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Description, characterization, and identification of stand structure classes in northeastern Ontario: the application of multi-cohort concepts in the classification of stands from four forest types to cohorts

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INTRODUCTION

Forest management that is based on natural disturbance regimes has been suggested as a coarse filter strategy to maintain biodiversity and ecological functions at multiple spatial and temporal scales in industrial forest landscapes (Attiwill 1994, Bergeron and Harvey 1997, Niemela 1999). At the stand level, this approach entails the maintenance of structural and biological legacies similar to those resulting from natural disturbances (Franklin et al. 2002, Harvey et al. 2002). At the landscape level, it involves managing the structural and compositional attributes of landscapes in order to emulate patterns and variability expected under regional natural disturbance regimes (Bergeron and Harvey 1997, Franklin 1993, Landres et al. 1999).

Fire, particularly its frequency, size, and severity, is a key element of the disturbance regime in boreal forests (Bergeron et al. 2002). Research indicates that many boreal stands persist beyond the average fire return interval and beyond the lifespan of the first post-disturbance cohort of trees, leading to the development of a multi-cohort age structure. For example, fire history studies in boreal forests of northwestern Quebec have shown that 55% of stands originated from fires >100 years B.P., and 27% from fires >200 years B.P. (Bergeron et al. 1999b,). In the Lake Abitibi Model Forest of northeastern Ontario, where fires historically have tended to affect large areas and where fire return intervals are long, 31% of stands had not burned for >200 years and 13% for >250 years (Gauthier et al. 2002). A review of several such studies suggests that almost 50% of the natural boreal forest mosaic in northwestern Quebec is composed of old growth and over-mature stands characterized by multi-cohort age structures (Bergeron et al. 2002).

These findings imply that traditional even-aged boreal forest management will have only limited applicability in emulating natural disturbance regimes in many areas of the boreal forest (Bergeron et al. 1999a, Bergeron and Harvey 1997, Bergeron et al. 2001). It follows that biodiversity maintenance in managed landscapes might also suffer as a result of a continued focus on even-aged boreal forest management. Commercial rotation ages are generally shorter than the mean return intervals of natural disturbances cycles in eastern boreal forests, and the regulation of age class structure under traditional even-aged management has the potential to eliminate the great majority of stands over the rotation age and to reduce average stand age to 40-60 years (Bergeron et al 2001, Harvey et al. 2002).

In response to this realization, Multi Cohort Forest Management (MCFM) has emerged as a forest management strategy to maintain biodiversity while continuing to manage forests for fibre production. Unlike traditional approaches to boreal forest management that rely almost exclusively on clearcutting and even-aged management (McRae et al. 2002), MCFM requires the use of various partial cutting techniques to emulate the multi-cohort structure of uneven-aged and relatively old boreal stands (Bergeron et al. 2002). The cohort concept integrates stand age, composition, and structural aspects into three broad successional or stand development phases (cohorts) for eastern boreal regions. Conceptually, the first cohort includes relatively young, even-aged stands of fire-adapted, pioneer tree species (e.g., black spruce, jack pine, trembling aspen, balsam poplar, and white birch) that tend to dominate during the first 100 years after a fire. The second cohort represents a mid-successional phase of 75-175 years where mixed stands dominate on mesic and mesic-hydric sites, or in the case of lowland black spruce, an irregular or uneven-aged stand structure has started to form. The third cohort begins sometime after 150 years at a time when virtually all first cohort pioneer trees have died, multi-cohort age structure is well developed, and stand renewal through gap dynamics is evident (Harvey et al. 2002, Bergeron et al. 2002). As envisioned, MCFM entails the development of strategic-level forest management planning approaches and stand-level silvicultural techniques to maintain a spectrum of forest compositions and structures at different scales across landscapes (Bergeron et al. 2002). One idea is to use theproportional representation of these cohorts to guide the proportional application of partial and even-age cutting systems. For example, cohort I stands could be maintained by clearcutting, whereas cohort II and III stands could be maintained by variable retention silvicultural systems that produce uneven-aged stands (Bergeron et al. 2002, Harvey et al. 2002).

Most research on MCFM has focussed on the identification and description of these cohorts and has taken place in boreal regions of Quebec (Nguyen 2000, Boucher et al. 2003). Cohort classification systems proposed to date have relied exclusively on the diameter distributions of live trees in stands to designate their membership to different cohorts. The focus has been on three main diameter structure types believed to be representative of progressive stages of forest development and analogous to cohorts: 1) even-sized structure, with a unimodal bell-shaped “normal” distribution that spans relatively few diameter classes; 2) uneven irregular structure, in which trees belong to several diameter classes and tend to exhibit multi-modal diameter distributions; and 3) uneven “inverse- J” structure, in which the majority of stems are in smaller diameter classes, and several larger diameter classes are represented but include relatively few trees, forming the tail of this type of distribution (Boucher et al. 2003, Nguyen et al. 2000, Smith et al. 1997). The inverse-J distribution is believed to coincide with a late development stage dominated by small-scale disturbances and senescence, and is thought to signal gap regeneration dynamics often attributed to old growth stands (Oliver and Larson 1996).

This report has three main objectives. First, we extend the cohort classification scheme developed in Quebec to the Claybelt Region of northeastern Ontario. Secondly, because previous cohort classification schemes relied heavily on a subjective classification of diameter distribution histograms(e.g., Boucher et al. 2003), we developed a quantitative cohort classification approach that was more objective. Finally, we incorporate a broader range of stand structural data in the classification system and investigated cohort-specific variation among stand attributes not used directly in the quantitative classification of cohorts in order to develop a better understanding of the structural and compositional variability that exists within and among the cohorts.

METHODS

Study sites

Study sites consisted of 97 permanent growth plots (PSPs) and 38 permanent sample plots (PGPs) selected from the OMNR Growth and Yield Plot Network for the northeast region. PSPs and PGPs are used by the OMNR and forest industry to monitor forest growth and yield in the region, and provide stand-level information at a finer scale than the forest resource inventory used in management planning. In order to obtain results that would be widely applicable in the region, the sites were located in various parts of Ecoregion 3E, including parts of Rowe's (1972) Northern Clay, Missinaibi-Cabonga, and Central Plateau boreal forest sections, and were spread across multiple crown forest management units. Sites were selected to represent a range of developmental conditions in four standard forest units commonly used in forest management planning in the region (Watt et al. 2003): black spruce stands growing on wet, deep organic soils or on moist, peaty-phase mineral soils in lower slope positions (SB1; $\underline{n} = 50$), mixed conifer stands of white spruce, balsam fir, black spruce and eastern white cedar growing on moist sandy to clayey soils (SF1; $\underline{n} = 52$); upland black spruce dominated conifer stands on fresh to moist, medium loamy to clayey soils (SP1; $\underline{n} = 11$), and mixed coniferous/deciduous stands comprised largely of trembling aspen, white birch, black and white spruce and balsam fir on moist, medium loamy to clayey soils (MW2; $\underline{n} = 22$).

Both plot types were fixed area sample plots, although they differed with respect to the total area sampled: PSPs typically include three separate 400 m^2 circular sample plots for trees, whereas PGPs include only one (Hayden et al. 1995, Hayden 2003). Eight of the PSP sites were established before data collection in the PSPs was standardized, and rather than containing 3 separate circular plots, they had a single 20 m x 20 m (400 m^2) or 32 m x 32 m (900 m^2) plot. In all cases, tree information from the sites was standardized to per hectare values.

Several sites had been re-measured since plot establishment, and only the most recent data was employed in the cohort classification analyses. The majority of sites were either established or re-measured between the years 2000 and 2002 ($\underline{n} = 109$). The remainder were established or re-measured in 1993 ($\underline{n} = 2$), 1994 ($\underline{n} = 22$), 1995 ($\underline{n} =1$), or 1997 ($\underline{n} = 1$).

Variables used in the analyses

A complete list of site-level variables used in the analyses is presented in Appendix I.

Live trees

Several key variables were calculated from the diameter distributions of live trees following previous cohort classification projects (e.g., Nguyen 2000, Boucher et al. 2003). As in these previous analyses, trees were placed into 2-cm classes, with the class identifier representing the class midpoint (for example, 9 – 11 cm dbh trees were identified as the 10-cm class). The minimum diameter at breast height of trees included in the sample was 2.5 cm dbh (Hayden et al. 1995, Hayden 2003). Diameter distributions of trees per hectare in 2-cm dbh classes were calculated and histograms prepared for each study site.

Several additional variables were calculated from the diameter distribution data. The Shannon-Wiener diversity index (H') described how stems were distributed among the various dbh classes:

$$H' = -\sum p_{cl} \cdot \log(p_{cl})$$

where p_{cl} is the proportion trees in each of the observed diameter classes (Legendre and Legendre 1998; Boucher et al. 2003). Diameter class richness (S) was determined from the number of dbh classes observed at each site. Diameter class evenness (E) compared the diversity to the corresponding maximum value at each site; the greater the value, the more evenly distributed trees are among diameter classes. Eveness was calculated using Pielou's formula (Legendre and Legendre 1998):

$$E = H'/H_{max} = H' / \log S$$

The coefficient of skewness (α_3) was used to quantify asymmetry of the diameter distributions. Skewness for a normal distribution is zero; positive skewness corresponds to a frequency distribution with a longer "tail" to the right than to the left; and negative skewness corresponds to a distribution with a longer "tail" to the left than to the right (Legendre and Legendre 1998). The coefficient of skewness was defined as:

$$\alpha_3 = [\sum (x_i - \text{mean})^3 / (n-1)] / s_x^3$$

where x_i is the observed diameter class, mean = mean diameter class, n = the number of diameter classes, and s_x is the standard deviation among diameter classes (Legendre and Legendre 1998; Boucher et al. 2003). The coefficient of variation (CV) was also calculated from the diameter distributions of each site ($CV = s_x \cdot 100/\text{mean}$; Boucher et al. 2003). All variables were calculated using the SAS system for windows statistical computer software package (SAS, v 8.2).

Two-parameter Weibull probability density functions were fit to the diameter distributions so that parameter estimates from the functions could be added to the suite of variables included in cohort analyses. In forestry, the Weibull distribution has been used successfully to model the size distribution of trees within tree populations (Van Laar 1991, Gove 2000). The Weibull function was fit to the diameter distributions from each site using the CAPABILITY procedure in SAS (SAS, v 8.2). In two-parameter Weibull functions, the location parameter (θ) is set to zero, allowing the shape (ß) and scale (α) parameters to describe the curve. The Weibull function approximates a normal curve when ß = 3.6 (Van Laar 1991). As values for the shape parameter increase from >0 to 3.6, the curve describes a progressively more normal distribution (Johnson 2000), as is expected for the even-aged or continuous diameter distributions of cohort I stands (Figure

1). For the same reason, cohort III stands characterized by inverse-j diameter distributions can be expected to have relatively low estimates for the shape parameter that distinguish them from cohort I stands (Figure 1). An increase in the scale parameter (α) describes a progressively broader and flatter curve (Johnson 2000) and is useful to distinguish cohort II stands with many diameter classes from cohort I stands with relatively few (Figure 1). In order to plot the predicted values for the location of the curve (Y) in units of trees/hectare directly over diameter distribution histograms, we used the USDA Forest Service BALANCE model (Gove 2003). The Balance model and capability procedure in SAS generated identical estimates for the shape and scale parameters of the Weibull functions, but only BALANCE provided estimated values for Y in units of trees per hectare (SAS fitted the curves to density percentages instead).

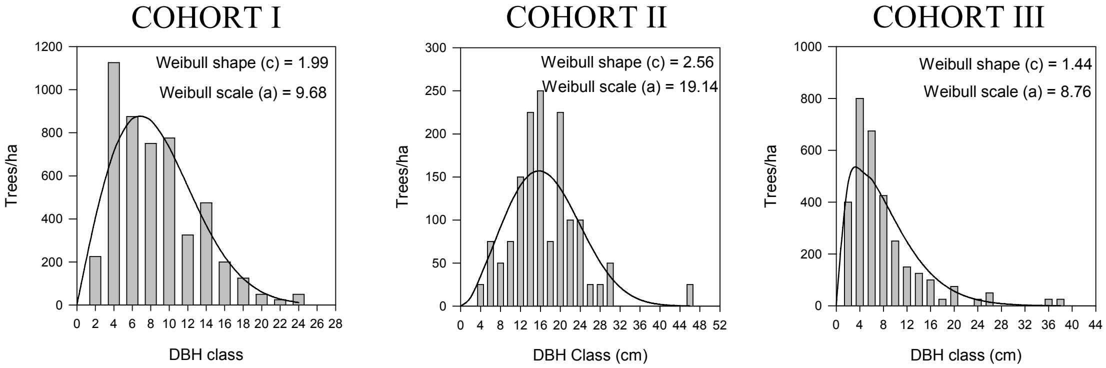

Figure 1. Diameter distributions typical of cohort I, II, and III stands with fitted Weibull function curves. Cohorts were assigned by the methods described below (Cohort I = plot ABI01005PGP; Cohort II = plot TEM01084; Cohort III = plot CHT02006).

Additional summary variables included total density (in trees/ha) and the relative percentage of small (<9 cm dbh), medium (9-20.9cm dbh) and large (> 21 cm dbh) diameter trees in the sample, obtained by summing trees/ha in small, medium and large classes and multiplying these values by 100/total density. In order to explore the statistical tool for cohort classification proposed by Boucher et al. (2003), 2-cm diameter classes also were summarized using the percentage of total density represented in each class rather than trees/ha (by dividing trees/ha in each class by total density and multiplying by100). Similarly, to test the classification functions proposed by Nguyen (2000), live trees in each site were assigned to a series of additional diameter and species-based trees/ha categories (see Appendix I).

Crown Class variables.—

Each tree inventoried in the PSPs and PGPs was assigned one of seven rown classes: Emergent (E), Dominant (D), Co-dominant (C), Intermediate (I), Overtopped-suppressed (OS), understory (U), and open understory (OU). Based on these assignments and a conversion to numerical classes (eg. E =1; D = 2; C = 3; etc.), crown class diversity (CCH), richness (CCR), and evenness (CCE) were calculated for each site (using the same formulas presented earlier). .

Snags

Standing dead trees (snags) within sample plots were inventoried by species, diameter, and decay class using a 5-class system (Hayden et al. 1995, Hayden 2003). Snag information of this type was available for all sites. Snags < 10.0 cm dbh were deleted from the data used in analyses. Snags counts were converted from fixed-area counts to trees per hectare using the appropriate conversion factors for each site. Snags per hectare in decay classes 1-3 were summed to create the "newsnags" variable and in decay classes 4 and 5 to create the "oldsnags" variable. These groups were further subdivided by size by grouping 10 –15 cm dbh snags as "small", 15-25 cm dbh snags as "medium", and >25 cm dbh snags as "large", resulting in a total of eight snag variables for each site (see Appendix I).

Downed woody debris, canopy openness, and veteran tree age.--

Downed woody debris (DWD), veteran tree age, and canopy openness data were collected at a subset of sites ($\underline{n} = 95$) in the fall of 2003. Because data of this type was not available for all sites, and some temporal variation existed between collection of this data and collection of tree data at the sites, it was not used directly to classify cohorts.

