps	5-24 og	3-5 og	---
Extended gaps (m^2)	392 (200-942) og	---	---
% area in extended gaps	12-47 og	7-14 og	---
Mean age gap tree (yr)	138 (127-153) og	---	---

* total= live trees + snags
** log decay states as described by MacMillan (1981): classes range from 1-5 in order of increasing stages of decay; class 5 logs have no bark, twigs or branches remaining, are at least 50% covered by mosses and oval in shape
*** gap tree= tree that falls resulting in cap creation, canopy gap= area directly under the canopy opening, extended gap= canopy gap + adjacent area extending to the bases of canopy trees that surround the gap

average, more species made up the majority in deciduous than mixed or coniferous forests. Only two species typically contributed more than 15% of the total number of canopy tree stems in deciduous forests. These results are similar to those of Keddy and Drummond (1994) who included a large portion of southern deciduous forests in their study.

4.2 Tree Size

The basal area of live canopy trees was highest in old-growth forests (36 m^2/ha) and it averaged 32 m^2/ha for all forests (old-growth combined with mature forests) not recently disturbed (Table 2). Young forests had basal areas from 10 to 24 m^2/ha. Keddy and Drummond (1994) reported a mean basal area of 21 m^2/ha for recently disturbed forests.

The density of live trees forming the canopy of old-growth deciduous forests (Table 2) was less (398 stems/ha) than the average determined for all forests recorded (496 stems/ha). Canopy tree densities for deciduous forests were less than those of mixed and coniferous forests.

4.3 Logs and Snags

In the studies examined, information on logs was presented in terms of number, weight, density and surface area. The amount of data available on logs is much more limited than that for canopy composition and tree size. In old-growth deciduous forests an average of 58 logs weighing a total of 32 tonnes are found on one hectare. One study showed that these logs covered about 2% of the forest floor. MacMillan (1981) noted for deciduous forests that large (>40 cm diameter), heavily decayed (decay class 5= no bark or twigs, with 50% bryophytic cover, oval in shape) logs would be indicative of old-growth forest. Keddy and Drummond (1994) suggested that the presence of large logs, both firm and decayed, would be indicative of a healthy, undisturbed forest. In a deciduous forest in Kentucky, Martin (1992) found an average of more than three logs ≥60 cm in diameter/ha and at least 70% of all logs in an advanced stage of decay. MacMillan (1981) reported 63% of the logs in a deciduous forest in Indiana were in decay class 4 or 5 (classes ranged from 1 (least decay) to 5, which was described above).

Since few of the forests for which snag data were available were specifically identified as old-growth, canopy snags were examined for mature and old-growth forest combined and, separately, for those forests noted as disturbed/young. The average density of snags in both categories was similar (98 vs. 99 stems/ha), although the maximum number of snags was greatest in the former group (245 stems/ha). The percentage of trees reaching canopy height (live trees + snags) that was snags ranged from 6 to 22 for mature and old-growth forests. Snags had a basal area of 4.9 m^2/ha which corresponds to an average of 11% of the total basal area (live trees + snags). The density of snags was lowest in deciduous forests. Basal area and the percentages of snags were similar for deciduous and mixed forests and much lower in deciduous than conifer forests.

For deciduous forests, Keddy and Drummond (1994) suggest that more than four large snags (wildlife trees, >50.8 cm DBH)/10 ha be considered typical in old-growth forest. Martin (1992) indicates that at old-growth forests typically have at least three snags/ha $\geq$ 60 cm DBH/ha.

4.4 Shrubs

Both the number and density of shrub species in the forest were examined (Table 2). Shrub species density (0.014 species/m^2) in deciduous forests was similar to that for mixed forests, but the mean number of species recorded in a stand was higher for deciduous (12) than mixed (6) forests.

4.5 Herbs

Both the number and density of herb species in the forest were examined (Table 2). Herb species density (0.271 species/m^2) was similar to that for mixed forests as was the mean number of species recorded in a stand. Keddy and Drummond (1994) provided data on spring ephemerals found in old-growth deciduous forests and showed that typically six to 11 species occur, with an average of eight species.

4.6 Mosses and Fungi

Keddy and Drummond (1994) listed corticulous mosses expected to be found in mesic old-growth beech-maple forests. Based on these data, they suggest that the presence of more than six species in a forest is an indication of biologically diverse forest.

Old-growth forests are hosts to macrofungi that are not found in other habitats (Keddy and Drummond 1994) and many late successional tree species depend upon them for regeneration and perpetuation (Perry *et al*. 1990). Insufficient information is currently available to establish macrofungi indicators of forest health for forests in the EOMF region.

4.7 Gaps

Although most old-growth northern hardwood stands are broadly uneven-aged and have a substantial component of small and medium sized trees, the incidence of recent canopy gaps is highly variable. In old-growth hardwoods in upper Michigan, Frelich and Lorimer (1991b) found that large trees (>45 cm DBH) generally occupied about half the canopy, mature trees (25-45 cm DBH) composed about one-third and the remainder was occupied by saplings and poles that had grown up in gaps.

Small gaps occur frequently in mesophytic hardwoods, covering an average of 0.4 to 2.0% of the land area annually (Runkle 1985, Lorimer and Frelich 1994). Gap formation can therefore cause nearly complete turnover in the canopy in less than 250 years.

In the forest data reviewed for this study, canopy gaps (area directly under the canopy opening) averaged 107 m^2 and covered 5 to 24% of the forest area at any one point in time (Table 2). Extended gaps (canopy gap plus adjacent area extending to the bases of canopy trees that surround the gap) averaged 392 m^2 and covered 12 to 47% of the forest area. Gap trees (the tree that falls, resulting in gap creation) averaged 138 years in age. Data for gaps in mixed and coniferous forests is insufficient for comparison.

