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Potential tree species dynamics in the arbor vitae association of Cedar Bog, a west-central Ohio fen¹

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COLLINS, S. L., J. L. VANKAT, and J. V. PERINO (Dept. Bot., Miami Univ., Oxford, OH 45056). Potential tree species dynamics in the arbor vitae association of Cedar Bog, a west-central Ohio fen. Bull. Torrey Bot. Club 106: 290-298. 1979.—Size association, population structure, density-diameter curve, and life history studies were used to evaluate possible successional trends in a *Thuja occidentalis* dominated association. It is predicted, in contrast to previous hypotheses, that *T. occidentalis* has a stable population structure and will continue to dominate, that *Fraxinus nigra* and *Acer rubrum* will increase in importance but remain subdominants, and that *Liriodendron tulipifera* will remain a minor component with temporary dominance in areas of canopy openings.

According to Gates (1942), boreal bog succession may involve the replacement of a lowland hardwood forest community of black ash (*Fraxinus nigra*) and red maple (*Acer rubrum*) by a climax community of arbor vitae (*Thuja occidentalis*) or black spruce (*Picea mariana*; nomenclature follows Weishaupt 1971). Sampson (1930) postulated that this successional sequence was reversed in northern Ohio, i.e. that black ash and red maple become established following the conifer stage.

Cedar Bog is a west-central Ohio fen with an arbor vitae association adjacent to a lowland forest of black ash, red maple, and tuliptree (*Liriodendron tulipifera*). It has been the object of several studies, some of which have briefly discussed successional dynamics. Dachnowski (1910) reported seedlings of trees such as red maple and tuliptree growing in arbor vitae stands, yet he suggested that some edaphic factor maintained the conifers in lieu of a deciduous forest climax. Braun (1928) hypothesized that Cedar Bog was undergoing succession to a deciduous forest climax via two seres: bog-arbor vitae-deciduous forest and bog-meadow-deciduous forest. The Environmental Control Corporation (1973)

reported hummocks where a few deciduous trees, particularly tuliptree and black ash, were much younger yet taller than the more common arbor vitae. They concluded that deciduous species were eliminating arbor vitae via succession. These reports and Sampson's hypothesis were based primarily upon nonquantitative field observation. The purpose of our study was to use quantitative techniques to investigate possible tree species dynamics in the arbor vitae association of Cedar Bog.

Cedar Bog Nature Preserve is located in southern Champaign County, west-central Ohio, at 40°03' north latitude and 83°47' west longitude; it is mapped on the Saint Paris Quadrangle of the United States Geological Survey 7.5' series. Braun (1950) estimated Cedar Bog to be "the most southerly of the well-preserved bog remnants" in North America. It is between two moraines in a depression filled with coarse, dolomitic glacial outwash; underground water flows through this gravel from the north and east, surfacing in the preserve (Forsyth 1974). This has resulted in a calcareous fen or "bog" with a pH ranging from 6.9 to 8.2 (Environmental Control Corporation 1973). The soils of the preserve are in the Carlisle Series and are poorly drained, highly organic, and dark colored.

The regional climate is continental; mean monthly temperatures for two weather stations near the bog range from -1.6° C in January to 23.2° C in July. Annual precipitation averages 92.5 cm and

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is distributed evenly throughout the year. The growing season is approximately 160 days (Environmental Control Corporation 1973). The microclimate of the preserve is affected by the cool temperature of the underground water supply (Frederick 1974).

The vegetation of Cedar Bog has been classified into six plant associations: marl meadow, bog meadow, arbor vitae, swamp forest, hardwood forest, and shrub (Frederick 1974). Only two of these directly relate to our study. One is the arbor vitae association which is on peaty, organic soils and consists of arbor vitae in pure stands or mixed with some deciduous trees. These stands are generally long and narrow in shape. The other association related to this study is the swamp forest; it occurs on organic mucks and is dominated by such species as red maple, black ash, and tulip-tree.