DWD sampling involved line intersect sampling and a 5-class DWD decay categorization (Marshall et al. 2000; Maser et al. 1979). In each sampled stand, three 45.14 m lines oriented at 120^0 to one another were extended from the plot center. Observers recorded all logs >7.5 cm in diameter at the point of intersection with the line, and assigned each individual log a decay class between 1 and 5 (Maser et al. 1979). Site-level variables derived from these data include the amount of DWD by decay class, the total amount of DWD in decay classes 1-2, and the total amount of DWD in decay classes 3-5 (see Appendix I). All DWD variables are volume estimates in m3/ha, which was calculated for each piece using a modified formula for estimating volume of logs from line intersect sampling:

$$\text{Vol} = (\pi^2 * \text{diameter}^2) / 8 * L$$

where diameter is the diameter of the log at the point of intersection with the line in cm and L is the total length of the sampling line in metres (Marshall et al. 2000). Individual piece volume estimates were calculated and summed according to decay class variables listed above using SAS (SAS v. 8.02).

Canopy overstory density was measured at the plot center and the end of each DWD sampling line, providing four sampling points per site. A "Model C" spherical densiometer (FOREST DENSIOMETERS, Bartlesville, OK) was employed for all overstory density sampling. Four readings were taken per sampling point facing magnetic North, East, South and West. The average of the counts made in each cardinal direction multiplied by 1.04 provides percent of overhead area not occupied by canopy. The difference between this and 100 is an estimation of overstory density in percent.

From these data, we determined five variables: Large-scale overstory density (mean overstory density from the 4 sampling points), large-scale overstory density variance and coefficient of variation (across the four sampling points), and fine-scale overstory density variance and coefficient of variation (across the 16 measures per site) (Appendix I).

Veteran trees were located within stands by searching the canopy for large, emergent trees. The search for veteran trees was limited to the stands that contained the fixed area sample plots, not the fixed-area plots themselves. One to three of the largest trees in the surrounding stand were cored at breast height using a tree increment corer. Tree ages were estimated by counting rings from bark to pith on mounted, sanded cores using Stem Analysis Measurement Increment Core Capture Version 1.1 equipment and software (Miller, 1994). Only the maximum age (maxage) of the cores collected at each site was included as a variable in the cohort classification analysis.

Exploratory Analyses

As a start, the cohort classification functions proposed by Nguyen (2000) and Boucher et al. (2003) were applied to the study sites. In order to test the classification function proposed by Nguyen (2000), sites were divided into two composition–based groups: Intolerant, in which intolerant species constituted more than 10% of the total basal area ($\underline{n} = 59$), and the SPD group, which had < 10% intolerant basal area ($\underline{n} = 76$) (Appendix I). Unfortunately, despite careful attention to the details in Nguyen (2000), we were unsuccessful in applying his functions. For the SPD group,75 of 76 sites were classified to cohort II, and no sites to cohort III. A comparison of our means revealed several discrepancies, not only for the 1-4.9 cm dbh class. In addition, when sites were plotted in relation to the Weibull shape and scale parameters, no patterns were evident among the cohort classes. Given these problems, the Nguyen classification functions were not further explored. One possible explanation for the failure of these classification functions is that they relied heavily on diameter class variables in units of trees/ha, which might vary considerably in relation to site productivity. More recent cohort classification work has used percentages of trees by diameter class when comparing sites to circumvent this problem (e.g., Boucher et al. 2003). Although the classification functions proposed by Nguyen (2000) were not further incorporated in this study, his study nonetheless provided valuable direction as to variable selection.

Exploration of the statistical tool for cohort classification proposed by Boucher et al. (2003) initially was hampered by errors in the paper (the authors neglected to mention that they were presenting standardized coefficients and they also presented typographic errors in one of their tables). Correspondence with the authors clarified these errors and allowed proper application of the classification functions. Unfortunately, the dbh data used in Boucher et al (2003) included only trees >9 cm dbh and they presented functions only for sites that contained >75% conifer basal area. Thus, use of their functions restricted us to a subset of our dbh data and a subset of our sites (103 of the 135).

Nonetheless, the Boucher et al. (2003) classification function provided valuable insights into the cohort classification problem. For example, the plot of sites in relation to

Weibull shape and scale parameters showed strong evidence of relationships between Weibull parameters and cohort classes (Figure 2).

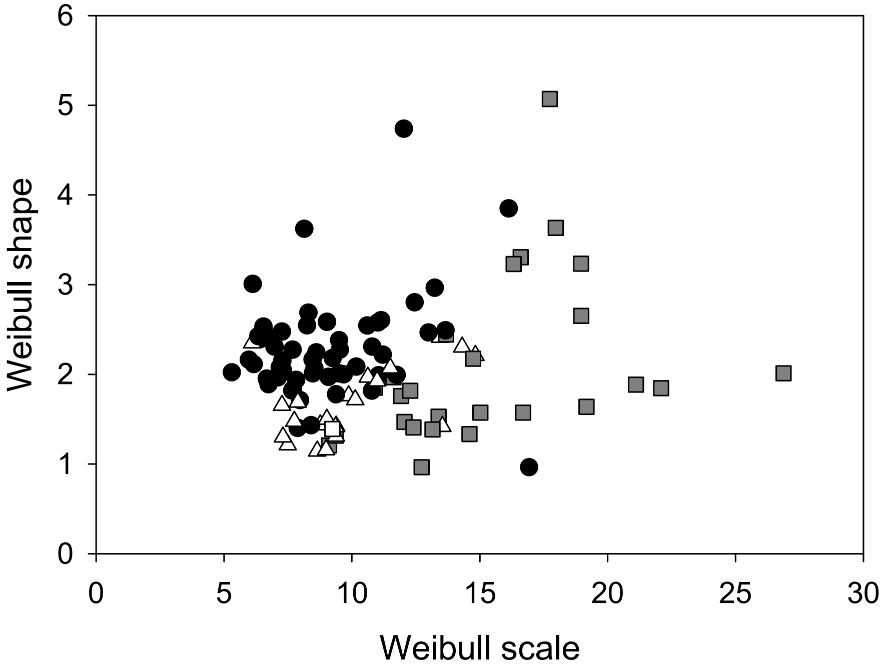

Figure 2. Weibull shape vs. scale parameters for 103 sites classified using Boucher et al.'s (2003) statistical tool. ● = cohort I ■ = cohort II ▲ = cohort III

Cohort III sites tended to be distinguished from cohort I sites along the shape axis and cohort I tended to be distinguished from cohort II sites along the scale axis, although exceptions are evident (Figure 2). This pattern is of particular interest because the Weibull parameters were not used in the Boucher et al. (2003) classification function.

The Boucher classification function used five diameter-class based variables: diversity, coefficient of skewness, coefficient of variation, and density (%) of 10-cm and 14-cm diameter classes. When the Boucher classification function was applied to Ontario data that included the smaller diameter classes, the density (%) of the 10-cm and 14-cm diameter classes was changed substantially (due to the inclusion of smaller diameter classes, which often represented a high percentage of the total density). The resulting cohort classification changed for many sites as a result. This confirmed that in order to be effective, the Boucher statistical tool must be applied to plot data that does not include smaller diameter classes.

We explored multivariate patterns in relation to the Boucher cohorts using SAS and CANOCO (v. 4.51)(SAS v. 8.02, ter braak and smilauer 2002). Principal component analysis (PCA) was performed using key structural variables as identified by our exploratory work and from the classification functions of Nguyen (2000) and Boucher et al. (2003). Variables used in this analysis were derived from data for all sites that included all trees > 2.5 cm. The variables included: diameter class diversity, richness, and evenness, the coefficient of skewness, the coefficient of variation, Weibull shape, and

Weibull scale; and symbols for sites in the PCA were assigned based on Boucher cohorts (Figure 3). Density (%) of trees in the 10-cm and 14 cm classes were not included as they were believed to be less indicative of cohort classes when calculated using all of the tree data. This PCA was also used to assess the relationship between Boucher cohorts and forest units by plotting symbols that represented the forest unit memberships (Figure 4).

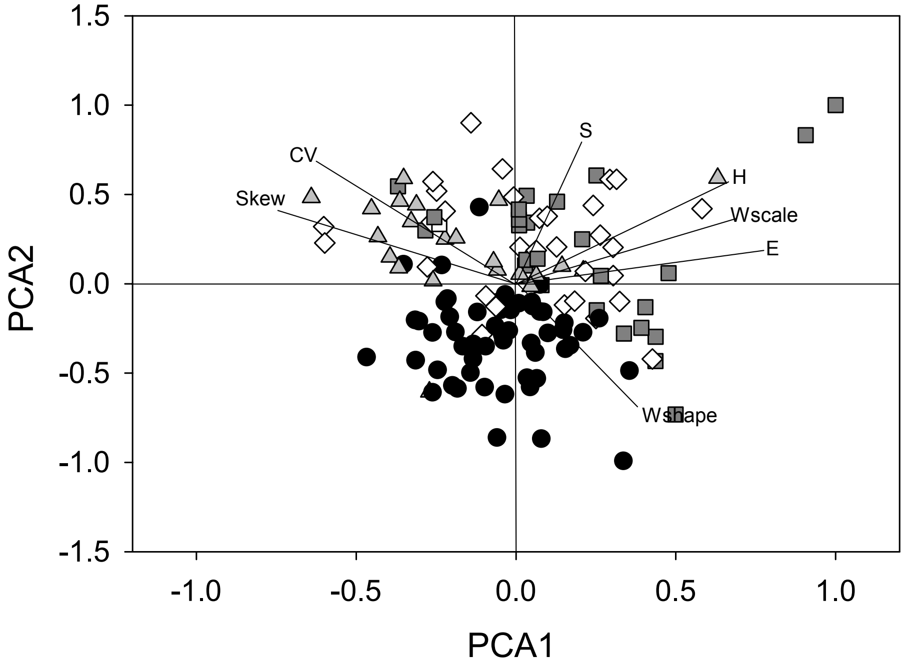

Figure 3. Principal component analysis of the 135 study sites, with vectors shown for key analysis variables. The first and second axes accounted for, respectively, 47 and 37% of the total variance. Symbols represent cohorts as assigned by Boucher et al.'s (2003) statistical cohort classification tool: ● = cohort **I** ■ = cohort **II** ▲ = cohort **III** ◊ = unclassified.

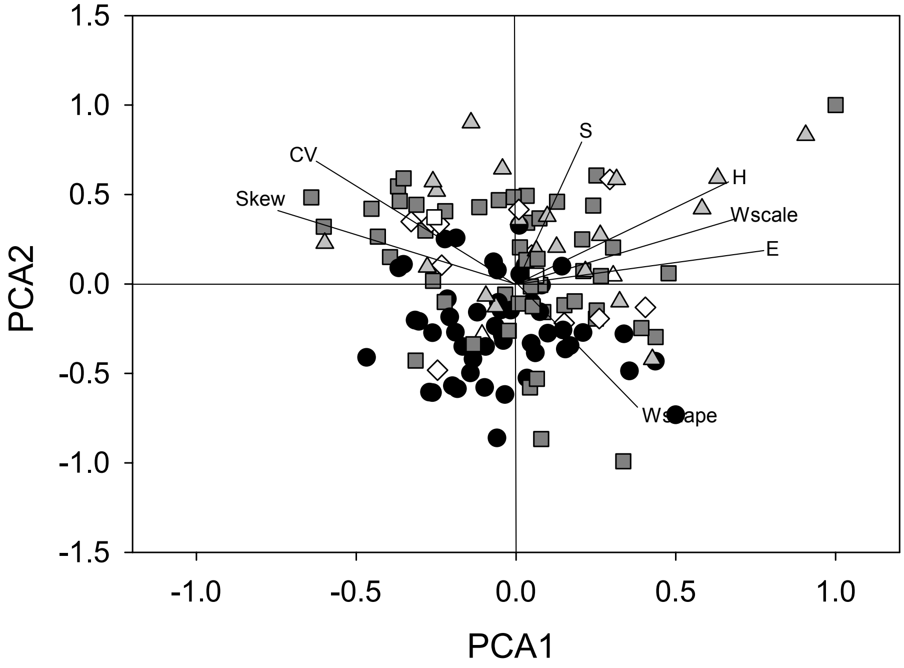

Figure 4. As Fig. 3 except that symbols represent forest units:
● = SB1 ■ = SF1 ▲ = MW2 ◊ = SP1.

This exploratory PCA demonstrated that PCA was an effective multivariate approach to distinguishing cohorts based on variables of known importance to cohort classification (Nguyen 2000, Boucher et al. 2003). It also provided a means to interpret which variables were associated with which cohorts by examining the direction and length of vectors. For example, cohort II sites were distinguished from cohort I sites by a stronger positive association with vectors for diameter distribution diversity (D), evenness (E), richness (S), and the Weibull scale parameter (Figure 3). Although some individual cohort III sites were dispersed throughout the ordination space, a small cluster of these was clearly present in positive association with the diameter distribution skewness (skew) and coefficient of variation (CV), and to a lesser degree richness (S). Cohort III sites were also strongly negatively related to increasing values for the Weibull shape parameter (Figure 3).

Of the four forest units involved in our study, only SB1 was not well represented in all regions of the ordination space, indicating that variability within the SB1 forest unit was less than that in other forest units (Figure 4). SB1 sites tended to be negatively associated with both principal component axes, indicating that the sites with greatest values for most variables did not include SB1 sites. This suggested that if site scores from the PCA were used to classify cohorts, and the analysis included sites from all forest units, the variability within the SB1 sites might not be detected. Analysis variables in SB1 sites might not even approach the median value for the same variable from other forest units. In other words, diameter distributions in SB1 sites appeared to vary on a smaller scale than for other forest units, a scale that might not be detected if analysed with sites from other forest units. Diameter distributions for SB1 sites supported this conclusion: most of these sites did not have large diameter trees, meaning less diameter classes are represented in SB1 sites compared to other forest units. Based on these observations, a decision was made to analyze the SB1 sites separately from the other forest units in further analyses. Therefore, the forest unit groupings decided upon for further cohort classification analyses were: 1) the SB1 group, which included only SB1 sites ($\underline{n} = 50$); and 2) the "NonSB1" group, which included SF1, SP1, and MW2 sites ($\underline{n} = 85$). The separation of the spruce-dominated SB1 forest units from other forest units is consistent with previous cohort classification studies (Nguyen 2000, Boucher et al. 2003).

PCA model selection

For both analysis groups, variables were incrementally added to those used in the first exploratory PCA to see how these additions influenced the separation of visually-assigned, Weibull-based, and Boucher-type cohorts. Visually-based cohort classes were assigned through examination of the diameter distribution histograms for each site and relating these to the expected distributions of cohort I, II and III stands (Figure 1). Typically, when alternative PCA models were explored, all the variables associated with a particular structural feature, such as snags, were added, and then multiple models were examined in which the variables were reduced to the ones that best contributed to cohort separation in ordination space. Variables that were not available for all sites, such as the downed woody debris variables, were explored in PCAs, but were not included in the final models (because including these carried the cost of dropping 40 sites from the analysis groups). These incremental variables were included in the PCA analysis "passively"; that is, they did not contribute to the definition of the site scores. As a result, their correlations with the original classification could be assessed.