5.0 STRUCTURE OF MIXED FORESTS

In eastern Ontario, the following mixed cover types have been described by Boysen (1994):

dry boreal mixedwood
rich boreal mixedwood
hemlock-red maple-white pine
white cedar-hemlock-yellow birch
boreal organic swamp

The majority of the mixed forests described in the literature for eastern North America were dominated by hemlock and northern hardwoods (Appendix B). Numerous studies have been conducted on white birch-red spruce dominated forests, particulary in New England and New York. This forest cover type is very restricted in southeastern Ontario. It is ecologically similar to the white spruce-balsam fir-white birch boreal forest. Of particular interest in the EOMF region are the studies of red spruce-yellow birch (and red spruce-northern hardwoods) forests since, in the past, this forest cover type occurred commonly in southeastern Ontario (Eyre 1980). There is a paucity of data on forests with white cedar as a dominant and wetland and lowland mixed forests.

There is insufficient information from the literature to make comparisons among mixed cover types on a structural basis. The majority of data published in the literature relate to old-growth forests, limiting the scope for making structural comparisons with younger forests.

Data on mixed forest structure are summarized in Table 2, while the original data are in Appendix B or discussed in the text below. Each of the structural characteristics discussed in section 3.0, for which data specific to mixed forests are available, will be briefly reviewed.

5.1 Canopy Composition

Table 2 shows that few species (3 on average) constituted the majority (70%) of the canopy tree stems in old-growth mixed forests of eastern North America. On average, fewer species made up the majority in mixed than deciduous forests and more species composed the majority of mixed than coniferous forests (Table 2). Only two species typically contributed more than 15% of the total number of canopy tree stems in mixed forests.

5.2 Tree Size

The total basal area of live canopy trees was highest in old-growth forests (36 m^2/ha) and it averaged 34 m^2/ha for all forests not recently disturbed (Table 2). No comparable data were found for young mixed forests. Martin (1992) suggested mixed old-growth forests could be characterized by basal areas of more than 25 m^2/ha (live trees).

The density of live trees forming the canopy of old-growth mixed forests (Table 2) was less (500 stems/ha) than the average determined for all forests (old-growth combined with mature forests) recorded (623 stems/ha). Canopy tree densities for mixed forests were more than those of deciduous forests and less than those for coniferous forests. Martin (1992) suggests a value of 250 stems/ha as an average expected density for old-growth mixed mesophytic forests.

5.3 Logs and Snags

Only one study (McFee and Stone 1966) provided data on weights or areas of logs in mixed forest (Table 2). This study of a red spruce-yellow birch forest in New York found 42 tonnes of logs/ha that covered an area of 300 m^2.

Since few of the forests for which snag data were available were specifically identified as old-growth, canopy snags were examined for mature and old-growth forest combined and, separately, for those forests noted as disturbed/young. The average density of snags in both categories was similar (129 vs. 125 stems/ha), although the maximum number of snags was greatest in the former group (489 stems/ha). In mixed forests snag density was higher than in deciduous forests, but lower than in coniferous forests. The percentage of canopy trees (live trees + snags) that was snags ranged from 5 to 24 for mature and old-growth forests. Snags had a mean basal area of 5.4 m^2/ha which corresponds to an average of 14% of the total (live trees + snags) basal area. Basal area and the percentages of snags were similar for mixed and deciduous forests and much lower in mixed than conifer forests.

5.4 Shrubs

Both the number and density of shrub species in the forest were examined (Table 2). Shrub species density (0.015 species/m^2) was similar to that for deciduous forests, but the mean number of species recorded in a stand was lower for mixed (6) than deciduous (12) forests.

5.5 Herbs

Both the number and density of herb species in the forest were examined (Table 2). Herb species density (0.330 species/m^2) was similar to that for deciduous forests as was the mean number of species recorded in a stand.

5.6 Gaps

Few data are available from the literature concerning canopy gaps in mixed forests. The results of two studies of beech-hemlock forest shown in Table 2 indicate that canopy gaps cover 3-5% and extended gaps cover 7-14% of the forest land area. Information on gap size is missing.

6.0 STRUCTURE OF CONIFEROUS FORESTS

In eastern Ontario, Boysen (1994) describes the following cover types which are entirely composed of conifers or have variants that are entirely composed of conifers:

jack pine
dry boreal mixedwood
rich boreal mixedwood
hemlock-white pine
eastern red cedar
boreal organic swamp

Studies from the literature for eastern North America covered the majority of the forest cover types listed above (Table 2) including both upland and lowland types. All except one of the red spruce-balsam fir stands were located in montane boreal forests for which there is no direct counterpart in eastern Ontario (Eyre 1980).

There is insufficient information from the literature to make comparisons among coniferous cover types on a structural basis. All the data published in the literature relate to old-growth and mature forests, making structural comparisons with younger forests impossible.

Data on mixed forest structure are summarized in Table 2, while the original data are in Appendix C or in the text below. Each of the structural characteristics discussed in section 3.0, for which data specific to coniferous forests are available, will be briefly reviewed.

6.1 Canopy Composition

Table 2 shows that few species (2 on average) constituted the majority (70%) of the canopy tree stems of old-growth coniferous forests of eastern North America. On average, fewer species made up the majority in coniferous than in deciduous and mixed forests (Table 2). Only two species typically made up more than 15% of the total number of canopy tree stems in coniferous forests.

6.2 Tree Size

The total basal area of live canopy trees was highest in old-growth forests (42 m^2/ha- uplands; 40 m^2/ha- lowland/wetlands) and it averaged 34 m^2/ha for all upland forests not recently disturbed (Table 2). No comparable data were found for young coniferous forests.

The density of live trees forming the canopy of old-growth coniferous forests (Table 2) was less (556 stems/ha) than the average determined for all forests (old-growth and mature combined, 721 stems/ha). Canopy tree densities for coniferous forests were higher than those for deciduous and mixed forests.

6.3 Logs and Snags

No information on the weight, density or surface area of logs was found for coniferous forests.

Since few of the forests for which snag data were available were specifically identified as old-growth, canopy snags were examined for mature and old-growth forest combined. Snags density ranged from 40 to 574 stems/ha and, on average was higher than in deciduous and mixed forests. The percentage of canopy trees (live trees + snags) that was snags ranged from 14 to 36 for mature and old-growth forests. Snags had a mean basal area of 20.5 m^2/ha which corresponds to an average of 35% of the total (live trees + snags) basal area. Basal area and the percentages of snags were higher for conifer forests than for deciduous and mixed forests.