The state government acquired the bog in the 1940s, by which time an estimated 2,830 hectares of peatland had been reduced to approximately 20 hectares of fen and swamp forest. Much of this reduction occurred when rivers and streams were dredged during 1910–1912 and 1915 to drain land for agriculture. Other human impacts on the bog include burning to reduce vegetation density and removing arbor vitae for landscaping materials, telephone poles, and Christmas trees (Franks 1931; Clark County Audubon Society 1972).

Materials and methods. Ten belt transects of 2 m width and variable length (7.5 to 100 m) were placed 50 m apart in an east-west direction through the arbor vitae association and into the swamp forest association. Each transect was divided into 2×7.5 m contiguous quadrats within which each woody plant (including those that fell on the edges of the quadrats) was recorded and trees were measured for diameter breast height (dbh). Quadrats of this size and shape were used because of the very high tree densities, the long, narrow shape of the arbor vitae stands, and the necessity of using the same quadrats to sample a wide range of size classes.

Importance Percentages (I. P.) were calculated for tree species by adding relative values of frequency, density, and basal area and dividing by three; values for

shrub and understory taxa were calculated by summing relative frequency and relative density and dividing by two. Successional trends were examined by use of detailed population size class structural diagrams, density-diameter curves, and size association analyses.

There are two methods of size association analysis, "2-D" and "3-D" (Zedler and Goff 1973). The former compares the different size classes of one species to the combined size classes of a second species. The latter compares all size classes of two species, e.g. seedling and seedling, seedling and sapling, etc. In both analyses, the three size classes of Johnson, Burgess, and Keamermer (1976) were used: trees (dbh ≥ 10.2 cm), saplings (dbh < 10.2 cm and height ≥ 30.5 cm), and seedlings (height < 30.5 cm). For 2-D analysis, the tree size class was subdivided into two diameter size classes: 10.2 to 25.4 cm and > 25.4 cm. For 3-D analysis, the same size classes as above were used for deciduous species and four were used for arbor vitae: 10.2 to 15.2, 15.3 to 20.3, 20.4 to 25.4, and > 25.4 cm. Cole's index of association (Cole 1949) was employed to determine interspecific relationships. A significance level of $\alpha = 0.15$ was used in 2-D and 3-D analyses.

Zedler and Goff (1973) presented three assumptions regarding size association analysis: (1) the vegetation sampled includes the various successional stages, (2) the older plots represent a potential vegetation for the younger plots, and (3) there is a correlation between age and dbh for each species. The first two assumptions were satisfied in our study by extending transects through the arbor vitae association into the swamp forest association. Studies in other locations, although reaching contrasting conclusions, indicated that one of these associations is more mature than the other and represents a later stage of the same sere (Sampson 1930; Gates 1942; Dansereau and Segadas-Vianna 1952; Curtis 1959). The third assumption is a frequent premise of plant population structure studies, and although size-age correlation usually is not precise, the assumption of such a correlation is valid when narrow size classes are avoided (Dau-bennire 1968).

Table 1. Relative values of basal area, density, and frequency and Importance Percentages for all species with at least one individual ≥ 10.2 cm dbh.

Species	Relative basal area	Relative density	Relative frequency	Importance percentage
<i>Thuja occidentalis</i>	62.7	54.8	31.6	49.7
<i>Fraxinus nigra</i>	6.2	13.4	18.8	12.8
<i>Liriodendron tulipifera</i>	17.5	7.0	9.8	11.4
<i>Acer rubrum</i>	2.9	9.5	12.0	8.1
<i>Acer saccharum</i>	5.7	2.7	5.3	4.6
<i>Ulmus americana</i>	2.3	3.0	6.0	3.8
<i>Ostrya virginiana</i>	0.9	3.9	5.3	3.4
<i>Carpinus caroliniana</i>	0.7	3.2	4.5	2.8
<i>Celtis occidentalis</i>	0.5	0.9	3.0	1.5
<i>Prunus serotina</i>	0.5	0.7	2.3	1.2
<i>Tilia americana</i>	0.2	0.9	1.5	0.9
Absolute total/750 m ²	4.96 m ²	440 individuals		
Absolute total/hectare	66.13 m ²	5,867 individuals		