For the NonSB1 group, the chosen PCA model included the following 17 variables: Wshape, Wscale, S, H, E, Skew, CV, dspct, dmpct, dlpct, dtot, oldsnags, newsnags, oldsnagL, newsnagL, CCR, CCE, and CCH (see Appendix I for variable descriptions). Compared to the original exploratory analysis, these 17 included measures of tree density, snags, and crown class variables. Including the density (%) of small, medium, and large trees in the PCA improved the separation of cohorts in ordinations. These relative density variables (%'s) were complimented by the addition of the absolute total density variable (trees/ha) and all four were included in the model. The model that included all snag size classes did not result in better separation of cohorts than one that included only large snags, hence variables for small and medium snags were not retained. However, including the size-independent total newsnags and oldsnags variables did result in slightly more distinct cohort groupings in ordination space, and presumably captured variability in snags of all sizes, so these variables also were included. All three crown class variables were included because of their potential in providing information related to the underlying cohort concept. For instance, high richness and diversity of crown classes would be expected in cohort III stands, and high crown class evenness values in densely treed, multi-aged cohort II (and possibly cohort III) stands.

For the SB1 group, the chosen PCA model included 13 variables: Wshape, Wscale, S, H, Skew, CV, dspct, dlpct, dtot, oldsnags, newsnags, CCR, and CCH (see Appendix I for variable descriptions). The main difference compared to the NonSB1 group was the omission of diameter class and crown class evenness variables. Exploratory PCAs that incorporated these variables showed evenness vectors that were almost orthogonal to the second principal component axis that best separated the cohort types, suggesting that while some variability among sites existed in relation to diameter and crown class evenness, it had little to do with cohort types. Removing the evenness variables also allowed for greater separation among cohorts. The density (%) of medium sized trees also was dropped because separation of cohorts on the second principal component axis was better without it. Again, this suggested that variability in the density of medium sized trees among sites had little to do with cohort classes. From an ecological perspective, due to the rarity of large trees in this forest unit, it is unlikely that the density of medium sized trees would distinguish cohorts if by default most trees are medium sized in mature stands because they tend not to grow as large. Including the variables for large snags did not better the separation of cohorts in ordinations, presumably for similar reasons. Snag variables included the chosen PCA were limited to the size-independent "newsnags" and "oldsnags" variables.

Cluster analysis

Several authors have suggested taking advantage of the characteristics of clustering and ordination by combining the two of analysis types using the same similarity or distance matrix (e.g., Legendre and Legendre 1998). Once PCA models were selected for the analysis groups, cluster analysis was performed on the matrix of site scores. A hierarchical, agglomerative clustering method called Ward's minimum variance method was used, in which each object is in a cluster of its own at the beginning of the procedure. To form clusters, the method minimizes an objective function equivalent to the same squared error criterion as that used in multivariate analysis if variance. At each clustering step, Ward's method finds the pair of objects or clusters whose fusion increases as little as possible the sum, over all objects, of the squared distances between objects and cluster centroids (Legendre and Legendre 1998). Ward's method was performed using CLUSTER in SAS, in which the number of clusters sought could be controlled, followed by the TREE procedure, which produces a dendrogram of the linkages among clusters as they grow (SAS v. 8.02). Dendrograms are useful to interpret the degree of similarity among objects in clusters, as each cluster level can be assessed along a scale of semi-partial R^2 values that underlies these diagrams. Semi-partial R^2 is computed as the between cluster sum of squares divided by the total sum of squares, which increases as clusters grow (Legendre and Legendre 1998).

The approach used to cluster site scores involved exploratory trials using different combinations of principal component axis scores and numbers of clusters. PCA plots in which symbols represented visual cohort classes and Boucher cohort classes were then examined to find the clustering approach that best grouped sites relative to cohorts. Dendrograms of the various cluster analyses were produced to assess cohort separation.

The clustering of sites using scores from one or more principal component axis provided a means to group sites based on differences in all of the analysis variables included in the PCA. Unlike previous studies that relied heavily on a visual classification of diameter distributions, followed by discriminant analysis to arrive at parsimonious classification functions for the cohorts, the cohorts defined by this clustering approach are less subjective and incorporate quantitative relationships among sites in the grouping of cohorts.

Cohort Comparisons of analysis variables

After cohort classes were assigned to the sites, all structural and composition variables were compared among cohorts by analysis group and forest unit using a Kruskal-Wallis test, a non-parametric one-way analysis of variance (Legendre and Legendre 1998). Forest unit and analysis group are the same for SB1 sites, but for the NonSB1 group forest unit specific comparisons were made to investigate intra-cohort differences unique to each forest unit type. These comparisons identified differences among the cohorts and were particularly useful for variables not used in the PCAs. Pair-wise Kruskal-Wallis tests among the three cohorts were adjusted using the Bonferroni correction to minimize the risk of type I errors (Legendre and Legendre 1998). For a three-class comparison, the correction is equivalent to replacing the significance level of 0.05 with 0.01695.

Cohort classification functions

Following the example of Boucher et al. (2003), classification functions were developed for each analysis group and forest unit based on the assigned cohort classes. Forest unit specific functions were derived to explore the possibility that these might provide lower misclassification probabilities than the global function for the NonSB1 group. A stepwise discriminant analysis, using the STEPDISC procedure in SAS, was performed to identify the best variables for discriminating among the three cohort types in each forest unit and analysis group. Prior to stepwise analysis, the size and composition class-based variables used in Nguyen's (2000) classification approach were removed to lessen the sensitivity of classification functions to productivity differences among sites, in part because of the difficulty encountered when applying Nguyen's functions to our data. In addition, DWD, overstory density, and age variables that were missing for some sites were dropped: DC1-DC5, newDWD, oldDWD, Fs_osdcv, Fs_osdvar, Ls_osdcv, Ls_osdvar. All other variables listed in Appendix I were included. The stepwise selection process stopped when all variables in the model met the criterion to stay (p=0.15) and none of the other variables met the criterion to enter (p=0.15) (SAS Institute 1999).

All of the variables identified in the stepwise discriminant analysis were subsequently included in the calculation of analysis group-specific and forest unit-specific classification functions using the DISCRIM procedure in SAS (SAS v. 8.02). This procedure develops a discriminant criterion to classify each observation into one of the predefined groups (cohorts). The DISCRIM procedure also provided measures of discrimination that can be considered probabilities of misclassification. The posterior probability error-rate estimates associated with classification functions for each group are reported with the classification results.

RESULTS

NonSB1 analysis group

The first principal component axis in the NonSB1 PCA explained 34% of the total variance and the second PCA axis explained 21%. Using visual cohort classes to identify cohorts in the ordination, vectors indicated that many visually classified cohort III sites are associated with high values for skewness and the coefficient of variation of the diameter classes, old snags, and high relative densities of small diameter trees (Figure 5). Remaining cohort III sites were associated with high amounts of new snags, diameter class richness, high scores for Weibull scale, and high relative density of large trees. Cohort I and cohort II sites tended to overlap in the PCA, but cohort I sites appeared to more strongly associated with high total stem density and high values for Weibull shape, whereas cohort II sites showed stronger positive associations with diameter class diversity, evenness, Weibull scale, and new snags. Cohort I sites tended to be in positive association with the first axis and in negative association with the second axis.

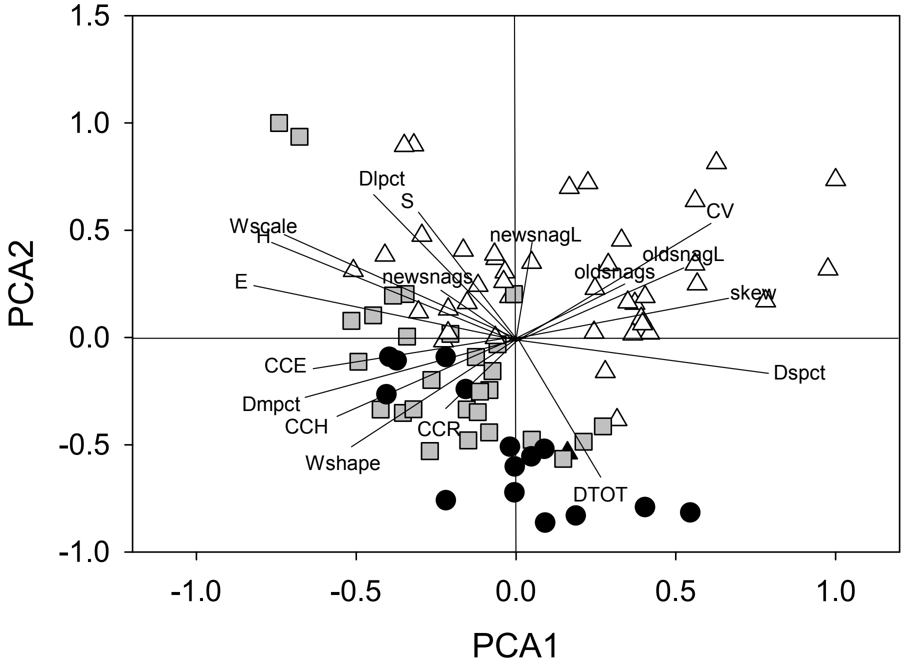

Figure 5. Principal component analysis biplot for the NonSB1 analysis group. Symbols represent cohorts as assigned visually by examination of diameter distributions:
● = cohort I; ■ = cohort II; ▲ = cohort III.

The clustering approach most consistent with visual and Boucher cohort classes used site scores from the first 6 PCA axes, which cumulatively accounted for 90% of the total variance. Using a three-cluster approach, many sites visually classified to cohort III that were negatively associated with the first PCA axis were clustered with visual cohort II's (compare Figure 5 vs. 6). Using a four-cluster approach, and combining clusters 3 and 4 to represent cohort III, resulted in a much better agreement between clusters and visually assigned cohorts (Figure 7).

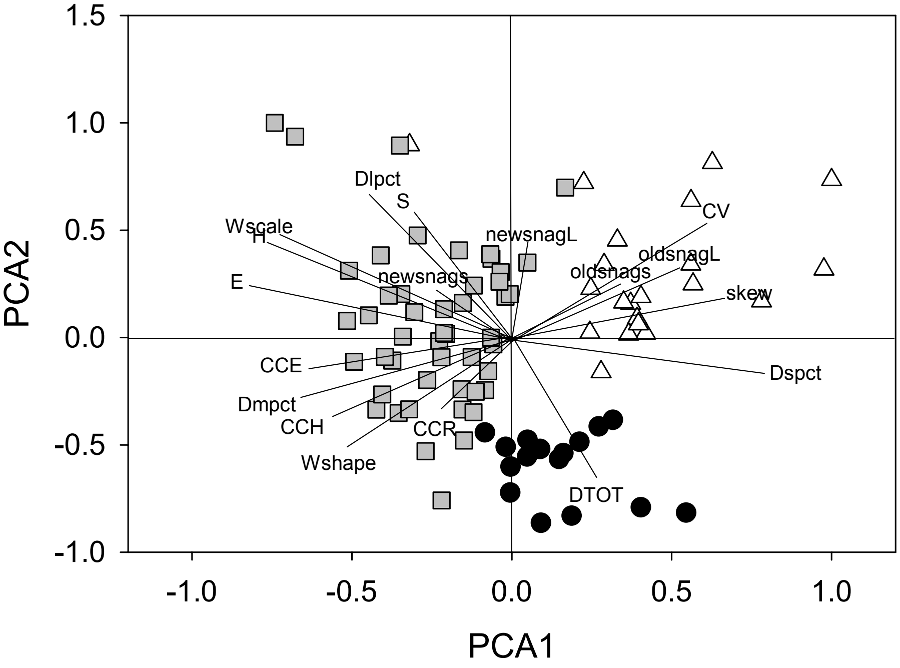

Figure 6. Principal component analysis biplot for the NonSB1 analysis group. Symbols represent clusters and cohorts grouped by cluster analysis using a 3-cluster approach:
● = cohort I; ■ = cohort II; ▲ = cohort III.

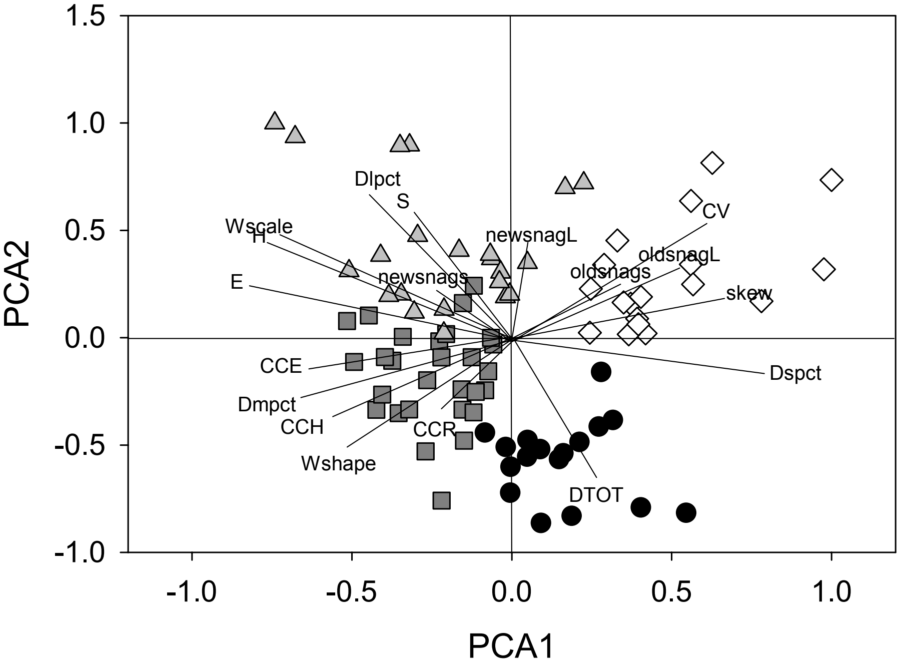

Figure 7. Principal component analysis biplot for the NonSB1 analysis group. Symbols represent clusters using a 4-cluster approach: ● = cluster I ; ■ = cluster II; ▲ = cluster III and ◊ = cluster IV.

Using either three or four clusters to define cohorts, cohort I sites formed a distinct cluster that was positively correlated with high tree density, weibull shape, and small tree density (Figure 7). However, cohort assignment varied for cohort II and III sites depending on how many clusters were assigned and how these were combined to represent cohorts. The choice between using a three-cluster approach to identify cohorts versus a four-cluster approach and combining clusters 3 and 4 as cohort III's was influenced by agreement with visually assigned cohort class, a review of field observations from a subset of sites, and by plotting the Weibull parameter relationship to the alternative clustering scenarios (Figure 8).