6.4 Shrubs

No information on the number and density of shrub species in coniferous forests was found during the literature review.

6.5 Herbs

No information on the number and density of herb species in coniferous forests was found during the literature review.

6.6 Gaps

Few data are available from the literature concerning canopy gaps in coniferous forests. In 17 spruce-balsam fir stands, canopy gaps averaged 38 m^2 and ranged in size from 9 to 147 m^2 (Table 2).

7.0 DEVELOPMENT OF FOREST STRUCTURE GUIDELINES

Based on the literature review, means and ranges of structural variables were determined for deciduous, mixed and coniferous forest cover types (Table 2). As far as possible these figures were generated using data from cover types found within the EOMF region to enhance their utility for applications to forest management. Most of these data are for old-growth forests or old-growth and mature forests combined and few concern young/disturbed forests. As well, one cannot assume that the shape of the curve for the relationship between a forest structure variable and forest age is simple as shown by the relationship between age and early successional species (Fig. 2). For these reasons, the guidelines presented in Table 3 take the form of providing numerical values for structural variables at the high end of the age spectrum (when a value can be determined based on information in this document or those by Keddy and Drummond (1994) and Martin (1992) and an indication of the direction of the trend from young to old forest. Old-growth values can be thought of as the closest one can get to control stands against which current forest conditions can be compared. In the absence of values from the literature for structural components of mixed forests, it is suggested that values for deciduous forests be used as first approximations for the former since both forest types have many similarities as shown in Table 2. The absence in the literature of structural data for coniferous forests in eastern North America cannot be dealt with in a similar manner because they differ in many ways from deciduous forests. Suggestions for further defining the structural variables in Table 3 and refining their relationships with forest development stage are provided in section 8.0.

The value of a structural variable for a particular forest can be compared to the value and trend in Table 3. If the stand value is beyond the value in the table, the variable is considered to be typical of old-growth/mature forest. Where a stand has not yet reached the value given in the table, management could incorporate action to enhance the progression of the forest toward the tabled value. Management recommendations should be based on the evaluation of these structural variables as a group, rather than singly.

The structural basis of forest management must also take into consideration other factors such as forest size. In small forest fragments, for example, the creation of a gap of a given size would have a more dramatic effect on forest structure than it would in large forest. Ideally, with refinement, the structural variables outlined in this document will be useful for predicting, comparing and evaluating forest structural characteristics and will promote the maintenance, restoration and regeneration of natural forest stands and the growth of old-growth forest in eastern Ontario.

Table 3. Structural guidelines for assessing and managing forests in eastern Ontario based on Table 2 and discussions in the text. (D= decrease from young to old forest, I= increase from young to old forest, NA= not applicable, *= recommended guideline not based on actual data, ?= no value/insufficient values found during literature search).

			Expected mature/old growth value		
Structural Characteristic	**Measurement**	**Trend**	**Deciduous**	**Mixed**	**Coniferous**
Canopy composition (live trees >10cm DBH)	No. species constituting majority (70%) of canopy tree stems	D	<4	<3	<3
	No. species contributing 15% of canopy tree stems	D	<3	<3	<3
	Percentage of shade-tolerant species*	I	>80%	>80%	?
	Tree density (stems/ha)	D	<450	<550	<600
	Tree basal area (m^2/ha)	I	>30	>30	>30
Snags (standing dead trees >10cm DBH)	Snag density (/ha)	D	100	125	300
	Large snag density (> 60 cm DBH/ha)	I	>3	>3	?
Logs**	Log density (/ha)	I	50	50	?
	Large log density (>60 cm diam/ha)	I	>3	>3	?
	Log decay state (% logs in classes 4+5)	I	60%	60%	60%

Structural Characteristic	Measurement	Trend	Expected mature/old growth value Deciduous	Mixed	Coniferous
Shrubs	Percentage of shade-tolerant species*	I	80%	80%	80%
	Percentage of typical species*	I	80%	80%	80%
Herbs	Percentage of shade-tolerant species*	I	80%	80%	80%
	Percentage of typical species*	I	80%	80%	80%
	No. spring ephemeral species	I	>6	>6	NA
Gaps***	Mean canopy gap area (m^2)	I	>100	>100	35
	% land area in canopy gaps	I	5-24	3-5	?
	Mean extended gap area (m^2)	I	>350	>350	?
	% land area in extended gaps (m^2)	I	12-47	7-14	?
	Mean age gap tree (yr)	I	130	130	?

**log decay states as described by MacMillan (1981): classes range from 1 to 5 in order of increasing stages of decay; class 5 logs have no bark, twigs or branches remaining, are at least 50% covered by mosses and oval in shape

*** gap tree= tree that falls resulting in gap creation, canopy gap= area directly under the canopy opening, extended gap= canopy gap + adjacent area extending to the bases of canopy trees that surround the gap tab2

8.0 FURTHER WORK

In order to proceed further in preparing a refined set of structural guidelines, further work should be undertaken in six areas as described below. Collection of additional data from Ontario stands would be most relevant.

1. Field Calibration of Structural Data

It is necessary to calibrate this work for particular mature and old-growth cover types which are currently found and potentially could be restored in the EOMF region. The values in Table 3 need to be further tuned to reflect variations in site conditions that will be reflected in growth characteristics of component species. On a dry site, for example, a forest cover type would likely have different structural characteristics than it would on a moist site. At the same time, the utility of the structural variables discussed in this report (as well as suggestions for additional variables) for characterizing all cover types found in eastern Ontario requires assessment.

2. Structural Data

The structure of deciduous forests was best covered in the literature. For mixed and coniferous forests, however, data were lacking or few for major structural variables including logs (weight, density, decomposition) and canopy gaps (size, % land area). Collection of data from Ontario stands would be most relevant.