Results. The transects included a total of 50 quadrats comprising an area of 0.075 ha, approximately 2% of the portions of the preserve that contain arbor vitae. Twenty-one woody species were encountered, 11 of which had at least one individual ≥ 10.2 cm dbh (Table 1). Based on I. P. values, the most important species with canopy potential are arbor vitae (49.7 I. P.), black ash (12.8), tuliptree (11.4), red maple (8.1), and sugar maple (*Acer saccharum*; 4.6). The great dominance of arbor vitae is to be expected because of the transect placement. The high I. P. for tuliptree is partly the result of the presence of one individual of 87.5 cm dbh, the largest tree sampled. Sugar maple occurred mainly where the transects were extended beyond the arbor vitae association into the swamp forest association. American elm (*Ulmus americana*) had greater dominance before the Dutch elm disease (Frederick

1974), and today most individuals appear unhealthy. The remaining five species in Table 1 usually occurred outside the arbor vitae association.

Data on the ten shrubs and tree species with no individuals ≥ 10.2 cm dbh are given in Table 2. The most important shrub is spice bush (*Lindera benzoin*; 60.8 I. P.). This species occurs throughout the entire preserve, often in dense thickets. The second-ranked species is alternate leaved dogwood (*Cornus alternifolia*; 16.0), the most abundant understory tree. Canada yew (*Taxus canadensis*; 8.1) was the only other understory species with an I. P. greater than 5.0. The other seven species occurred primarily where the transects extended into the swamp fore association or to the edge of the bog meadow.

Figure 1 presents the results of 2-D size association analysis, i.e. regression lines of plots of interspecific association values for

Table 2. Relative frequency, relative density, and Importance Percentages for shrubs and tree species in the study area with no individuals ≥ 10.2 cm dbh.

Species	Relative density	Relative frequency	Importance percentage
<i>Lindera benzoin</i>	66.5	55.0	60.8
<i>Cornus alternifolia</i>	13.1	18.8	16.0
<i>Taxus canadensis</i>	7.4	8.8	8.1
<i>Quercus bicolor</i>	2.8	5.0	3.9
<i>Sambucus canadensis</i>	2.8	3.8	3.3
<i>Betula pumila</i>	4.0	2.5	3.3
<i>Fraxinus pennsylvanica</i>	1.1	2.5	1.8
<i>Euonymus americanus</i>	1.1	1.3	1.2
<i>Potentilla fruticosa</i>	0.6	1.3	1.0
<i>Salix</i> sp.	0.6	1.3	1.0
Absolute total/750 m ²	106 individuals		
Absolute total/hectare	2,133 individuals		