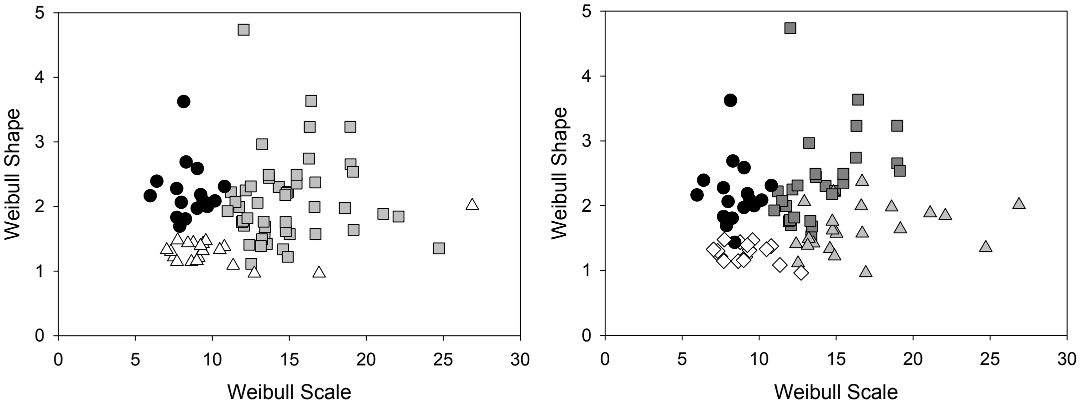

Figure 8. Comparison of three-cluster (left) and four-cluster (right) classification results in relation to Weibull shape and scale parameters. ● = cluster I; ■ = cluster II ; ▲ = cluster III; ◊ = cluster IV.

Using a 3-cluster approach, a cluster consistent with many visually assigned cohort III sites was formed (Figure 6), but membership in this group (except for two sites) appeared to be limited to sites with relatively low values for the Weibull scale parameter (Figure 7). When a 4-cluster approach to cohort classification was used, and clusters 3 and 4 were combined to define cohort III, cohort III sites include sites that spanned the range of the Weibull scale axis (Figure 8). From a theoretical perspective, there is little reason to expect that cohort III stands will only include stands that showed a limited number of diameter classes (as a low value for Weibull scale indicates). If anything, one would expect the opposite: many cohort III stands with predominantly high values for the Weibull scale parameter as these stands persist in the absence of stand replacing disturbances. For this reason, and because of the agreement between the 4-cluster approach and the visually assigned cohorts, the 4-cluster approach that combined clusters three and four to define cohort III was selected for the classification of NonSB1 sites.

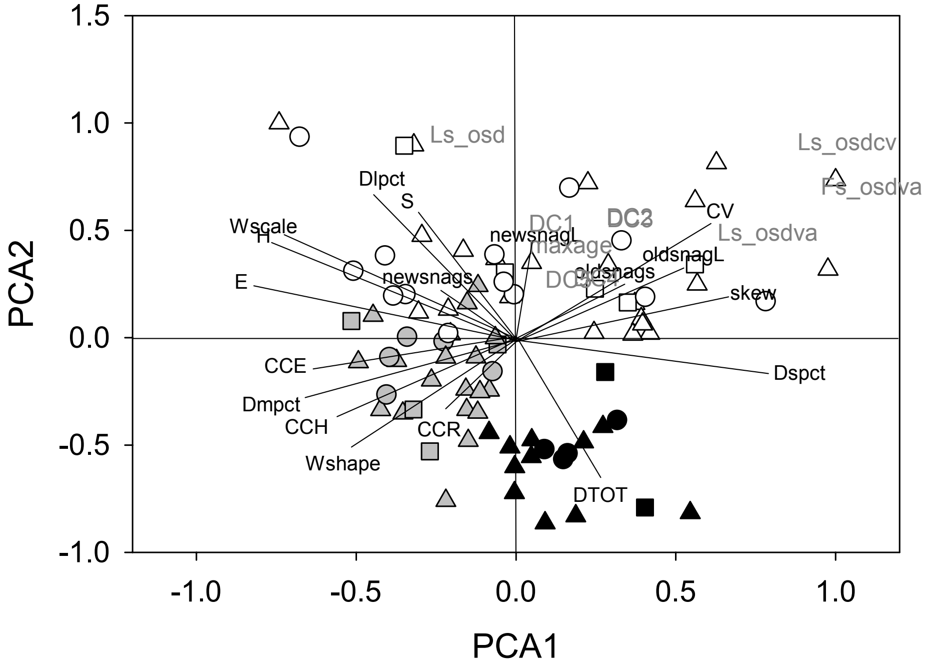

Figure 9. Final PCA biplot for the NonSB1 analysis group with vectors for analysis variables. Downed woody debris, age and canopy overstory variables are plotted passively (in grey text). Cohorts were defined by cluster analysis using a 4-cluster approach and combining clusters 3 and 4 to represent cohort III sites: cohort I = black;
cohort II = grey; cohort III = white. Symbols represent forest unit: ● = MW2; ■ = SP1; ▲ = SF1

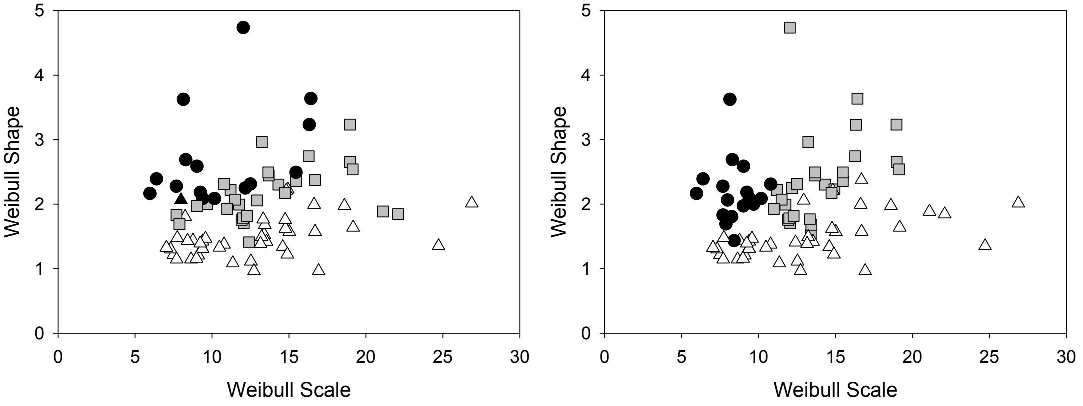

Figure 10. Comparison of visually assigned cohorts (left) and cluster-based cohorts (right) in relation to Weibull shape and scale parameters for the NonSB1 group.
● = cohort I; ■ = cohort II ; ▲ = cohort III;

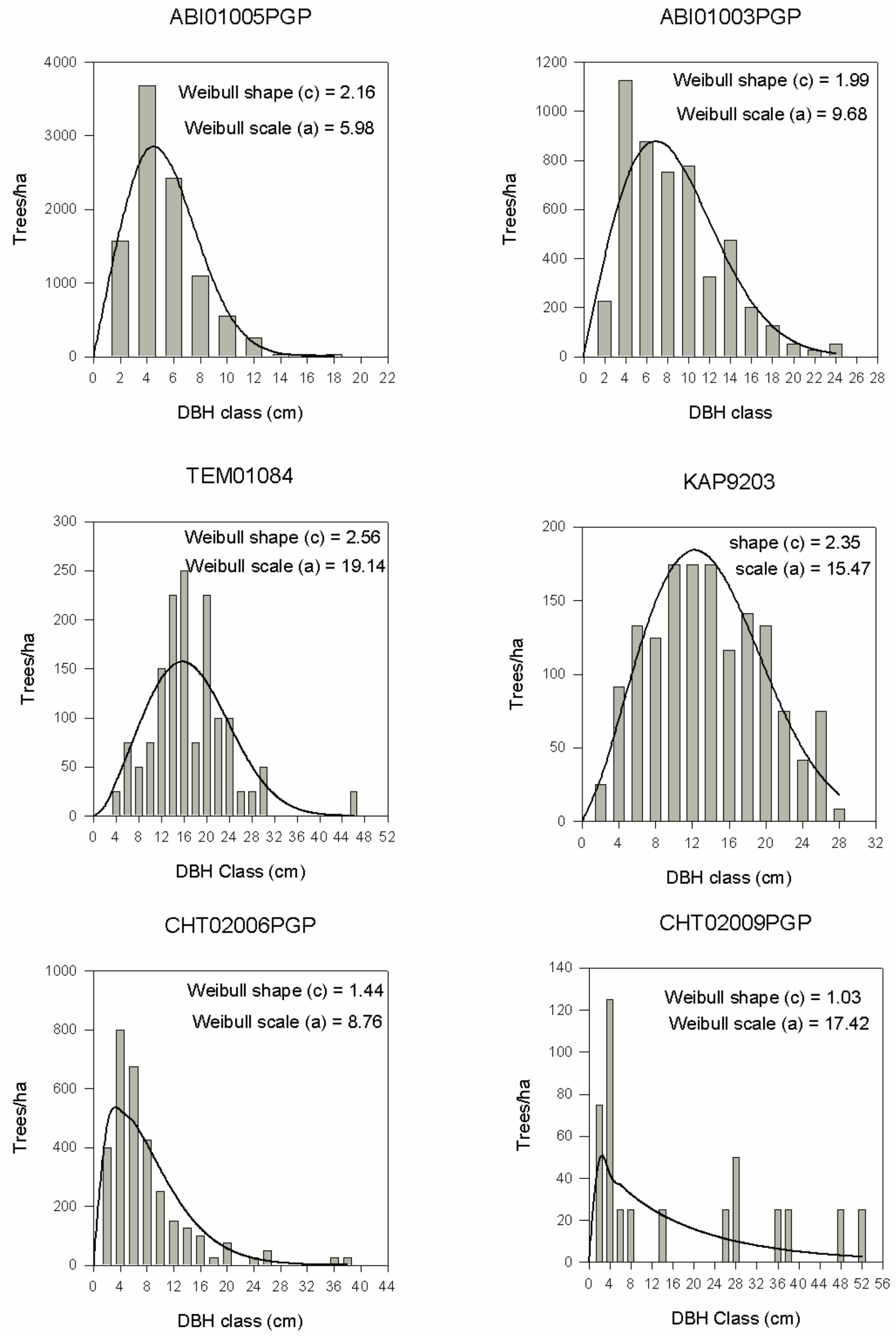

Figure 11. Diameter distributions with Weibull curves for sites in the NonSB1 analysis group after cohort assignment. Top row = cohort I, middle row = cohort II, and the bottom row= cohort III

Cohort I was strongly positively associated with high total tree density and, to a lesser degree, with the Weibull shape parameter (Figure 9). Cohort I was negatively associated with the majority of analysis variable vectors. Cohort III was positively associated with vectors for diameter class skewness, coefficient of variation, richness, the abundance of most snags, and to a lesser degree Weibull scale, diameter class diversity, and eveness. Cohort II was positively associated with diameter class diversity, evenness, the abundance of newsnags, crown class evenness, crown class richness, and Weibull shape. Including overstory density, age, and dwd variables passively in the ordination reveals an association of cohort III with high overstory density variance and coefficient of variation, high overstory density, and high amounts of DWD in all stages of decay (Figure 9). The positive association of cohort III sites with maximum tree age supported the assumption that sites with cohort III structure tend to be older than sites in cohorts I or II.

The clustering approach decreased overlap of cohort groups in ordination space compared to the visually assigned cohort groups, while still maintaining the relationship of the visually-based cohort groups to the analysis vectors (Figure 9). The relationship of the cluster-based cohort groups to Weibull parameters confirmed expectations that the scale parameter is useful in distinguishing cohorts I and II, and the shape parameter in distinguishing cohort III from the other cohorts (Figure 10). The diameter distributions of randomly selected sites in each cluster-based cohort group agreed with expected distributions according to the cohort concept, and demonstrated that including additional parameters to define cohort groups did not result in a departure from the underlying concept (Figure 11).

SB1 analysis group

The first PCA axis for the SB1 group explained 41% of the total variation and the second PCA axis explained 21% (Figure 12). Many visually classified cohort III sites were associated with high values for the coefficient of variation and richness of the diameter classes, old snags, diameter class diversity, and skewness. Cohort II sites appear to be positively associated with the same analysis variables and vectors, but not as strongly as the cohort IIIs. Other vectors associated with cohort II sites include crown class richness and diversity, the density of large trees, and, to a lesser extent, total density and Weibull scale. Visually classified cohort I sites were grouped in the PCA due to their negative relationship with diameter class richness, diversity, and the abundance of old snags. Cohort I sites tend to be grouped on the positive side of the second PCA axis, and because the only vector positively associated with this axis was for Weibull shape, a positive relationship between high values for Weibulll shape and cohort I sites can also be inferred.

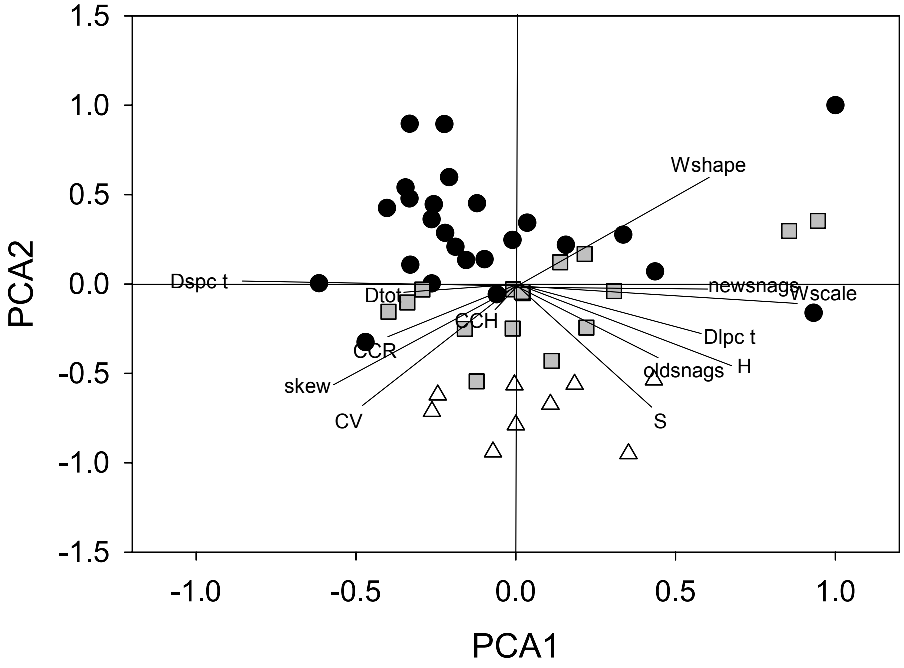

Figure 12. Principal component analysis biplot of sites from the SB1 analysis group. Symbols represent cohorts assigned by visual assessment of diameter distribution histograms. ● = cohort I; ■ = cohort II; ▲ = cohort III.

The Boucher cohort classes for this analysis group did not form any distinct grouping patterns in the exploratory PCAs and the classification function only identified 6 cohort IIs and 8 cohort IIIs among the 50 SB1 sites. By comparison, visually assigned cohort classes identified 16 potential cohort II's and 9 cohort III's from this group, and the pattern of separation along the second PCA axis was clear (Figure 12). For these reasons, the Boucher cohort classes were not considered further in the clustering of sites to form cohort groups. Instead, a clustering approach was sought that best distinguished the visually assigned cohort classes plotted in Figure 12.