3. Cover Type Representation

To date, the literature has focused mainly on upland forests and generally neglected lowland and wetland forests. In eastern Ontario, cover types with white cedar are important, yet little structural information was available. The collection of data for all structural variables is required for these cover types.

4. Structure-Age Relationship

Little information on the structural characteristics of young forests was found in the literature. In order to understand trends in the structural variables over time and make management recommendations to guide the future management of a stand, it is important to collect and examine structural data for variables from forests covering a range of successional stages.

5. Shrubs and Herbs

Due to the considerable geographical variation in the forests examined, shrub and herb data were summarized in terms of density and numbers of species rather than by the presence or absence of particular species or groups of species (except for spring ephemerals in deciduous forests). By examining the relationship between these measures and forest age/disturbance, their utility as structural indicators for forest management could be clarified.

There is a need to prepare lists of herbs and shrubs typical of young, mature and old-growth forest cover types found in eastern Ontario against which particular forest stands can be compared and evaluated. Species could be assigned a `value' which would indicate their significance as indicators of particular (e.g., old-growth) conditions.

6. Other Variables

To this point, only the physical structure of the forest has been considered in relation to management guidelines. An examination of the relationship between physical structure and wildlife species as integrators of forest integrity should be made. Keddy and Drummond (1994) have laid a foundation for this work through their discussions of cavity-dwelling birds and mammals, avian diversity and large vertebrates.

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APPENDIX A

STRUCTURAL DATA FOR DECIDUOUS FORESTS

Table 4. Canopy species composition (% total number of live stems) for old-growth deciduous forests (+= <0.5%).

	Study							
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	
Acer rubrum			10	4		+		9
Acer saccharum	24	8	19	28	15	45	1	
Betula allegheniensis						5	1	
Fagus grandifolia			11	21		3	21	56
Tsuga canadensis						4	8	
Fraxinus americana			1	4	3	2		
Fraxinus nigra						23	+	
Prunus serotina					1			
Ostrya virginiana		1	1	6	2	2	13	
Populus grandidentata					1			
Quercus alba			32	10	18			7
Quercus bicolor							+	
Quercus macrocarpa						+		
Quercus michauxii								2
Quercus rubra			4	5				1
Quercus shumardii								+
Quercus velutina		1	1	10				
Tilia americana		55				11	8	
Ulmus americana		20			2	26	1	1
Ulmus flava				2	1			
Ulmus rubra							+	
Carya cordiformis				1	5	8	2	
Carya glabra			6	7	9			+
Carya laciniosa			1					
Carya ovata			7	2	14			+
Liriodendron tulipifera			4					4

	Study							
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	
Morus rubra			1					
Juglans cineria						+	+	
Juglans nigra					2			
Nyssa sylvatica			4	3				6
Liquidambar styraciflua								13
Cornus florida			9	15	4			
Carpinus caroliniana								+
No. species constituting 70% of canopy stems	**2**	**6**	**5**	**4**	**4**	**3**	**3**	
No. species contributing 15% of canopy stems	**3**	**1**	**3**	**2**	**3**	**2**	**1**	

Study	Forest Type	Minimum DBH (cm)	Location	Reference
1	smaple-basswood-elm	10.2	Minnesota	Kittredge (1934)
2	woak	"	Indiana	Cain (1932)
3	beech-smaple-ash	7.6	"	Potzger and Chandler (1953)
4	oak-hickory	"	"	"
5	elm-ash*	15	Quebec	Brisson *et al*. (1992)
6	smaple-beech	"	"	"
7	beech-swgum-rmaple	10	Indiana	Jackson and Barnes (1975)

*before Dutch Elm Disease

Table 5. Density of live trees in deciduous forests.

Density (stems/ha)	**Forest Type**	**Tree Size** (DBH, cm)	**Age** (yr)	**Location**	**Reference**
300	woak	≥10.2	og	Indiana	Cain (1932)
250	woak	>2.5	"	Ohio	McCarthy *et al*. (1987)
475 (mean)	woak-bloak-roak	≥ 10	>40	Connecticut	Tritton and Siccama (1990)*
462 (mean)	"	"	"	"	"
626	"	"	"	"	"
500	oak-hickory	≥7.6	og	Indiana	Potzger and Chandler (1953)
418	oak-hickory	≥10.2	"	"	Potzger and Friesner (1934)
277	smaple-beech	>15	"	Quebec	Brisson *et al*. (1992)
530 (mean)	smaple-beech-ybirch	≥10	>40	New Hampshire	Tritton and Siccama (1990)
444	"	"	"	Vermont	"
613	"	"	"	New Hampshire	"
627	"	"	"	"	"
844	"	"	"	"	"
545	"	"	"	"	"
669	"	"	"	Vermont	"
633 (mean)	"	"	"	"	"
649	"	"	"	New York	"
1127	smaple-basswood-elm	>10.2	og	Minnesota	Kittredge (1934)

Density (stems/ha)	**Forest Type**	**Tree Size** (DBH, cm)	**Age** (yr)	**Location**	**Reference**
363	elm-ash (L)	>15	og	Quebec	Brisson *et al.* (1992)
275	swgum-tulip-rmaple (L)	≥10.2	"	Indiana	Jackson (1969)
242	beech-swgum-rmaple (L)	>10	"	"	Jackson and Barnes (1975)
184	beech-swgum-rmaple (L)	"	"	"	"
315	smaple-basswood-tulip	≥12.5	"	Kentucky	Martin (1975)
525	beech-smaple-ash	≥7.6	"	Indiana	Potzger and Chandler (1953)

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants
DBH= diameter breast height, tree size= minimum DBH of trees used to determine density, og= old growth

Table 6. Basal area of live trees in deciduous forests.