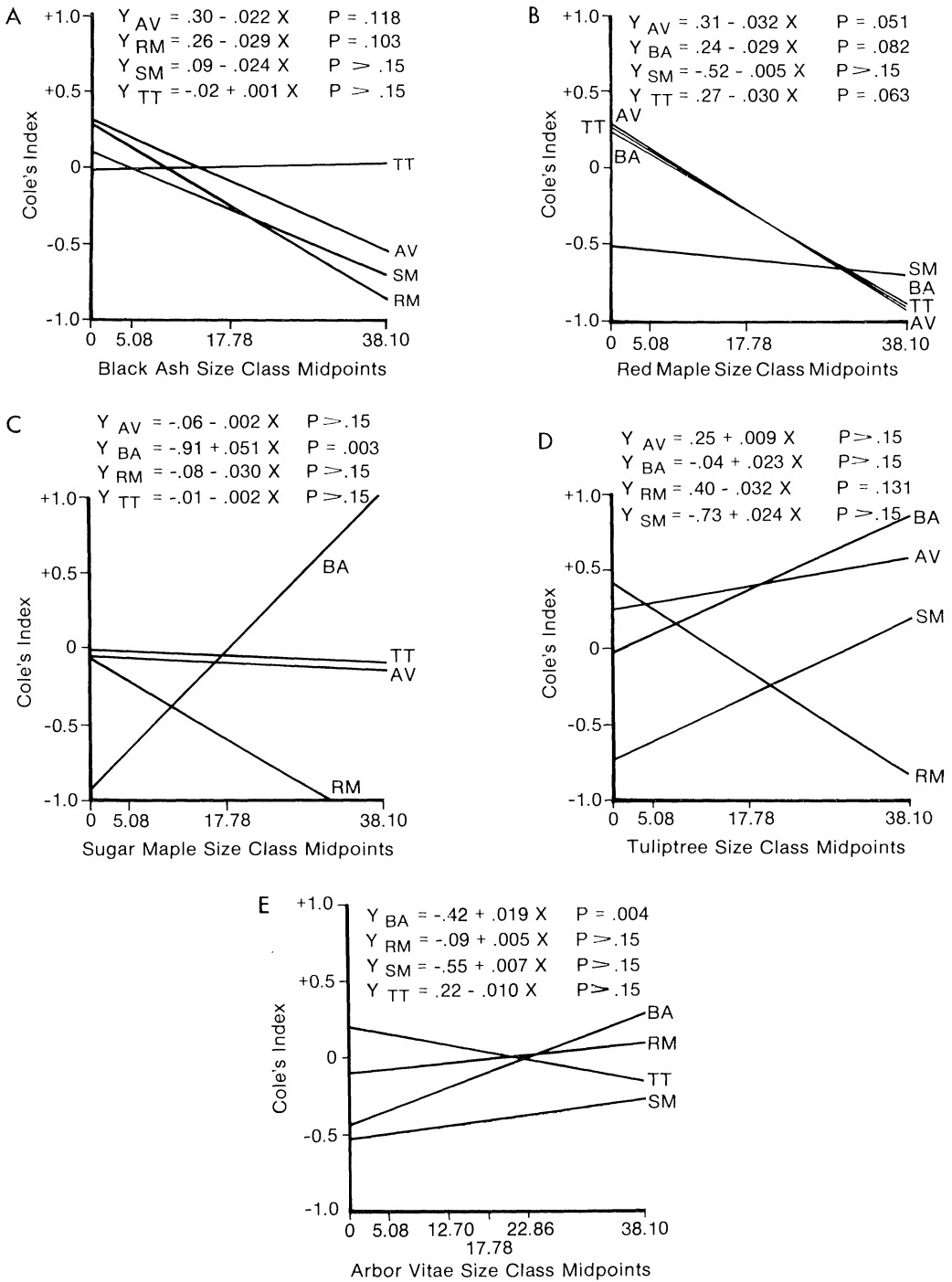


Fig. 1. Regression lines for the 2-D size association analysis. The ordinate is Cole's index of association. The abscissa represents the size classes of the species indicated: arbor vitae (AV), black ash (BA), red maple (RM), sugar maple (SM), and tuliptree (TT).

Table 3. Regression coefficients resulting from 3-D size association analysis.