The Cluster analysis selected to group cohorts in the SB1 analysis group was based solely on site scores from the second principal component axis of the PCA, which explained 21% of the total variance (Figure 13). Clearly, the first PCA axis had little to do with cohort separation in this analysis group. Worse yet, if it was included in the analysis, the outliers on this axis formed independent clusters. Including scores from axes 3, 4 and 5 resulted in clusters that differed greatly from those assigned visually. For example, by including scores from the 3rd principal component axis, a large cluster formed in the centre of the ordination space, and half of the group of sites visually classified to cohorts I and III became members of this cluster. Similar shifts in the proportions of sites in the three clusters were obtained when using various combinations of site scores from principal component axes 2-6. Ultimately, only the clustering based on the second PCA axis alone showed a relatively high degree of correspondence with visual cohort classes.

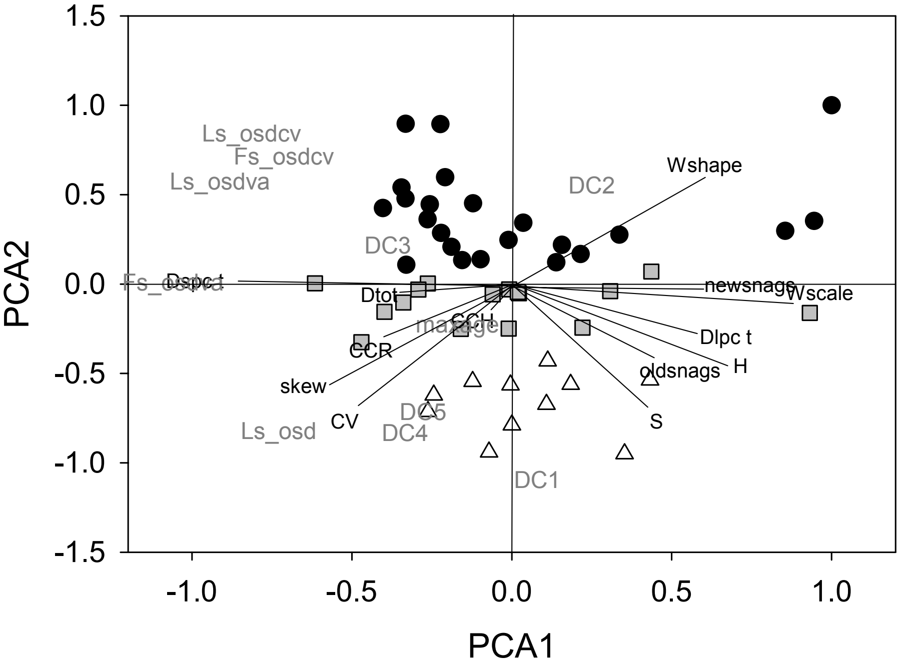

Figure 13. Final Principal component analysis biplot of sites from the SB1 group. Downed woody debris and canopy overstory density variables are plotted passively (in grey text). Symbols and colors represent cohorts assigned by cluster analysis of scores on PCA2. ● = cohort I; ■ = cohort II; ▲ = cohort III.

Definition of cohorts on the second principal component axis agreed well with visually-based cohort groups (compare Figures 12 and 13), with the exception of two visual cohort II outliers that became cohort I's in the clustering approach. According to clustering, some visually assigned cohort I's were more like cohort II's, and some cohort II's more like cohort III's, and these were re-assigned, but the pattern was maintained. The relationship of cluster-based cohorts to analysis variable vectors is therefore the same as that described above for visually based SB1 cohorts. The passive ordination of downed woody debris and age variables accorded with expectations in that these variables showed positive associations with cohort II and III sites (Figure 13). However, the results for overstory density variables were not entirely consistent with expectations. Overstory density variance and coefficient of variation were more strongly associated with cohort I and II than cohort III sites according to the ordination, although they also appeared to be negatively related to the first PCA axis, which had little to do with cohort separation. High overtory density was related to cohort II as might be expected, but also to some degree to cohort III sites (Figure 13).

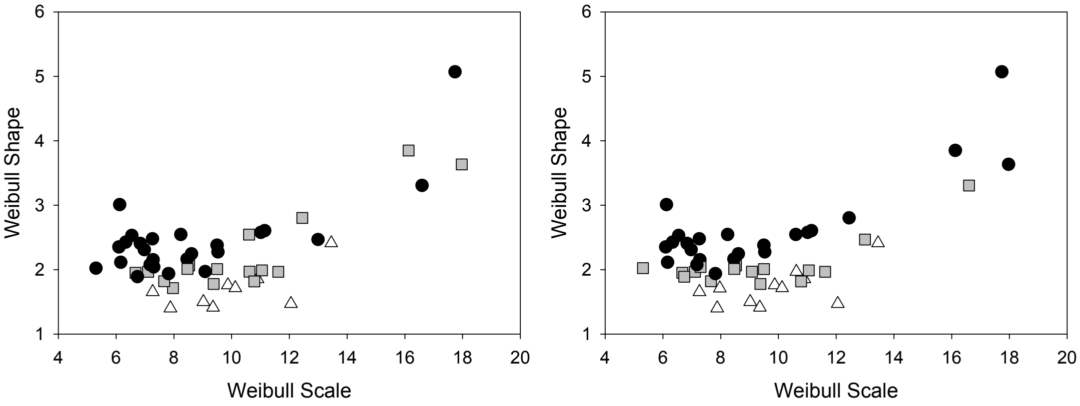

Figure 14. Comparison of visually assigned cohorts (left) and the cluster-based cohorts (right) in relation to Weibull shape and scale parameters for the SB1 analysis group.
● = cohort I; ■ = cohort II; ▲ = cohort III.

The relationship of visually assigned cohorts and cluster-based cohorts to the Weibull shape and scale parameters were similar to each other, but different from the relationships evidenced for the NonSB1 group (compare Figures 10 and 14). For the pure conifer SB1 group, Weibull scale appeared to be less useful in distinguishing cohorts than for the NonSB1 group. The scale parameter separated all cohorts in the SB1 group, contrary to just cohort III's from I's and II's as seen in the NonSB1 group.

Diameter distributions for randomly selected sites again were as expected from cohort theory (Figure 15). These plots confirm that Weibull scale varied little in relation to SB1 cohort types, and that SB1 sites tended to not support large trees in comparison to NonSB1 sites. The plots in Figure 15 also show that cohorts within the SB1 forest unit are somewhat less distinctive in terms of their signature diameter distributions and the shapes of their Weibull curves than was true within the NonSB1 group. The implication is that cohorts are more difficult to detect in this forest unit. Nonetheless, Figure 15 shows that cohort concepts can be applied to distinguish cohort types in SB1 forests, and that the use of variables in addition to those that describe diameter distributions can strengthen differences among cohort types. In other words, the use of variables in addition to those that describe diameter distributions can help distinguish cohorts when variability in diameter distribution related variables is limited.

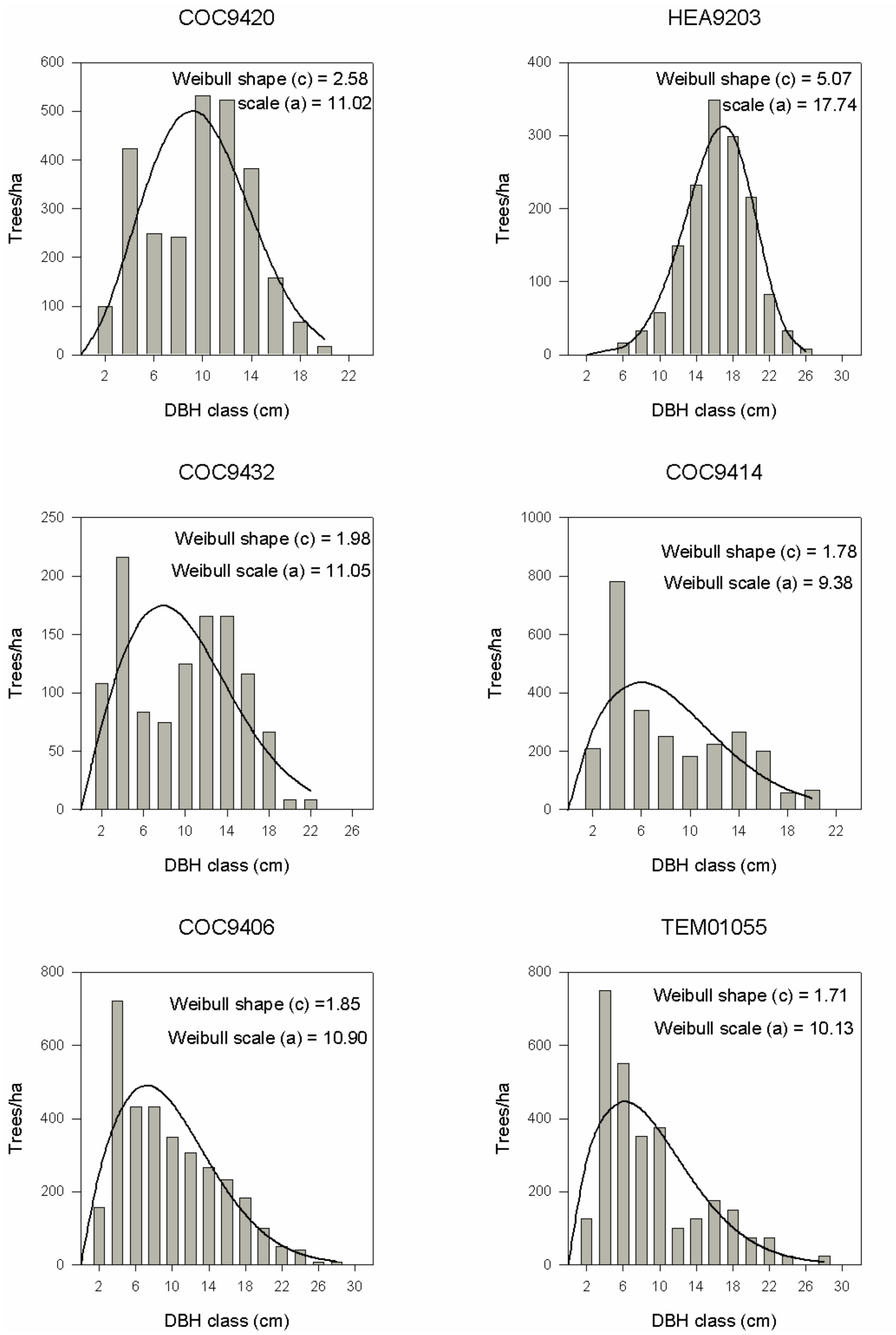

Figure 15. Diameter distributions with Weibull function curves for sites in the SB1 analysis group. Top row = cohort I; middle row = cohort II; and bottom row = cohort III .

Comparisons of analysis variables among cohorts

The Bonferroni correction appeared to be very conservative, and for this reason the unadjusted p-values from the Kruskal-Wallis tests are presented alongside the Bonferroni values in the tables that follow. All variables used in analyses are included in these tables. Recall that the number of sites compared varied depending upon the variable, as certain data were only collected at 95 of the 135 sites. These variables, and the corresponding sample size in each cohort, are indicated by an asterix in the tables that follow.

Table 1. Results of the Kruskal-Wallis tests for the NonSB1 analysis group. Variables are described in Appendix I.

Variable	**Cohort I (n=17) (*n=10)**	**Cohort II (n=28) (*n=22)**	**Cohort III (n=40) (*n=35)**	**Kruskal-Wallis *p*-value**	**Bonferroni *p*-value**
BAITOT	4.05	7.61	6.75	0.0294	0.0855
BASTOT	22.12	23.26	17.93	0.0172	0.0508
CCE	0.60	0.62	0.54	0.0404	0.1163
CCH	1.11	1.15	0.88	<0.0001	**0.0001**
CCR	4.06	4.00	3.65	0.0022	0.0067
CV	51.12	47.94	77.76	<0.0001	**<0.0001**
ConBA	22.38	23.81	18.66	0.0211	0.0620
DC1*	2.09	16.59	35.88	<0.0001	**<0.0001**
DC2*	19.09	26.66	59.59	<0.0001	**<0.0001**
DC3*	12.30	16.78	43.79	<0.0001	**0.0001**
DC4*	14.38	9.25	17.09	0.0133	**0.0394**
DC5*	2.11	2.47	6.20	0.1210	0.3209
DTOT	4946.46	2181.96	1607.52	<0.0001	**<0.0001**
DecBA	3.79	7.06	6.01	0.0365	0.1057
Dlpct	0.65	9.45	18.85	<0.0001	**<0.0001**
Dmpct	30.48	58.16	27.68	<0.0001	**<0.0001**
Dspct	68.87	32.39	53.46	<0.0001	**<0.0001**
E	0.77	0.89	0.85	<0.0001	**0.0001**
Fs_osdcv*	24.54	16.46	24.24	0.0992	0.2691
Fs_osdvar*	510.53	256.09	387.61	0.1175	0.3127
H	1.70	2.19	2.25	<0.0001	**<0.0001**
INTDBH1	128.89	16.65	84.24	0.0421	0.1211
INTDBH2	185.69	71.69	31.82	0.0219	0.0643
INTDBH3	160.16	128.22	31.36	0.0013	**0.0038**
INTDBH4	41.15	103.82	31.86	0.0014	**0.0043**
INTDBH5	8.82	62.18	71.93	0.0002	**0.0005**
Ls_osd*	85.26	88.48	79.71	0.0430	0.1236
Ls_osdcv*	19.38	13.28	18.41	0.2317	0.5465
Ls_osdvar*	356.18	199.90	257.88	0.3521	0.7280
S	9.29	11.89	14.10	<0.0001	**<0.0001**
SLratio	96.96	6.53	5.95	<0.0001	**<0.0001**
SMratio	3.11	0.61	3.98	<0.0001	**<0.0001**

SPDDBH1	1581.13	268.41	465.30	<0.0001	**<0.0001**
SPDDBH2	1653.45	388.05	352.80	<0.0001	**<0.0001**
SPDDBH3	1016.19	654.96	240.45	<0.0001	**<0.0001**
SPDDBH4	153.83	382.36	144.54	<0.0001	**<0.0001**
SPDDBH5	17.15	105.61	153.22	<0.0001	**<0.0001**
TotBaha	26.17	30.87	24.67	0.0121	**0.0359**
Wscale	8.47	14.01	13.28	<0.0001	**<0.0001**
Wshape	2.19	2.39	1.48	<0.0001	**<0.0001**
maxage*	76.40	92.50	119.09	0.0015	0.0046
newDWD*	33.48	60.03	139.26	<0.0001	**<0.0001**
newsnagL	0.00	0.89	12.71	0.0001	**0.0003**
newsnagM	2.44	36.01	25.72	0.0138	**0.0408**
newsnagS	10.27	74.38	30.80	0.0002	**0.0005**
newsnags1	12.71	111.28	69.23	0.0003	**0.0008**
oldDWD*	16.49	11.72	23.29	0.0133	**0.0395**
oldsnagL	14.71	7.14	36.53	0.0127	**0.0377**
oldsnagM	7.35	29.15	31.21	0.0105	**0.0310**
oldsnagS	12.24	47.29	15.68	0.0049	**0.0146**
oldsnags1	34.29	83.58	83.41	0.0493	0.1407
skew	0.90	0.41	1.35	<0.0001	**0.0001**

Table 2. Results of the Kruskal-Wallis tests for the SB1 analysis group and SB1 forest unit in northeastern Ontario. Variables are described in Appendix I.