Basal Area (m^2/ha)	Forest Type	Tree Size (DBH, cm)	Age (yr)	Location	Reference
22 (mean)	woak-bloak-roak	≥ 10	>40	Connecticut	Tritton and Siccama (1990)*
19 (mean)	"	"	"	"	"
19	"	"	"	"	"
28	woak-bloak	>10	og	Wisconsin	McCune and Cottam (1985)
41	woak	?	"	Indiana	Cain (1932)
32	rmaple-smaple-roak	>10	"	Michigan	Pregitzer and Barnes (1984)
47	rmaple-ybirch-roak	"	"	"	"
36	smaple-beech	?	"	New York	Beatty (1984)
29	"	>15	"	Quebec	Brisson *et al*. (1992)
37	beech-smaple	>15	og	Michigan + Ohio	Woods (1984)
27 (mean)	smaple-beech-ybirch	≥10	>40	New Hampshire	Tritton and Siccama (1990)
31	"	"	"	"	"
28	"	"	"	"	"
38	"	"	"	"	"
31	"	"	"	"	"
32	"	"	"	"	"
27	"	"	"	Vermont	"
30 (mean)	"	"	"	"	"
40	"	"	"	New York	"
35	smaple-ybirch	>10	og	Michigan	Pregitzer and Barnes (1984)
39	"	"	"	"	"
36	"	"	"	"	"

Basal Area (m^2/ha)	**Forest Type**	**Tree Size (DBH, cm)**	**Age (yr)**	**Location**	**Reference**
39	smaple-basswood	>10	og	Michigan	Pregitzer and Barnes (1984)
27	"	"	"	"	Pregitzer *et al*. (1983)
45	"	>15	"	Minnesota	Woods (1984)
31	elm-ash	>15	"	Quebec	Brisson *et al*. (1992)

10	pin cherry	all trees	15	New Hampshire	Gore and Patterson (1986)
24	wbirch-trembling aspen	"	50	"	"

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants
DBH= diameter breast height, tree size= minimum DBH of trees used to determine basal area, og = old growth

Table 7. Density of snags in deciduous forests.

Density (stems/ha)	(% total)	Forest Type	Tree Size (DBH, cm)	Age (yr)	Location	Reference
49 (mean)	9	woak-bloak-roak	≥ 10	>40	Connecticut	Tritton and Siccama (1990)*
88 (mean)	16	"	"	"	"	"
93	12	"	"	"	"	"
71 (mean)	11	smaple-beech-ybirch	"	"	New Hampshire	"
51	10	"	"	"	Vermont	"
90	13	"	"	"	New Hampshire	"
131	17	"	"	"	"	"
245	22	"	"	"	"	"
87	14	"	"	"	"	"
116	15	"	"	"	Vermont	"
74 (mean)	10	"	"	"	"	"
123	16	"	"	"	New York	"
70	?	beech-smaple	> 5	og	New York	Leopold *et al*. (1988)
21	5	smaple-basswood-ash	"	"	Illinois	Jackson and Petty (1971)
168	?	oak-hickory	2	> 100	Virginia	Rosenberg *et al*. (1988)
?	11	smaple-beech	?	94-126	West Virginia	Carey (1983)
?	6	"	"	206	"	"

164	?	oak-hickory	2	60-79	Virginia	Rosenberg *et al*. (1988)
146	"	"	"	80-99	Virginia	"
?	10	smaple-beech	?	61-69	West Virginia	Carey (1983)
50	?	upland hardwood	> 10.2	40->60	South Carolina	Carmichael and Guynn (1983)
37	"	cove hardwood	"	"	"	"

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants
total= density of live trees + snags, DBH= diameter breast height, tree size= minimum DBH of trees used to determine density, og= old growth

Table 8. Basal area of snags in deciduous forests.

Basal Area (m^2/ha)		Forest Type (% total)	Tree Size (DBH, cm)	Age (yr)	Location	Reference
1.5 (mean)	6	woak-bloak-roak	≥ 10	>40	Connecticut	Tritton and Siccama (1990)*
2.7 (mean)	12	"	"	"	"	"
2.2	10	"	"	"	"	"
3.6 (mean)	11	smaple-beech-ybirch	"	"	New Hampshire	"
3.6	10	"	"	"	Vermont	"
1.9	6	"	"	"	New Hampshire	"
4.4	11	"	"	"	"	"
16.0	34	"	"	"	"	"
5.4	14	"	"	"	"	"
4.0	13	"	"	"	Vermont	"
2.1 (mean)	6	"	"	"	"	"
7.1	15	"	"	"	New York	"
19.3	7	smaple-basswood-ash	>5	og	Illinois	Jackson and Petty (1971)
0.78	2	beech-smaple	>5	"	New York	Leopold *et al*. (1988)
2.2	?	oak-hickory	≥2	60-79	Virginia	Rosenberg *et al*. (1988)**
2.8	?	"	"	80-99	"	"
4.5	?	"	"	>100	"	"

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants
**mean DBH (cm) of snags for three age classes from youngest to oldest= 10.7, 12.2, 14.1
total= basal area of live trees + snags, DBH= diameter breast height, tree size= minimum DBH of trees used to determine basal area, og = old growth

Table 9. Logs in deciduous forests.

Forest Type	Weight (tonnes/ha)	Density (logs/ha)	Log Size (diam. cm)	Surface **Area** (m²/ha)	Forest Age (yr)		Location Reference
smaple-wbirch-beech	54		all		100	NH	Gore and Patterson (1986)
beech-ybirch-smaple	42		"		og	"	"
beech-birch	29		7.5		"	?	Keddy and Drummond (1994)
oak-hickory-maple	16		5	164	"	IND	MacMillan (1981)
n hardwood	28-34		?		170	NH	Bormann and Likens (1979)
mixed oak	27		?		og	NJ	Lang and Forman (1978)
mixed oak	21		7.5		"	?	Keddy and Drummond (1994)
oak-hickory		54	$\geq$20		149	ILL	Thompson (1980)
smaple-roak		50	"		180	"	"
"		70	"		240	"	"
-------------------------							
wbirch-tremaspen	32		all?		50	NH	Gore and Patterson (1986)
pin cherry	32		"		15	"	"
no trees	86		-		1	"	"

log size= minimum diameter of logs used to determine structural measures

Table 10. Richness of herb and shrub species in old growth deciduous forests.