Species pair	Coefficient associated with	
	First species	Arbor vitae
Black Ash—Arbor Vitae	-0.022*	0.010
Red Maple—Arbor Vitae	-0.027*	0.005
Tuliptree—Arbor Vitae	-0.005	-0.004
Sugar Maple—Arbor Vitae	0.002	0.015

* Significant at the 0.15 level

individual size classes of a single species and a second species considered as a whole. The interpretation of the size association regression lines depends on whether they have a positive or negative slope (Zedler and Goff 1973). If, for example, the regression line for species A has a positive slope when compared with the size classes of species B and the regression line for species B has a negative slope when compared with the size classes of species A, then a potential successional replacement of B by A is indicated. If instead the regression lines for both A and B have positive slopes, then the relationship is convergent, indicating a temporally increasing association of species A and B. If both A and B have negative slopes, their relationship is divergent, indicating that joint occurrence will become less likely. If the slope of one regression line is not significantly different from zero and the slope of the other is positive (negative) a situation intermediate between successional replacement and convergence (divergence) is indicated.

The regression line for black ash in Figure 1E has a positive slope (0.019, $P = 0.004$), illustrating an increasing association of black ash with larger arbor vitae. The regression line for arbor vitae in Figure 1A is negative (-0.022 , $P = 0.118$). Together, the two regression lines indicate an increase in black ash and potential successional replacement of arbor vitae. The regression lines for red maple and arbor vitae indicate a situation intermediate between successional replacement by red maple and divergence of the two species, since the regression line for red maple in Figure 1E has a slope not significantly different from zero and that for arbor vitae in Figure 1B has a negative slope (-0.032 , $P = 0.051$). In the comparison of red

maple and black ash (Figure 1A and 1B), both regression lines have negative slopes, -0.029 ($P = 0.103$) and -0.029 ($P = 0.082$) respectively; therefore, this analysis predicts divergence, i.e. that black ash and red maple will develop primarily in different areas. Thus, 2-D analysis indicates a potential for replacement of the arbor vitae association by separate red maple and black ash associations.

The 3-D size association analysis was limited to comparing arbor vitae with the other four species studied in 2-D analysis, since only arbor vitae had a sufficient sample size. Interpretation of 3-D analysis is analogous to that explained for 2-D analysis.

Table 3 presents the regression coefficients from 3-D analysis. In the cases of black ash-arbor vitae and red maple-arbor vitae, the results indicate a situation intermediate between successional replacement of arbor vitae and divergence. None of the coefficients comparing arbor vitae and the other two species are significantly different from zero, so no successional pattern is indicated for them.

The relationship between arbor vitae, black ash, and red maple can be elucidated further by evaluation of the size class distributions given in Table 4. Arbor vitae has the greatest number of individuals in all size classes. When percentages are calculated, arbor vitae (using its total of 201 individuals as a base) has percentage values in all tree size classes that are equal to or greater than those calculated for the combination of all species (percentage of 329 individuals). Although arbor vitae has only 57% of its individuals in the sapling class, the number of arbor vitae saplings is so large (115), that they make up a majority (54%) of the total saplings sampled (212).

Both black ash and red maple have low numbers of saplings (30 and 21, representing 14 and 10% of the total saplings, respectively). However, in both species the sapling size class makes up a very high percentage of the total number of individuals of the species; 77% of the black ashes and 91% of the red maples are saplings. Black ash is represented in most of the tree size classes, but red maple is present in only two of them.

Table 4. Population size class structures (number of individuals).

Species	Saplings*	Trees (dbh in cm)							Totals
		10.2- 15.0	15.1- 20.0	20.1- 25.0	25.1- 30.0	30.1- 35.0	35.1- 40.0	>40.0	
<i>Thuja occidentalis</i>	115	30	20	16	11	4	3	2	201
<i>Fraxinus nigra</i>	30	2	2	1	3	—	1	—	39
<i>Acer rubrum</i>	21	—	—	—	1	1	—	—	23
<i>Liriodendron tulipifera</i>	5	1	—	1	—	—	—	2	9
<i>Ostrya virginiana</i>	11	1	1	—	—	—	—	—	13
<i>Carpinus caroliniana</i>	8	—	1	—	—	—	—	—	9
<i>Ulmus americana</i>	7	2	1	2	—	—	—	—	12
<i>Acer saccharum</i>	6	—	2	—	1	—	—	1	10
<i>Quercus bicolor</i>	2	—	—	—	—	—	—	—	2
<i>Celtis occidentalis</i>	2	—	1	—	—	—	—	—	3
<i>Tilia americana</i>	3	1	—	—	—	—	—	—	4
<i>Prunus serotina</i>	—	2	—	—	—	—	—	—	2
<i>Fraxinus pennsylvanica</i>	2	—	—	—	—	—	—	—	2
Total/750 m ²	212	39	28	20	16	5	4	5	329
Total/hectare	2,827	520	373	267	213	67	53	67	4,387