Variable	**Cohort I (n=23) (*n=10)**	**Cohort II (n=16) (*n=12)**	**Cohort III (n=11) (*n=6)**	**Kruskal-Wallis *p*-value**	**Bonferroni *p*-value**
BAITOT	0.18	0.11	0.27	0.2817	0.6293
BASTOT	19.11	20.24	22.37	0.7538	0.9851
CCE	0.60	0.55	0.57	0.1751	0.4387
CCH	0.99	0.98	1.03	0.5814	0.9266
CCR	3.83	4.19	4.00	0.0204	0.0599
CV	43.24	52.71	64.43	<0.0001	**<0.0001**
ConBA	19.11	20.24	22.37	0.7538	0.9851
DC1*	4.50	4.53	14.11	0.1652	0.4181
DC2*	22.38	8.16	11.37	0.5280	0.8949
DC3*	8.95	6.35	4.90	0.4685	0.8499
DC4*	1.76	2.45	6.07	0.4829	0.8617
DC5*	1.17	1.07	2.60	0.5582	0.9138
DTOT	2984.60	3296.22	2671.10	0.7452	0.9835
DecBA	0.18	0.11	0.27	0.2817	0.6293
Dlpct	1.44	0.77	4.45	0.0001	**0.0002**
Dmpct	37.02	36.41	34.40	0.9708	1.0000
Dspct	61.54	62.82	61.16	0.7989	0.9919
E	0.83	0.78	0.77	0.0717	0.2000
Fs_osdcv*	72.04	53.08	30.18	0.6038	0.9378
Fs_osdvar*	455.56	436.63	391.72	0.9562	0.9999

H	1.64	1.75	1.94	0.0242	0.0708
INTDBH1	5.43	7.28	3.77	0.0993	0.2692
INTDBH2	1.09	13.52	4.53	0.1941	0.4766
INTDBH3	1.08	5.73	9.81	0.4264	0.8113
INTDBH4	1.09	0.00	2.26	0.1531	0.3925
INTDBH5	2.17	0.00	1.51	0.1530	0.3924
Ls_osd*	55.60	61.98	71.81	0.5728	0.9221
Ls_osdcv*	47.93	31.94	14.17	0.1628	0.4132
Ls_osdvar*	304.31	239.44	106.44	0.7351	0.9814
S	7.48	9.44	12.45	<0.0001	**<0.0001**
SLratio	19.57	139.87	19.66	0.0410	0.1181
SMratio	4.07	3.34	2.29	0.9537	0.9999
SPDDBH1	900.38	1262.51	903.61	0.3824	0.7644
SPDDBH2	995.98	981.21	716.57	0.8340	0.9954
SPDDBH3	869.35	711.73	627.78	0.7388	0.9822
SPDDBH4	186.30	294.99	299.98	0.0249	0.0728
SPDDBH5	21.71	19.26	101.27	<0.0001	**0.0001**
TotBaha	19.29	20.35	22.64	0.7538	0.9851
Wscale	9.39	9.30	9.87	0.3726	0.7530
Wshape	2.63	2.07	1.71	<0.0001	**<0.0001**
maxage*	92.60	133.58	110.00	0.1492	0.3841
newDWD*	35.82	19.04	30.38	0.4571	0.8400
newsnagL	0.00	0.00	0.75	0.1699	0.4279
newsnagM	5.78	17.69	16.61	0.0358	0.1035
newsnagS	43.04	59.78	29.45	0.3323	0.7024
newsnags1	48.83	77.47	46.81	0.2086	0.5043
oldDWD*	2.94	3.51	8.68	0.3700	0.7499
oldsnagL	1.09	0.00	0.00	0.5560	0.9125
oldsnagM	5.43	10.40	33.28	0.0002	**0.0005**
oldsnagS	8.68	24.44	27.18	0.0457	0.1309
oldsnags1	15.20	34.84	60.46	0.0015	**0.0044**
skew	0.41	0.78	1.16	0.0003	**0.0008**

Table 3. Results of the Kruskal-Wallis tests for the MW2 forest unit in northeastern Ontario. Variables are described in Appendix I.

Variable	**Cohort I (n=4) (*n=4)**	**Cohort II (n=5) (*n=5)**	**Cohort III (n=13) (*n=10)**	**Kruskal-Wallis p-value**	**Bonferroni p-value**
BAITOT	12.12	13.37	11.15	0.7706	0.9879
BASTOT	18.37	18.66	15.69	0.4541	0.8373
CCE	0.60	0.60	0.57	0.7446	0.9833
CCH	1.13	1.11	0.95	0.2970	0.6525
CCR	4.25	3.80	3.69	0.1788	0.4461
ConBA	18.37	18.66	15.78	0.4541	0.8373
CV	54.24	45.68	70.37	0.0231	0.0677
DC1*	2.73	8.57	48.66	0.0335	0.0970
DC2*	20.93	23.05	42.96	0.1162	0.3098

DC3*	15.23	10.47	35.76	0.0955	0.2600
DC4*	19.23	2.92	15.93	0.0317	0.0921
DC5*	1.01	0.66	8.46	0.1317	0.3454
DecBA	12.12	13.37	11.06	0.7706	0.9879
Dlpct	0.61	9.15	17.67	0.0033	**0.0100**
Dmpct	31.92	62.58	37.67	0.0247	0.0724
Dspct	67.47	28.27	44.66	0.0195	0.0575
DTOT	5094.65	1992.14	1521.18	0.0048	**0.0143**
E	0.78	0.90	0.95	0.0903	0.2472
Fs_osdcv*	22.79	12.47	20.01	0.6351	0.9514
Fs_osdvar*	509.53	170.82	309.26	0.5691	0.9200
H	1.79	2.28	2.57	0.0222	0.0653
INTDBH1	304.05	16.60	61.64	0.0106	**0.0315**
INTDBH2	647.60	66.50	39.24	0.0061	**0.0183**
INTDBH3	514.23	156.38	43.23	0.0011	**0.0032**
INTDBH4	104.08	273.10	61.50	0.0109	**0.0323**
INTDBH5	24.98	86.56	114.73	0.0272	0.0794
Ls_osd*	87.98	92.19	84.17	0.3977	0.7815
Ls_osdcv*	18.30	10.01	16.85	0.5691	0.9200
Ls_osdvar*	339.63	121.98	239.76	0.6723	0.9648
maxage*	102.25	109.00	105.30	0.9955	1.0000
newDWD*	38.88	42.10	127.37	0.0880	0.2415
newsnagL	0.00	0.00	7.59	0.0708	0.1977
newsnagM	2.08	31.66	32.36	0.2690	0.6094
newsnagS	18.73	91.56	40.50	0.1639	0.4154
newsnags1	20.80	123.22	80.46	0.2167	0.5195
oldDWD*	20.24	3.58	24.39	0.0233	0.0683
oldsnagL	18.75	9.98	18.59	0.5501	0.9090
oldsnagM	18.75	36.62	31.06	0.5018	0.8763
oldsnagS	22.90	61.62	25.16	0.0519	0.1479
oldsnags1	60.40	108.22	74.82	0.4423	0.8265
S	10.25	12.60	15.31	0.0094	**0.0279**
skew	1.29	0.15	1.17	0.0155	**0.0459**
SLratio	84.83	3.36	4.04	0.0250	0.0732
SMratio	2.18	0.50	2.63	0.0218	0.0640
SPDDBH1	1325.20	206.64	327.04	0.0099	**0.0294**
SPDDBH2	1138.05	319.96	273.63	0.0087	**0.0260**
SPDDBH3	855.43	438.20	295.00	0.0133	**0.0393**
SPDDBH4	172.73	339.92	195.88	0.2406	0.5621
SPDDBH5	8.33	88.28	109.31	0.0227	0.0667
TotBaha	30.49	32.03	26.84	0.4411	0.8254
Wscale	8.66	14.86	14.05	0.0157	**0.0464**
Wshape	1.98	2.50	1.65	0.0213	0.0625

Table 4. Results of the Kruskal-Wallis tests for the SF1 forest unit in northeastern Ontario. Variables are described in Appendix I.

Variable	**Cohort I (n=11) (*n=4)**	**Cohort II (n=19) (*n=13)**	**Cohort III (n=22) (*n=20)**	**Kruskal-Wallis *p*-value**	**Bonferroni *p*-value**
BAITOT	1.19	5.83	3.75	0.0015	**0.0045**
BASTOT	24.47	24.62	19.93	0.1102	0.2956
CCE	0.62	0.61	0.53	0.0169	**0.0497**
CCH	1.15	1.15	0.85	0.0006	**0.0017**
CCR	4.00	4.05	3.68	0.0508	0.1447
CV	48.48	49.01	82.07	<0.0001	**<0.0001**
ConBA	24.47	24.62	19.93	0.1102	0.2956
DC1*	0.66	21.77	32.87	0.0050	**0.0149**
DC2*	21.10	31.94	69.66	0.0152	**0.0448**
DC3*	10.33	20.75	48.99	0.0017	**0.0050**
DC4*	13.84	13.82	18.13	0.5274	0.8944
DC5*	2.72	2.79	6.14	0.5141	0.8853
DTOT	4852.31	2221.54	1616.68	<0.0001	**<0.0001**
DecBA	1.19	5.83	3.75	0.0015	**0.0045**
Dlpct	0.53	8.31	20.09	<0.0001	**<0.0001**
Dmpct	31.91	57.87	22.70	<0.0001	**<0.0001**
Dspct	67.56	33.82	57.21	<0.0001	**<0.0001**
E	0.79	0.89	0.80	0.0003	**0.0008**
Fs_osdcv*	33.26	16.04	25.11	0.0524	0.1491
Fs_osdvar*	720.49	250.85	419.72	0.0365	0.1054
H	1.70	2.18	2.09	0.0007	**0.0021**
INTDBH1	86.36	16.23	101.97	0.3974	0.7811
INTDBH2	36.36	69.73	33.54	0.2048	0.4971
INTDBH3	29.55	126.75	29.19	0.0050	**0.0150**
INTDBH4	18.18	64.03	18.18	0.0100	**0.0296**
INTDBH5	2.27	43.86	36.12	0.0081	**0.0241**
Ls_osd*	79.82	88.77	79.58	0.0526	0.1496
Ls_osdcv*	27.53	13.63	18.92	0.1460	0.3773
Ls_osdvar*	539.46	232.51	280.58	0.1198	0.3181
S	8.91	11.79	13.50	0.0002	**0.0005**
SLratio	118.90	7.69	6.69	0.0018	**0.0053**
SMratio	2.92	0.64	5.02	<0.0001	**<0.0001**
SPDDBH1	1518.27	306.96	524.11	0.0002	**0.0006**
SPDDBH2	1807.11	402.14	351.48	<0.0001	**<0.0001**
SPDDBH3	1178.52	680.16	208.36	<0.0001	**<0.0001**
SPDDBH4	156.75	397.71	120.93	<0.0001	**<0.0001**
SPDDBH5	18.94	113.99	192.79	<0.0001	**<0.0001**
TotBaha	25.65	30.45	23.67	0.0283	0.0825
Wscale	8.60	13.68	12.87	0.0004	**0.0011**
Wshape	2.31	2.35	1.40	<0.0001	**<0.0001**
maxage*	48.75	83.54	125.55	0.0006	**0.0018**
newDWD*	32.08	74.45	151.51	0.0021	**0.0062**
newsnagL	0.00	1.32	8.40	0.0437	0.1256

newsnagM	2.26	38.15	17.44	0.0484	0.1384
newsnagS	2.26	78.94	30.18	0.0003	**0.0010**
newsnags1	4.53	118.41	56.02	0.0008	**0.0023**
oldDWD*	16.56	16.61	24.27	0.4386	0.8231
oldsnagL	13.64	7.89	54.30	0.0146	**0.0430**
oldsnagM	4.55	29.37	36.12	0.0383	0.1107
oldsnagS	3.78	42.95	13.64	0.0594	0.1678
oldsnags1	21.96	80.22	104.05	0.0230	0.0674
skew	0.73	0.50	1.43	0.0044	**0.0131**

Table 5. Results of the Kruskal-Wallis tests for the SP1 forest unit in northeastern Ontario. Variables are described in Appendix I.

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Variable	**Cohort I (n=2) (*n=2)**	**Cohort II (n=4) (*n=4)**	**Cohort III (n=5) (*n=5)**	**Kruskal-Wallis *p*-value**	**Bonferroni *p*-value**
BAITOT	3.67	8.87	8.49	0.1033	0.2789
BASTOT	16.76	22.55	14.96	0.7630	0.9867
CCE	0.54	0.67	0.53	0.1225	0.3242
CCH	0.88	1.23	0.84	0.0707	0.1973
CCR	4.00	4.00	3.40	0.1054	0.2840
CV	59.40	45.68	77.96	0.0173	0.0510
ConBA	18.98	26.37	20.58	0.4988	0.8741
DC1*	3.67	9.80	22.36	0.0911	0.2492
DC2*	11.38	14.01	52.59	0.0227	0.0667
DC3*	10.40	11.76	39.06	0.0589	0.1665
DC4*	5.76	2.31	15.23	0.0526	0.1497
DC5*	3.10	3.68	1.95	0.8612	0.9973
DTOT	5167.90	2231.25	1791.66	0.2416	0.5637
DecBA	1.45	5.05	2.86	0.5016	0.8762
Dlpct	1.42	15.23	16.48	0.1609	0.4091
Dmpct	19.74	54.05	23.65	0.0293	0.0852
Dspct	78.85	30.72	59.87	0.0889	0.2436
E	0.69	0.89	0.79	0.1261	0.3327
Fs_osdcv*	10.60	22.80	29.23	0.0760	0.2111
Fs_osdvar*	92.61	379.70	415.84	0.0877	0.2406
H	1.54	2.16	2.07	0.0877	0.2406
INTDBH1	12.50	18.75	65.00	0.5448	0.9057
INTDBH2	83.20	87.50	5.00	0.1425	0.3696
INTDBH3	170.40	100.00	10.00	0.0717	0.2001
INTDBH4	41.60	81.25	14.98	0.0332	0.0963
INTDBH5	12.50	118.75	118.26	0.0910	0.2488
Ls_osd*	90.71	82.92	71.28	0.1503	0.3864
Ls_osdcv*	5.24	16.25	19.51	0.0632	0.1779
Ls_osdvar*	22.75	191.32	203.32	0.0760	0.2111