Forest Type	Herbs (sp./m^2)	Herbs (sp./stand)	Shrubs (sp./m^2)	Shrubs (sp./stand)	Location	Reference
northern hardwood		19			?	Rogers (1982)
central hardwood		37			"	"
smaple-beech	.978	84		14	VT	Bormann and Buell (1964)
smaple-beech	.005	25	.001	5	MI	Zager and Pippen (1977)
smaple-beech-basswood	.005	29	.001	5	MI	"
smaple-basswood			.023		MN	Daubenmire (1936)
"			.023	14	WI	Eggler (1938)
"	.35	40	.025	11	"	"
"			.013	8	"	"
beech-smaple	.016	41			MI	Brewer (1980)
"		79		16	OH	Williams (1936)
beech-tulip-smaple		78		19	KY	Braun (1942)

Table 11. Canopy gaps in deciduous forests. Canopy gap sizes are means, followed by the range in sizes.

Forest Type	**Canopy Gap*** (m^2)	(% land area)	**Extended Gap** (m^2)	(% land area)	**Mean Age Gap Tree**	**Location**	**Reference**
oak-maple			925, 909-942			Indiana	Parker and Sherwood (1982)
smaple-ybirch	126, 9-385					Quebec	Payette *et al*. (1990)
smaple-ybuckeye-beech	113	9-24	273	22-47	127	sAppalachians	Runkle (1982)
smaple-buckeye-beech	124	8	281	21		North Carolina	"
beech-smaple	102	7	281	14	153	Ohio	"
smaple-beech	69	5	200	12	135	Pennsylvania	"

* canopy gap= area directly under the canopy opening, extended gap= canopy gap + adjacent area extending to the bases of canopy trees that surround the gap, gap tree= tree that falls resulting in gap creation

APPENDIX B

STRUCTURAL DATA FOR MIXED FORESTS

Table 12. Canopy species composition (% total number of live stems) for old-growth mixed forests (+= <0.5%).

	Study													
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Abies balsamea	+				1	5	2	9	9	1	+			
Acer pennsylvanicum				15	8					5	1			
Acer rubrum		10	17			5	+	4	1	4	7			
Acer saccharum	22	+	23	4	52	6	9	4	7	8	12	12	44	24
Acer spicatum					7									
Betula allegheniensis	23	1			15	20	19	17	4	7			16	28
Betula lenta		6										7		
Betula papyrifera	2		40											
Fagus grandifolia		37		38		10	7	9	9	43	37	10		
Picea rubens				5	16	48	62	45	46	18	30			
Tsuga canadensis	34	25		38	1	7	1	9	9	17	3	38	28	19
Fraxinus americana		+												1
Fraxinus nigra							+	+						
Pinus strobus	2	6	4			+		+	1	+	+		2	2
Pinus resinosa	+		2											
Prunus serotina		1				+		+			1			
Thuja occidentalis									1					3
Ostrya virginiana			2								1			
Populus grandidentata			4								+			
Quercus alba		1												
Quercus macrocarpa												1		
Quercus rubra		1	4											
Ulmus americana	2												3	+
Tilia americana	14		4									14	7	22
Cornus sp.												3		
Halesia sp.												5		
Aesculus sp.		9										2		

							Study							
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Magnolia acuminata		2										3		
Liriodendron tulipifera												5		
Other species							+		+					
No. species constituting 70% of canopy stems	**3**	**3**	**3**	**2**	**3**	**3**	**2**	**3**	**3**	**3**	**3**	**4**	**2**	**3**
No. species contributing 15% of canopy stems	**3**	**2**	**3**	**3**	**3**	**2**	**2**	**2**	**2**	**2**	**2**	**1**	**3**	**4**

Study	Forest Type	Minimum DBH (cm)	Location	Reference
1	smaple-hemlock-ybirch	25	Wisconsin	Stearns (1951)
2	hemlock-wpine-beech	10.2	Pennsylvania	Morey (1936)
3	smaple-wpine	10.2	Minnesota	Kittredge (1934)
4	hemlock-n hardwoods	5	New York	Leopold *et al*. (1988)
5	spruce-n hardwood	5	"	"
6	"	25.4	"	Graves (1899)
7	"	"	"	Hosmer and Bruce (1901)
8	"	"	"	Graves (1899)
9	"	"	"	Hosmer and Bruce (1901)
10	hardwood-conifer	5.1	"	Cutler (1975)
11	upland mixed	10.2	"	Roman (1980)
12	hemlock-basswood-tulip	12.5	North Carolina	Oosting and Bourdeau (1975)
13	smaple-hemlock-ybirch	25	Wisconsin	Stearns (1951)
14	"	"	"	"

Table 13. Density of live trees in mixed forests.

Density (stems/ha)	**Forest Type**	**Tree Size** (DBH, cm)	**Age** (yr)	**Location**	**Reference**
366	hemlock-ybirch	≥ 10	>40	Pennsylvania	Tritton and Siccama (1990)*
447	"	"	"	Connecticut	"
609	"	"	"	Vermont	"
910	"	"	"	New Hampshire	"
802	"	"	"	"	"
333	hemlock-ybirch-beech	>10.2	og	Pennsylvania	Morey (1936)
301	smaple-hemlock-beech	"	"	"	Morey (1936)
200	beech-birch-maple-heml	≥20.3	"	"	Meyer and Stevenson (1943)
642	smaple-wpine	≥10.2	og	Minnesota	Kittredge (1934)
956 (mean)	wbirch-rspruce-bfir	≥10	>40	New Hampshire	Tritton and Siccama (1990)
1029	"	"	"	"	"
517	"	"	"	Vermont	"
599 (mean)	"	"	"	"	"
1938 (mean)	"	"	"	New York	"
627	"	"	"	"	"
321	hemlock-beech-rmaple	≥ 12.5	og	Kentucky	Martin 1975
1450	rspruce-ybirch-beech	"	"	West Virginia	Adams and Stephenson (1989)
478	hemlock-woak-beech	"	"	"	"
287	hemlock-basswood-tulip	"	"	North Carolina	Oosting and Bourdeau (1955)

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants
DBH= diameter breast height, tree size= minimum DBH of trees used to determine density, og= old growth

Table 14. Basal area of live trees in mixed forests.