* Woody plants with a height ≥ 30.5 cm and a dbh < 10.2 cm.

Only 22% of the saplings and 17% of the trees are of species other than arbor vitae, black ash, or red maple. Included are species that in this region normally do not reach canopy height, e.g. hop hornbeam (*Ostrya virginiana*) and hornbeam (*Carpinus caroliniana*). Also included is American elm, a species whose larger individuals have a few, scattered leaves and numerous dead branches which indicate that their survival is doubtful.

Four density-diameter curves are presented in Figure 2: (×) arbor vitae; (○) black ash and red maple combined; (●) all species combined; and (+) all species combined, less arbor vitae, black ash, and red maple. In general outline, the four curves have an inverted J-shape; however, curves B and D approach an inverted L-shape, reflecting the relatively small numbers of individuals in the tree size classes. Thus, the inverted J-shape of the composite curve for the entire stand is largely a product of the size class distribution of the only species with a true inverted J-shaped curve, i.e. arbor vitae, the dominant. An inverted J-shaped density-diameter curve is thought to be indicative of a relatively balanced population structure (Meyer 1952). It is possible to interpret an inverted J-shaped density-diameter curve in two different ways: either the species has very high mortality in the smaller size classes or the species has had a

presumably relatively recent population increase.

Population structures also can be examined by graphing the logarithm of density against diameter. A straight-line, negative exponential form is characteristic of populations with a constant rate of mortality between different size classes. This form has been reported as characteristic of natural, undisturbed forests (Meyer 1952). Goff and West (1975) concluded that a rotated sigmoid curve described an equilibrium population structure within small stands in which the mortality rate is high in the understory, low in the vigorous overstory, and high in the senescent overstory. Arbor vitae has a curve that, although it does not differ statistically from a straight line, is somewhat intermediate between the two generalized forms (Figure 3) and can be interpreted as indicating a stable population structure. In the cases of black ash and red maple, this type of analysis (not shown) did not resolve the question posed in the previous paragraph of whether they have high mortality in the smaller size classes or have had relatively recent population increases.

In summary, the results of 2-D size association analysis indicated increasing importance of black ash and possibly red maple relative to arbor vitae. The 3-D size association analysis may be interpreted as indicating similar findings or divergence

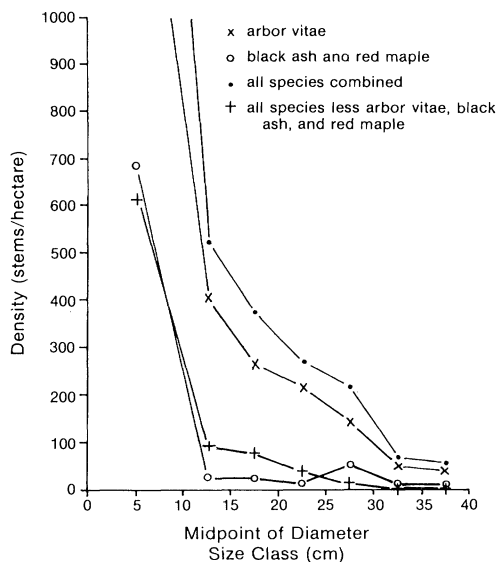


Fig. 2. Density-diameter curves for arbor vitae and selected combinations of species. The density values for the smallest size class midpoint (5 cm) of arbor vitae and all species combined are 1,533 and 2,827 stems/hectare, respectively.

between arbor vitae and both black ash and red maple. Density-diameter curve analyses can also be interpreted as indicating a relatively recent increase in the combination of black ash and red maple, although an alternative interpretation is that these species have high mortality in the smaller size classes. Density-diameter curve analyses applied to arbor vitae indicated a stable population structure.