S	9.50	11.50	13.60	0.0148	**0.0439**
SLratio	23.67	5.28	7.68	0.2657	0.6040
SMratio	5.99	0.61	2.94	0.0464	0.1328
SPDDBH1	2438.70	162.50	565.98	0.0498	0.1420
SPDDBH2	1839.10	406.25	564.46	0.6331	0.9506
SPDDBH3	444.90	806.25	239.82	0.4813	0.8605
SPDDBH4	100.00	362.50	114.90	0.1919	0.4724
SPDDBH5	25.00	87.50	93.26	0.3050	0.6643
TotBaha	20.43	31.42	23.44	0.3131	0.6758
Wscale	7.40	14.48	13.09	0.0632	0.1779
Wshape	1.91	2.45	1.41	0.0315	0.0916
maxage*	80.00	101.00	120.80	0.0911	0.2492
newDWD*	25.45	35.56	114.01	0.0227	0.0667
newsnagL	0.00	0.00	44.98	0.0400	0.1152
newsnagM	4.15	31.25	44.88	0.6808	0.9675
newsnagS	37.40	31.25	8.32	0.1379	0.3593
newsnags1	41.55	62.50	98.18	0.5384	0.9016
oldDWD*	8.86	5.99	17.18	0.4299	0.8147
oldsnagL	12.50	0.00	5.00	0.3578	0.7351
oldsnagM	0.00	18.75	9.98	0.4473	0.8312
oldsnagS	37.40	50.00	0.00	0.0129	**0.0381**
oldsnags1	49.90	68.75	14.98	0.0719	0.2006
skew	1.05	0.29	1.43	0.1676	0.4232

Many structural variables were significantly different among cohorts in the NonSB1 analysis group, and these differences were not limited to variables used directly in cohort classification for this group (Table 1). For instance, trees/ha in Nguyen's (2000) size classes 1 – 3 were highly significantly different among cohorts, and these differences were found in both tolerant and intolerant size class groupings. The diameter size classes proposed by Nguyen were assumed to represent height classes based on the positive diameter to height relationship inherent in trees (Nguyen 2000). Following that assumption, results suggest that the height structure of different cohorts in the NonSB1 analysis group is significantly different. The smallest diameter intolerant trees were most abundant in cohort I, least abundant in cohort II, and slightly more abundant again in cohort III sites from the NonSB1 group. The number of trees in intolerant size classes 2 and 3 decreased between cohort I and II, and cohort II and III, respectively, and these differences were significant (Table 1). A significant similar trend of decreasing abundance of trees when comparing cohorts I through III was evidenced by the tolerant trees in Nguyen's first three size classes (Table 1). Variables used in cohort classification that were significantly different among cohorts included the diameter class skewness, richness, total tree density, the density (%) of large trees, and Weibull scale. According to means for each cohort, diameter class richness increased with increasing cohort class, as did the relative density of large trees. Conversely, total density decreased in cohorts I through III (Table 1). Low mean skewness distinguished cohort II from the other cohort types, and Weibull scale cohort I from cohorts II and III. Near significant differences, evidenced by unadjusted p-values, abounded in this comparison (Table 1).

For the SB1 analysis group, which only included sites from the SB1 forest unit, significant differences among cohorts were limited to variables used in the ordination and clustering analysis, with the exception of medium sized old snags and trees in Nguyen's SPDDBH5 diameter class group (Table 2). Diameter class richness, coefficient of variation, skewness, total old snags, and medium sized old snags all increased in cohorts I through III and were significantly different among cohorts. The Weibull shape parameter decreased significantly in cohorts I through III. Near significant increases in cohorts I through III in diameter class diversity and crown class richness also were detected by the Kruskal-Wallis tests (Table 2). Medium-sized new snags and trees per ha in the SPDDBH4 tolerant diameter class had similar means in cohorts II and III that were much greater than in cohort I, and differences among cohorts for these variables also were nearly significant. Old DWD increased across cohorts, and new DWD was observed in similar amounts in cohorts I and III that were greater than those in cohort II, but these trends were not significant (Table 2). The trends in overstory density and maximum tree age were counterintuitive, with the highest overstory densities observed in cohort III stands, and the greatest maximum tree age in cohort II stands. Large and fine-scale overstory density coefficient of variation and variance also decreased progressively from cohorts I through III, but not significantly so.

For the MW2 forest unit, as observed in the comparisons for the NonSB1 analysis group to which sites in this forest unit belong, most significant variables summarized trees per ha in the size classes and compositional groupings used by Nguyen (2000) in his cohort classification work in Quebec (Table 1; also see Appendix I). However, there were slight differences between the analysis group and forest unit specific comparisons. For example, the density of trees in Nguyen's first three size classes all decreased progressively from cohort I to III when comparing MW2 sites exclusively (Table 3). For both the intolerant and tolerant compositional groups (INT and SPD, respectively), Cohort II had the highest density of trees in size class 4, and Cohort III had the highest density size class 5 trees in both compositional groups. Not surprisingly, total density and the % density of large diameter trees also were significantly different according to Bonferroni adjusted *p*-values. The remaining highly significant differences were in variables used in the ordination and clustering analyses that included this stand type: diameter class richness, skewness, and the Weibull scale parameter (Table 3).

Near significant results were obtained for old downed woody debris, and downed woody debris in decay classes 1 and 4, suggesting that DWD also varies in a predictable fashion among cohorts in the MW2 forest unit (and as indicated in the PCA analysis). Judging by the means, cohort III stands have substantially more DWD in early stages of decay, and both cohorts I and III showed high amounts of decay class 4 DWD compared to a near absence of class 4 logs in cohort II. Lastly, the maximum tree age was quite similar among cohorts; in fact, all ages were within a standard deviation of the mean.

The greatest number of forest unit-specific significant differences among cohorts was detected in the SF1 forest unit (Table 4). Not surprisingly, many of the analysis variables used in ordination and clustering analyses to group cohorts were significantly different.

Among these, diameter class richness, skewness, coefficient of variation, total old snags, and large new snags increased significantly in cohorts I through III (Table 4). Crown class richness and diversity were also significantly different among cohorts, with similar means observed in cohorts I and II, and a trend toward lower richness and diversity of crown classes in cohort III. Weibull shape and scale parameters were significantly different among cohorts as well; shape being similar in cohorts I and II, and scale is similar in cohorts II and III. Diameter class diversity, eveness, Weibull shape, and Weibull scale were all greatest in cohort II and significantly different among cohorts. Total density decreased significantly in cohorts I through III. Many of the variables related to absolute or relative differences in tree densities by size class were also significantly different among SF1 cohorts. Similar to the trend in the MW2 forest unit, smaller size class groupings of trees (eg. INTDBH1-3, SPDDBH1-3) tended to be most abundant in cohort I and to decrease in cohorts II and III (Table 3). Tolerant and intolerant medium sized trees in the classes INTDBH4 and SPDDBH4, as well as large intolerant trees in the INTDBH5 class, were significantly most abundant in cohort II's. (Table 4). Large tolerant trees (SPDDBH5) were significantly most abundant in cohort III, as was the relative density of all large trees. Other tree density variables that were significantly different among cohorts included the relative density of medium sized trees (greatest in cohort II), and the density (%) of small trees, which was relatively high in cohorts I and III, and low in cohort II (Table 4).

The significant differences detected among cohorts in terms of deciduous and intolerant basal area (DECBA, BAITOT) were of particular interest in the SF1 forest unit, because such differences were not detected in other forest units. These two variables are essentially the same thing because they differ only with respect to the inclusion of jack pine in the intolerant group (BAITOT), an infrequently observed species in this forest unit. Deciduous basal area was lowest in cohort I, highest in cohort II, and intermediate in cohort III (Table 4). Downed woody debris in early stages of decay was significantly most abundant in cohort III, and amounts observed more or less doubled between cohorts I and II, and between cohorts II and III. DWD in late stages of decay was found in similar amounts in cohorts I and II, and was significantly more abundant in cohort III (Table 4). The mean maximum age increased with cohort class and was significantly different among cohorts. The difference in overstory density among cohorts was near significant, with the highest values observed in cohort II, and similar mean overstory densities in cohorts I and III.

Considerably fewer significant differences among cohorts were detected in the SP1 forest unit. Only diameter class richness, which increased with cohort class, and the number of small old snags were significantly different among SP1 cohorts (Table 5). Near significant differences, however, were observed for several variables. These included the diameter class coefficient of variation and amounts DWD in early stages of decay, which both increased in cohorts I though III. Large old snags were only found in cohort III. Medium sized trees were most abundant in cohort II (INTDBH4 and Dmpct). The Weibull shape parameter also was nearly significantly different among cohorts and was lowest in cohort III (Table 5).

Cohort classification functions

The stepwise discriminant analysis identified variables with the best discriminating power to predict cohort types for each analysis group and forest unit. Depending on the analysis group and/or forest unit, the stepwise selection process identified between 3 and 10 variables to include in the classification functions.

Table 6. Results of the stepwise discriminant analysis by analysis group and forest unit.

MW2		**SB1**		**SF1**		**SP1**		**NonSB1**	
Variable	R^2 value	Variable	R^2 value	Variable	R^2 value	Variable	R^2 value	Variable	R^2 value
DTOT	0.85	S	0.54	Dmpct	0.64	CV	0.73	DTOT	0.59
Skew	0.42	CV	0.59	DTOT	0.58	DTOT	0.66	Dmpct	0.51
H	0.38	SMratio	0.17	S	0.34	Dlpct	0.47	S	0.29
Totbaha	0.33	Oldsnags1	0.24	newsnagM	0.19			CV	0.11
Dlpct	0.33	SLratio	0.13	CV	0.19			SLratio	0.12
		CCR	0.16	CCH	0.19			newsnags1	0.11
		CCH	0.15	SLratio	0.19			CCR	0.07
		OldsnagS	0.10	Wscale	0.09			E	0.06
				newsnagS	0.10			H	0.09
								Wshape	0.06

The stepwise selection of variables appeared to be sensitive to sample size, as evidenced by the small number of variables that met the selection criteria in the MW2 (n = 22) and SP1 (n = 11) forest units. The discrimination criteria for the analysis groups and forest units are presented in Tables 7-10. The constants and coefficients for classification variables are the data required to build classification functions to assign unclassified sites to cohorts. According to the posterior probability error-rate estimates associated with the classification functions, most appeared to be quite robust. The estimated probabilities of misclassification were p = 0.06 for the NonSB1 group (Table 6), and p= 0.01 for the SB1 group and forest unit (Table 7). Forest unit-specific derivation of functions lessened the probability of misclassification compared to the group function for two of the three forest units in the NonSB1 group: p=0.03 for the MW2 forest unit (Table 8); and p= 0.03 for SF1 forest unit (Table 9). The misclassification probability was greater for the SP1 forest unit specific function (p= 0.17) than for the NonSB1 group classification function (Tables 6 & 10). Low sample size presumably contributed to the high error rate for the forest unit-specific function calculated for SP1 stands.

Table 6. Constants and coefficients of the classification functions calculated by discriminant analysis for the NonSB1 analysis group.

Variable	**Cohort I**	**Cohort II**	**Cohort III**
`Constant`	-629.700	-614.369	-656.517

Dmpct	0.595	0.790	0.655
DTOT	0.021	0.019	0.019
S	38.431	36.673	38.966
newsnags1	-0.010	0.002	-0.016
CV	4.530	4.734	5.012
E	1675.000	1584.000	1642.000
H	-541.337	-508.284	-524.781
SLratio	0.168	0.125	0.115
CCR	7.166	6.313	2.303
Wshape	62.366	66.081	68.109

Table 7. Constants and coefficients of the classification functions calculated by discriminant analysis for the SB1 analysis group and forest unit.

Variable	Cohort I	Cohort II	Cohort III
Constant	-115.370	-160.281	-231.040
S	1.765	2.174	2.816
CV	8.638	10.242	14.222
SMratio	2.046	2.400	3.518
Oldsnags1	0.206	0.250	0.374
SLratio	-0.006	0.007	-0.017
CCR	13.213	15.393	7.976
CCH	28.285	27.761	42.423
OldsnagS	-0.020	0.014	-0.092

Table 8. Constants and coefficients of the classification functions calculated by discriminant analysis for the MW2 forest unit.

Variable	Cohort I	Cohort II	Cohort III
Constant	-63.347	-17.674	-29.683
DTOT	0.030	0.003	-0.002
Skew	-2.464	5.432	13.246
H	-0.206	7.369	12.548
Totbaha	-0.677	0.304	0.419
Dlpct	1.033	0.188	0.203

Table 9. Constants and coefficients of the classification functions calculated by discriminant analysis for the SF1 forest unit.

Variable	Cohort I	Cohort II	Cohort III
Constant	-132.978	-168.300	-173.265
Dmpct	1.583	1.914	1.595

DTOT	0.015	0.015	0.013
S	-2.216	-1.712	0.192
newsnagM	-0.005	-0.023	-0.082
CV	2.036	2.387	2.495
CCH	5.189	-2.103	-10.053
SLratio	0.038	0.012	-0.012
Wscale	6.287	7.065	7.129
newsnagS	0.008	0.036	0.031

Table 10. Constants and coefficients of the classification functions calculated by discriminant analysis for the SP1 forest unit.

Variable	Cohort I	Cohort II	Cohort III
Constant	-181.321	-91.470	-187.805
CV	3.711	2.643	3.825
DTOT	0.027	0.019	0.027
Dlpct	1.768	1.308	1.812

DISCUSSION

This study provided an excellent opportunity to build upon previous cohort classification work and further elucidate cohort relationships to additional structural and compositional variables. In the course of exploratory analyses, it became clear that reliance on a reduced set of diameter distribution related parameters to classify cohorts may not result in cohort assignments that group the most related sites when additional structural variables are considered. Classification functions proposed to date may not be transferable to other forests and regions due to their dependence on classification variables that are correlated with site productivity (eg. Nguyen 2000), or their use of a limited number of classification variables and/or limited data availability for classification (eg. Boucher et al. 2003).

One of our primary objectives was to reduce subjectivity in cohort classification, which we achieved through combined use of principal components analyses and cluster analyses. The resulting clusters captured a high amount of structural and compositional variability among sites/cohorts. Although guided to some degree by a visual classification during exploratory analyses, the ultimate cohort classification used here depended entirely on quantitative differences among sites to group them into cohorts. The clustering approach relied on gradients among sites relative to all of the classification variables (site scores on PCA axes), so, fundamentally, it is built upon the combined variability in all of the analysis variables, not strictly differences in diameter distributions. Although the clustering of SB1 sites relied on scores from the second PCA axis alone and therefore less of the total variability among sites that the NonSB1 cluters, the classification proposed for SB1 was still based on differences in all analysis variables. The most important advantage of the approach described here may be that it has established an objective basis for cohort classification that to date has been subjective at its core (Nguyen et al. 2000, Boucher et al. 2003).

Including snag and crown class variables directly into the cohort classification analyses demonstrated that more than diameter distributions vary in a predictable fashion among cohorts, and that these differences complement the variables derived from diameter distributions. Moreover, this study demonstrated that many features commonly associated with older forests, such as snags and DWD are strongly related to cohort type, irrespective of whether these features are used directly in the cohort classification. For example, old snags were associated with cohort III sites in all forest units, and new snags tended to abound in cohort II sites. When all snag variables were compared among cohorts in K-W ANOVAs, the trend was evident even though many snag variables were not used directly in the cohort classification. Similarly, greater abundances of DWD were consistently found in cohort III sites even though DWD variables were not directly included in the classification approach. In the NonSB1 analysis group, overstory density variance and covariance was associated in ordinations and ANOVAs with cohort III stands as well, as one might expect if these are though of as more open forests dominated by small-scale gap disturbances. However, the weak relationship of cohort III sites to overstory density variance and coefficient of variation evidenced in the SB1 group suggests that some alternative means to measure gap size and frequency may be better suited to detecting gap differences among cohorts in this forest type; or, alternatively, that the evolution of cohorts in SB1 stands may not follow the assumption that cohort III stands are the most "open" ones. Nevertheless, several of the inter-cohort differences detected in our analysis support the underlying theory that cohort II and III stands represent progressively older forests characterized by more abundant snags, dwd, and increasing gap sizes and frequency.