Basal Area (m^2/ha)	Forest Type	Tree Size (DBH, cm)	Age (yr)	Location	Reference
37	hemlock-wpine-beech	10.2	og	Pennsylvania	Morey (1936)
27	smaple-hemlock-beech	≥10	"	New York	Beatty (1984)
24	beech-birch-maple-hem	≥17.8	"	Pennsylvania	Meyer and Stevenson (1943)
32	hemlock-beech	>10.2	"	"	Hough (1936)
44	hemock-ybirch	≥10	>40	Connecticut	Tritton and Siccama (1990)*
39	"	"	"	Vermont	"
34	"	"	"	New Hampshire	"
29	"	"	"	"	"
25 (mean)	wbirch-rspruce-bfir	"	"	"	"
28	"	"	"	"	"
22	"	"	"	Vermont	"
30 (mean)	"	"	"	"	"
30 (mean)	"	"	"	New York	"
35	"	"	"	"	"
57	wpine-ybirch-roak	>10	og	Michigan	Pregitzer and Barnes (1984)
50	ybirch-hemlock-rmaple	"	"	"	"
29	wpine-oak-smaple	"	"	"	"
35	upland mixed	>10.2	"	"	Roman (1980)
42	hemlock-beech-rmaple	≥12.5	"	Kentucky	Martin (1975)
22	hemlock-woak-beech	"	"	"	"

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants

DBH= diameter breast height, tree size= minimum DBH of trees used to determine basal area, og = old growth

Table 16. Basal area of snags in mixed forests.

Basal Area (m^2/ha)	(% total)	**Forest Type**	**Tree Size** (DBH, cm)	**Age** (yr)	**Location**	**Reference**
6.7	14	hemock-ybirch	≥10	>40	Pennsylvania	Tritton and Siccama (1990)*
4.5	9	"	"	"	Connecticut	"
4.1	9	"	"	"	Vermont	"
0.9	3	"	"	"	New Hampshire	"
2.3	7	"	"	"	"	
?	8	hemlock-beech-smaple	>2.5	og	Pennsylvania	Lutz (1930)
10.4	20	hemlock-n hardwoods	>5	"	New York	Leopold *et al*. (1988)
1.7	7	roak-wpine-rmaple	>2.5	88	Massachussets	Welch *et al*. 1992
7.5	21	spruce-n hardwoods	>5	og	New York	Leopold *et al*. (1988)
3.6 (mean)	13	wbirch-rspruce-bfir	≥10	>40	New Hampshire	Tritton and Siccama (1990)
5.0	15	"	"	"	"	"
5.1 (mean)	15	"	"	"	New York	"
6.5	16	"	"	"	"	"
12.0	35	"	"	"	Vermont	"
4.8 (mean)	14	"	"	"	"	"

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants
total= basal area of live trees + snags, DBH= diameter breast height, tree size= minimum DBH of trees used to determine basal area, og = old growth

Table 17. Logs in mixed forests.

Forest Type	**Weight** (tonnes/ha)	**Density** (logs/ha)	**Log Size** (diam. cm)	**Surface Area** (m^2/ha)	**Forest Age** (yr)	**Location**	**Reference**
rspruce-ybirch	42			300		NY	McFee and Stone (1966)

Table 18. Richness of herb and shrub species in old growth mixed forests.

Forest Type	Herbs (sp./m^2)	Herbs (sp./stand)	Shrubs (sp./m^2)	Shrubs (sp./stand)	Location	Reference
hemlock-beech-smaple	.020	54	.002	5	PE	Hough (1936)
beech-hemlock		11		8	OH	Williams (1936)
smaple-hemlock-ybirch	.257	54	.011	6	WI	Stearns (1951)
"	.292	46	.008	4	"	"
"	.296	42	.012	5	"	"
hemplock-tulip	.783	47	.042	10	VA	Oosting and Bourdeau (1955)

Table 19. Canopy gaps in mixed forests.

Forest Type	Canopy Gap* (m^2)	Canopy Gap* (% land area)	Extended Gap (m^2)	Extended Gap (% land area)	Mean Age Gap Tree	Location	Reference
beech-hemlock		3		7		"	Runkle 1982
"		5		14		"	"

* canopy gap= area directly under the canopy opening, extended gap= canopy gap + adjacent area extending to the bases of canopy trees that surround the gap, gap tree= tree that falls resulting in gap creation

APPENDIX C

STRUCTURAL DATA FOR CONIFEROUS FORESTS

Table 20. Canopy species composition (% total number of live stems) for old-growth coniferous forests (+=<0.5%).

	Study												
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Abies balsamea							4	13	26	11	28	80	77
Acer rubrum	1	2				5	35	4	1	15	2		
Acer saccharum						37		3	1	5			
Betula allegheniensis		12					1	19	7	8	3		
Betula papyrifera						26				1	16	19	15
Fagus grandifolia	6	11						3	+				
Picea glauca										2	29	1	1
Picea mariana											10		
Picea rubens							7	48	40				
Tsuga canadensis	58	60						7	5	16			
Larix laracina											5		
Fraxinus nigra								1					
Fraxinus americana		1											
Pinus strobus	34	3			42	27	51	+	3	30			
Pinus banksiana			94										
Pinus resinosa			6	100	58	5				10			
Prunus serotina		2					2	+					
Thuja occidentalis								1	16		7		
Populus balsamifera										1			
Populus tremuloides													4
Quercus alba	+												
Quercus rubra										+			
Castanea dentata	+												
Betula lenta		7											
Magnolia acuminata		2											
Amelanchier sp.			+										

Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Sorbus sp.													3
Other species									1				
No. species constituting 70% of canopy stems	**2**	**2**	**1**	**1**	**2**	**3**	**2**	**3**	**3**	**4**	**3**	**1**	**1**
No. species contributing 15% of canopy stems	**2**	**1**	**1**	**1**	**2**	**3**	**2**	**2**	**3**	**3**	**3**	**2**	**2**

Study	Forest Type	Minimum DBH (cm)	Location	Reference
1	hemlock-wpine	10.2	Pennsylvania	Morey (1936)
2	wpine-hemlock	"	"	"
3	jpine	"	Minnesota	Kittredge (1934)
4	rpine	20.4	"	"
5	rpine-wpine	"	"	"
6	wpine	10.2	"	"
7	wpine	"	New York	Roman (1980)
8	rspruce-bfir	"	"	Graves (1899)
9	spruce-hemlock	25.4	"	Hosmer and Bruce (1901)
10	wpine-hemlock	10	Michigan	Bourdo (1961)
11	wspruce-bfir	10.2	"	Jones and Zicker (1955)
12	bfir-spruce-birch	"	Minnesota	Buell and Niering (1957)
13	"	"	"	"

Table 21. Density of live trees in coniferous forests.

Density (stems/ha)	**Forest Type**	**Tree Size** (DBH, cm)	**Age** (yr)	**Location**	**Reference**
323	hemlock-wpine	>10.2	og	Pennsylvania	Morey (1936)
586	wpine-hemlock	>10	"	Michigan	Stearns (1950)
419	"	≥10	"	"	Bourdo (1961)
1267	rspruce-bfir (L)	"	>40	Maine	Tritton and Siccama (1990)*
921	rspruce-bfir	"	"	Vermont	"
1002	"	"	"	"	"
1038	"	"	"	New York	"
953	"	"	"	"	"
677	"	"	"	"	"
848	"	"	"	"	"
643	jpine-rpine	≥10.2	og	Minnesota	Kittredge (1934)
494	rpine	≥20.4	"	"	"
257	rpine-wpine	"	"	"	"
187	wpine	≥10.2	"	"	"
855	rspruce	"	"	West Virginia	Adams and Stephenson (1989)
875	hemlock-rspruce	"	"	"	"
925	"	"	"	"	"

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants
DBH= diameter breast height, tree size= minimum DBH of trees used to determine density, og= old growth, L= lowland

Table 22. Basal area of live trees in coniferous forests.

Basal Area (m^2/ha)	Forest Type	Tree Size (DBH, cm)	Age (yr)	Location	Reference
44	wpine	>10.2	og	New York	Roman (1980)
33	"	>10	"	Michigan	Pregitzer *et al*. (1983)
42	hemlock-wpine	10.2	"	Pennsylvania	Morey (1936)
64	wpine-hemlock	10.2	og	Pennsulvania	Morey (1936)
62	"	>10	"	Michigan	Pregitzer and Barnes (1984)
40	rspruce-bfir (L)	$\geq$10	>40	Maine	Tritton and Siccama (1990)*
23	rspruce-bfir	"	"	Vermont	"
24	"	"	"	"	"
21	"	"	"	New York	"
28	"	"	"	"	"
25	"	"	"	"	"
34	cedar	$\geq$2.5	>175	Michigan	Abrams and Scott (1989)
29	jpine	"	>55	"	"
19	"	>10	og	Michigan	Pregitzer and Barnes (1984)
36	cedar-blash-wspruce (L)	"	"	"	Pregitzer *et al*. (1983)
37	wpine-cedar (L)	"	"	"	Pregitzer and Barnes (1984)
14	blspruce-rspruce-larch (poor fen)	>10.2	"	New York	Roman (1980)
47	rspruce-bfir-rmaple (rich fen)	"	"	"	"

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants

DBH= diameter breast height, tree size= minimum DBH of trees used to determine basal area, og = old growth, L= lowland

Table 23. Density of snags in coniferous forest.

Density (stems/ha)	(% total)	**Forest Type**	**Tree Size** (DBH, cm)	**Age** (yr)	**Location**	**Reference**
210	14	rspruce-bfir (L)	≥ 10	>40	Maine	Tritton and Siccama (1990)*
439	32	rspruce-bfir	"	"	Vermont	"
461	32	"	"	"	"	"
574	36	"	"	"	New York	"
486	34	"	"	"	"	"
280	29	"	"	"	"	"
300	23	"	"	"	"	"
40	?	hemlock-rspruce	≥ 2.5	og	West Virginia	Adams & Stephenson (1989)
165	?	rspruce	"	"	"	"

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants
total= density of live trees + snags, DBH= diameter breast height, tree size= minimum DBH of trees used to determine density, og= old growth, L= lowland

Table 24. Basal area of snags in coniferous forests.

Basal Area (m^2/ha)	(% total)	Forest Type	Tree Size (DBH, cm)	Age (yr)	Location	Reference
4.9	11	rspruce-bfir (L)	≥10	>40	Maine	Tritton and Siccama (1990)*
17.4	43	rspruce-bfir	"	"	Vermont	"
23.8	33	"	"	"	"	"
20.7	39	"	"	"	New York	"
28.3	36	"	"	"	"	"
24.8	37	"	"	"	"	"
35.0	23	"	"	"	"	"
13.2	32	rspruce	≥2.5	og	West Virginia	Adams and Stephenson (1989)
16.6	58	"	"	"	"	"

*dominant trees >40 yr at DBH, most stands included 100-200 yr old dominants
total= basal area of live trees + snags, DBH= diameter breast height, tree size= minimum DBH of trees used to determine basal area, og = old growth, L= lowland

Table 25. Canopy gaps in coniferous forests. Canopy gap size is a mean, followed by the range in sizes.

Forest Type	**Canopy Gap*** (m^2)	(% land area)	**Extended Gap** (m^2)	(% land area)	**Mean Age Gap Tree**	**Location**	**Reference**
spruce-bfir	38, 9-147					NH	Foster and Reiners (1986)

* canopy gap= area directly under the canopy opening, extended gap= canopy gap + adjacent area extending to the bases of canopy trees that surround the gap, gap tree= tree that falls resulting in gap creation