Discussion. The results of our statistical analyses may be discussed species-by-species. In the case of arbor vitae, the results are contradictory, but there is reason to support the finding of a stable population structure as determined by density-diameter curve analyses. First, greater emphasis is warranted on density-diameter curve analyses than on size association analyses because quadrat size should have a greater influence on the latter than the former and, in our study, the factors mentioned in the materials and methods section necessitated sampling by relatively small quadrats. Second, life history observations provide support for the hypothesis that the arbor vitae population is stable. Much of the reproduction of this species is asexual from branch layering and

wind thrown trees. Nelson (1951) described a similar situation in a Michigan swamp. Individuals produced vegetatively may be expected to have comparatively low mortality in the smaller size classes since they may be partially supported by the reserves of the parent plants. Such low mortality would tend to produce straightening in a rotated sigmoid density-diameter curve. Therefore, an equilibrium population structure for a species in a small stand could be illustrated by a shape intermediate between a straight line and a rotated sigmoid form (when plotted on a semi-logarithmic basis). The curve for the arbor vitae population at Cedar Bog has such a shape (Figure 3), as mentioned in the previous section.

Our field observations of vegetative reproduction also suggest that arbor vitae has the potential of expanding in adjacent stands of the swamp forest and bog meadow associations; several individuals were observed in the swamp forest and all were from branch layering. Gates (1942) stated that well developed lowland deciduous forests in Michigan may be replaced by arbor vitae, and Clausen (1957) reported that arbor vitae invaded adjacent stands (of spruce and tamarack, *Larix laricina*) in Wisconsin bogs by branch layering.

Black ash is the second most important species in the arbor vitae association of

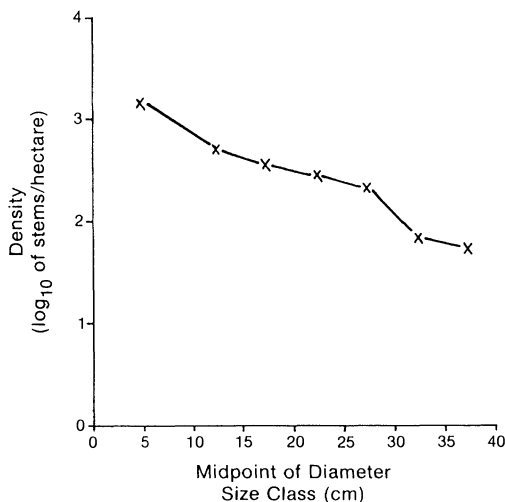


Fig. 3. Density-diameter curve for arbor vitae on a semi-logarithmic graph ($Y = 3.36 - 0.044X$; $r^2 = 0.96$).

Cedar Bog. The presence of some black ash was expected, since the maple-ash swamp forest of Cedar Bog is adjacent to the arbor vitae association. Gates (1942) also determined that arbor vitae communities in Michigan bogs contain low percentages of black ash, and Curtis (1959) cited black ash as a secondary species in the northern lowland conifer forests of Wisconsin. Goff and Zedler (1972) and Zedler and Goff (1973) predicted an increasing association of arbor vitae and black ash in Wisconsin forests.