The Weibull function and associated parameter estimates were shown to be strongly related to cohort class, and in the case of the NonSB1 analysis group, Weibull scale emerged as an important determinant of the distinction between cohort I and cohort II stands. To date, the shape parameter has been considered in cohort classification (Nguyen 2000), but not the scale parameter, so this finding may contribute to our understanding of cohort distinctions and may provide a relatively simple means to classify cohorts with limited data in the future. Of interest was the absence of such a relationship with the scale parameter in the SB1 sites. Weibull function curves fit to diameter distributions in this forest type did not produce as wide a range of scale parameter estimates, apparently due to the fact that SB1 stands did not tend to support trees in large diameter classes. This observation means that we should be cautious in seeking blanket cohort classification functions applicable to multiple forest types.

While most of the findings from this work supported the cohort concept and the assumed relationship of the three diameter distributions types to forests in progressively later stages of development, some counterintuitive results merit further exploration. For example, in SB1 sites the mean maximum tree age in cohort II was 133 ± 30 years, compared to 110 ± 35 years in SB1 cohort III. Judging by their standard deviations, these means are not really that different, but this result still begs the question as to whether the oldest SB1 stands can be assumed to show an inverse-j diameter distribution. Is it possible that uneven-irregular diameter distributions are more common to lowland spruce forests in late stages of development than the cohort concept assumes? A similar result was obtained for the MW2 forest unit, where mean maximum tree age was greatest in cohort II. However, the inter-cohort differences in this case were less extreme, and in fact mean maximum tree age was quite similar among all three cohorts in this forest unit (Table 1). Nonetheless, it points to the possibility that successive cohorts of trees may establish, grow, senesce and be replaced without the stand taking on a diameter distribution that necessarily accords with the inverse-j distribution associated with the conceptual cohort III. In other forest units, maximum mean tree age increased with the cohort class as one might expect, and was significantly different among cohorts in the SF1 forest unit.

One of the limitations Boucher et al. (2003) identified in their cohort classification work was the relatively small plot-sizes from which stand diameter distributions were derived, which may make bi-modal diameter distributions difficult to detect. This study shares that limitation to some degree, as all PGP tree data was from single 400 m2 circular fixed area sample plots. In most cases, PSP data was calculated from three such plots, but that still may not be enough to capture the variability of diameter distributions at the stand scale. Boucher et al. (2003) also recognized that by not having data from trees <9 cm dbh, some of the strongest signals of the inverse-j distributions may not have been detected in their analysis. In this study, data from trees as small as 2.5 cm dbh was included, and the availability of these data no doubt influenced classification outcomes, hopefully making inverse-j distributions easier to detect than had the data been limited to trees > 9.0 cm dbh.

We must also recognize that none of the methods proposed to date, including ours, can evaluate the successional element of the cohort concept because all rely upon structural characteristics of stands measured at a single point in time. In the case of forest types that undergo compositional change through succession, there is little doubt that a classification system so heavily weighted on structural variables could detect cohorts that might not accord with the assumed relationship of latter cohorts to latter stages of succession. For instance, all three diameter distributions that characterize cohorts structurally might be detected in stands of pioneer tree species that from the long-term successional perspective that underlies the cohort concept would always be considered the first cohort (sensu Harvey et al. 2002). We must therefore be cautious when associating structurally-based cohorts with successional stage. Otherwise, stand composition would have to be considered a primary distinction when classifying cohorts in managed landscapes, and structural variability within successional cohorts ignored. From a management perspective, we must ask what it is that we hope multi-cohort management can achieve in terms of the maintenance of biodiversity and function, and whether emulating a diversity of succesional stages in managed landscapes is as critical as maintaining structural diversity throughout stages of succession. From a biodiversity perspective, managing for structural variability in all forest types, irrespective of long-term successional stage, holds greater promise as a means to guard against biodiversity loss at the stand scale (Hansen et al. 1991). This is not to say that successional and structural cohorts are necessarily mutually exclusive concepts, but managers should recognize the complexity and limited ability of structural cohorts to infer successional when determining the proportional representation of cohorts at the landscape scale.

Lastly, perhaps importantly, this study differed from previous cohort definition studies in that no control was exercised with respect to stand management history. While other cohort definition studies focussed on stands natural origin, this study included several sites (> 25%) with a history of logging disturbance. There is therefore a possibility that residual structures from the logging disturbances remained at certain sites and influenced their classification. This may account for some of the counterintuitive age results for some sites and forest units. The relationship between cohort class and harvesting history certainly merits further exploration. More importantly, we should ask what influence logging history exerts on stand structure and to what degree disturbance history interacts with structural development in these forests. In a general sense, do the post-harvest structures in managed stands fulfill the ecological roles of such structures in their natural counterparts? The real issue is whether harvest-induced structural analogues of latter cohorts provide habitat similar to their natural counterparts. More research is needed to assess the relationship between these cohort classes and the biodiversity of the underlying stands. It will be of particular interest to see to what extent structurally-based cohorts correspond to biodiversity-based cohorts.

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REFERENCES

Attiwill, P.M., 1994. The disturbance of forest ecosystems—the ecological basis for conservation management. For. Ecol. Manage. 63, 247–300.

Bergeron, Y., Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. 92: 235-242.

Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fennica 36: 81-95.

Niemelä, J. 1999. Management in relation to disturbance in the boreal forest. Forest Ecology and Management 115: 127-134.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. 31: 384-391.

Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S. 1999a. Forest management guidelines based on natural disturbance dynamics: Stand and forest-level considerations. For. Chron. 75: 49-54.

Bergeron, Y., Gauthier, S., Carcaillet, C., Flannigan, M., Prairie, Y., Richard, P.J.H., 1999b. Variability in fire frequency and forest composition in Canada's southeastern boreal forest: a challenge for sustainable forest management. In: Veeman, T.S., Smith, D.W., Purdy, B.G., Salkie, F.J. (Eds.), Proceedings of the 1999 Sustainable Forest Management Network Conference, pp. 74–80.

Boucher, D., De Grandpré, L., and Gauthier, S. 2003. Développement d'un outil de classification de la structure des peuplements et comparaison de deux territories de la pessière à mousses du Québec.

Franklin, J.F., 1993. Preserving biodiversity: species, ecosystems or landscapes. Ecol. Applic. 3, 202–205.

Franklin JF, Spies TA, Van Pelt R, Carey AB, Thornburgh DA, Berg DR, Lindenmayer DB, Harmon ME, Keeton WS, Shaw DC, Bible K, Chen JQ. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol Manage. 155(1-3): 399-423.

Gauthier, S., Lefort, P., Bergeron, Y., Drapeau, P. 2002. Time since fire map, age-class distribution and forest dynamics in the Lake Abitibi Model Forest. Nat. Res. Can., Can. For. Serv., Laurentian For. Cent., Sainte-Foy, Que. Inf. Rep. LAU-X-125E.

Gove, J.H. 2003. Balance: a System for Fitting Diameter Distribution Models. General Technical Report. NE-xx, USDA Forest Service (in press).

Hansen, A.J., T.A. Spies, F.J. Swanson, and J.L. Ohmann. 1991. Conserving biodiversity in managed forests: Lessons from natural forests. BioScience 41: 382-392.

Harvey, B.D., Leduc, A., Gauthier, S., Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For. Ecol. Manage. 155: 369-385.

Hayden, J. Kerley, J. Carr, D., Kenedi, T., Hallarn, J. 1995. Ontario Forest Growth and Yield Program Field Manual. Ontario Ministry of Natural Resources. Ontario Forest Research Institute. Sault Ste. Marie, Ontario.

Hayden, J. 2003. Ontario Growth and Yield Program Permanent Growth Plot Reference Manual. DRAFT. Ontario Ministry of Natural Resources. Ontario Forest Research Institute. Sault Ste. Marie, Ontario.

Johnson, E.W. 2000. Forest Sampling Desk Reference. CRC press. 985 p.

Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managed ecological systems. Ecol. Appl. 9 (4), 1179–1188.

Legendre, P. and L. Legendre. 1998. Numerical Ecology. Elsevier Science B.V., New York, US.

Marshall, P.L., Davis, G., and LeMay. V.M. 2000. Using Line Intersect Sampling for Coarse Woody Debris. B.C. Forest Service. Technical Report TR-003. Nanaimo, B.C.

Maser, C., G. Anderson, K. Cromack, Jr., J.T. Williams, and R.E. Martin. 1979. Dead and downed woody material. *In:* J.W. Thomas, editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agriculture Handbook, No. 553. U.S. Department of Agriculture, Washington, DC.

Miller, R.J. 1994. Stem Analysis Measurement System (SAMSYSTEM). Stem Analysis Measurement Increment Core Capture Version 1.1. Ontario Forest Research Institute, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario.

McRae, D.J., L.C. Duchesne, B. Freedman, T.J. Lynham, and S. Woodley, 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. Environmental Reviews 9: 223-260.

Nguyen, T. 2000. Classification of Northern Abititbi's spruce-moss forest stands according to their internal structure. Preliminary report to the Quebec Ministry of Natural Resources. July 2000.

Oliver, C.D., and Larson, C.B., 1996. Forest Stand Dynamics. Update Edition. John Wiley and Sons, Inc., NY.

Rowe, J.S. 1972. Forest regions of Canada. Can. Dep. Environ., Can. For. Serv., Ottawa, ON. Publ. No. 1300. 172 pp.

SAS Institute Inc. 1999. SAS/STAT® user's guide, version 8. SAS Institute Inc., Cary, NC.

Smith, D.M., Larson, B.C., Kelty, M.J., and Ashton, P.M.S. 1997. The practice of silviculture: applied forest ecology. 9th edition. John Riley & Sons, New York.

ter Braak, C.J.F. and P. Smilauer. 2002. Canoco for Windows Version 4.51. Centre for Biometry, Wageningen, CPRO-DLO, Wageningen, The Netherlands.

Van Laar, A. 1991. Forest Biometry. University of Stellenbosch. 590 p.

Watt, W. R., Parton, J., Vasiliauskas, S., Chen, H., Lucking, G., and Houle, N. 2003. Standard forest units for northeastern Ontario boreal forests. OMNR Northeast Science & Information Info. Rep. DRAFT.

APPENDIX I

Analysis Variable	Units	Description
BAITOT	m2/ha	basal area of intolerant tree species (Pj, Pb, Po, Bw)
BASTOT	m2/ha	basal area of tolerant tree species (Bf, Cw, Pr, La, Sb, Sw)
CCE		crown class eveness
CCH		crown class diversity
CCR		crown class richness
CV		coefficient of variation of the diameter class distribubtion
ConBA	m2/ha	basal area of conifer species (Bf, Cw, La, Pj, Pr, Sb, Sw)
DC1	m3/ha	volume of logs in decay class 1
DC2	m3/ha	volume of logs in decay class 2
DC3	m3/ha	volume of logs in decay class 3
DC4	m3/ha	volume of logs in decay class 4
DC5	m3/ha	volume of logs in decay class 5
DTOT	trees/ha	total tree density
DecBA	m2/ha	basal area of decidous species (Pb, Po, Bw)
Dlpct	%	relative density of large-sized trees (trees > 21.0 cm dbh/DTOT)
Dmpct	%	relative density of medium-sized trees (9.0 cm dbh - 21.0 cm dbh trees/DTOT)
Dspct	%	relative density of small-sized trees (2.5 cm dbh - 9.0 cm dbh trees/DTOT)
E		eveness (equitability) of diameter classes
Fs_osdcv		fine-scale overstory density coefficient of variation
Fs_osdvar		fine-scale overstory density variance
H		diversity of the diameter classes
INTDBH1	trees/ha	intolerant trees 2.5 - 4.9 cm dbh
INTDBH2	trees/ha	intolerant trees 5.0 - 8.9 cm dbh
INTDBH3	trees/ha	intolerant trees 9.0 - 14.9 cm dbh
INTDBH4	trees/ha	intolerant trees 15.0 - 20.9 cm dbh
INTDBH5	trees/ha	intolerant trees >21.0 cm dbh
Ls_osd	%	Large-scale overstory density
Ls_osdcv		Large-scale overstory density coefficient of variation
Ls_osdvar		Large-scale overstory density variance
S		richness of diameter classes
SLratio		small to large tree ratio (sum of small trees/sum of large trees)
SMratio		small to medium tree ratio (sum of small trees/sum of medium trees)
SPDDBH1	trees/ha	tolerant trees 2.5 - 4.9 cm dbh
SPDDBH2	trees/ha	tolerant trees 5.0 - 8.9 cm dbh
SPDDBH3	trees/ha	tolerant trees 9.0 - 14.9 cm dbh
SPDDBH4	trees/ha	tolerant trees 15.0 - 20.9 cm dbh
SPDDBH5	trees/ha	tolerant trees >21.0 cm dbh
TotBaha	m2/ha	Total basal area
Wscale		scale parameter from two parameter Weibull probability density function
Wshape		shape parameter from two parameter Weibull probability density function
maxage	years	maximum age from tree core samples
newDWD	m3/ha	downed woody debris (log) volume in decay classes 1-3

newsnagL	trees/ha	snags in decay classes 1-3 > 25.0 cm dbh
Analysis Variable	**Units**	**Description**
newsnagM	trees/ha	snags in decay classes 1-3 > 15.0 cm dbh < 25.0 cm dbh
newsnagS	trees/ha	snags in decay classes 1-3 > 10.0 cm dbh < 15.0 cm dbh
newsnags1	trees/ha	total snags in decay classes 1-3
oldDWD	m3/ha	downed woody debris (log) volume in decay classes 4-5
oldsnagL	trees/ha	snags in decay classes 4 & 5 > 25.0 cm dbh
oldsnagM	trees/ha	snags in decay classes 4 & 5 > 15.0 cm dbh < 25.0 cm dbh
oldsnagS	trees/ha	snags in decay classes 4 & 5 > 10.0 cm dbh < 15.0 cm dbh
oldsnags1	trees/ha	total snags in decay classes 4 & 5
skew		skewness of the diameter class distribution

Tree species	**codes**
Bf	balsam fir
Bw	white birch
Cw	eastern white cedar
La	larch
Pb	balsam poplar
Pj	jack pine
Po	trembling aspen
Pr	red pine
Sb	black spruce
Sw	white spruce

Note: Diameter class variables used in Boucher et al. (2003) cohort classification required removal of trees < 9.0 cm dbh from the data and conversion of diameter class units from trees/ha in 2-cm diameter classes to the percentage of trees (# trees/ total tree density) in 2-cm diameter classes.