The 2-D size association analysis for Cedar Bog indicates successional replacement of arbor vitae by black ash, but 3-D analysis has two interpretations: replacement of arbor vitae by black ash or divergence of the two species. Density-diameter curve analysis for black ash and red maple combined also permits two alternative interpretations: an increase in population size or high mortality as individuals grow out of the sapling size class. Because of the relatively small number of black ash individuals sampled (a total of 39 as opposed to 201 arbor vitae) and because of our findings of a stable population distribution for arbor vitae, we interpret our analyses as indicating an increase in importance of black ash without successional replacement of arbor vitae in the foreseeable future.

Red maple also has been reported to co-occur to a limited extent with arbor vitae in wetlands (Gates 1942; Fowells 1965). The 2-D and 3-D size association analyses at Cedar Bog suggest an increase in red maple relative to arbor vitae or divergence of the two species. Again, there also are two interpretations possible for the findings of density-diameter curve analysis. We believe that although red maple may increase in importance in the stand, it will not replace arbor vitae in the foreseeable future. In fact, it is likely that the mortality of small red maples is quite high (the alternative interpretations of its combined density-diameter curve). Red maple seedlings and saplings are shade intolerant (Fowells 1965), and the light intensity beneath a dense arbor vitae canopy can be less than 4 foot candles (Curtis 1959). Also, soil conditions at Cedar Bog may contribute to the mortality of young red maples, since

development reportedly is stunted on saturated soils (Fowells 1965).

A fourth species, tuliptree, has been suggested as a key species in the predicted replacement of arbor vitae by hardwoods (Environmental Control Corporation 1973). This hypothesis was based on the field observation of a few tuliptree saplings growing in sites exposed by fallen canopy trees and on the extrapolation of these scattered observations to the entire stand. Sampson (1930) also proposed that tuliptree is common late in the swamp forest serere of northern Ohio, but did not provide quantitative evidence to support his statement. We hypothesize that tuliptree will not show a general increase in the arbor vitae association of Cedar Bog in the near future, based primarily on the finding that, despite observance of tuliptree in Cedar Bog nearly 70 years ago (Dachnowski 1910), the species still has a low frequency and makes up only a small proportion of the trees in the study area (only 3% of the sample). Also, neither 2-D nor 3-D size association analyses indicate successional relationships between arbor vitae and tuliptree (although the small population size makes these findings open to question). We do recognize that tuliptrees occasionally will acquire canopy status, primarily by replacing fallen conifers. However, we anticipate that since arbor vitae exhibits a stable population structure and is shade tolerant, it is capable of persisting beneath such sites of tuliptrees and later regaining canopy position.

Conclusions. Our conclusions contrast with the earlier hypotheses of replacement of the arbor vitae dominated community of Cedar Bog by hardwoods, including black ash, red maple, and tuliptree (Braun 1928; Environmental Control Corporation 1973). Braun's (1928) hypothesis of the existence of two seres, bog-arbor vitae-deciduous forest and bog-prairie-deciduous forest, was based on the co-occurrence of several communities at Cedar Bog and her attempt to place them in a successional framework in accord with the view of the development of a regional climatic climax. More recently, the Environmental Control Corporation (1973) also concluded that the arbor vitae association is successional to a forest dominated by hardwoods. This group did not

attempt statistical methods as used in this study, but based their hypothesis largely on field observation of a few tuliptrees where the canopy of arbor vitae had been opened.

Based on size association, population structure, density-diameter curve, and life history studies, we conclude that the arbor vitae population is essentially stable within the arbor vitae association. Thus, our findings do not support the earlier hypothesis concerning Cedar Bog, Gates' (1942) placement of a black ash-red maple hardwood forest as seral to an arbor vitae community, nor Sampson's (1930) suggestion that this sequence is reversed in northern Ohio. Instead, assuming there is no significant alteration in the ground water conditions that are considered essential for the existence of the vegetation of Cedar Bog (Forsyth 1974), we propose that arbor vitae will continue to be the dominant in the arbor vitae association, that black ash and red maple will increase as important subdominants, and that tuliptree will remain as a minor component temporarily important in the closure of canopy openings.

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