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Population Age Structures of Tree Species in Four Plant Communities in the Great Dismal Swamp, Virginia

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ABSTRACT

The age structures of four different plant communities (cedar, cypress, maple-gum and mixed hardwood) in the Great Dismal Swamp were determined from increment cores. The oldest stand was determined to be the cypress which also had the greatest standing crop biomass of the four communities. Red maple (*Acer rubrum* L.) was found to be an expanding population in the maple-gum, cypress and cedar stands, while bald cypress (*Taxodium distichum* (L.) Richard) and Atlantic white cedar (*Chamaecyparis thyoides* (L.) BSP) were determined to be declining in numbers in the cypress and cedar stands respectively. Linear correlations between age and relative cumulative frequency were determined and the median ecological longevity estimated for each species.

INTRODUCTION

The utility of understanding the structure and function of an ecosystem lies in application towards the interpretation of the ecological effects man has on that ecosystem and the development of management policies. An important functional feature of forest ecosystems is plant population dynamics determined by vegetation age structure. Odum (1971) states that the ratio of various age groups in a population determines the current reproductive status of a species population in addition to its future role in the ecosystem, i.e., whether or not the species will be maintained or phased out.

The primary objective of the present study was to determine the age structures of species occurring in four plant communities in the Great Dismal Swamp, Virginia, by enumerating

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annual rings in increment cores, and to interpret the reproductive status of individual species within each stand. In addition, an intercommunity comparison of age data was made to examine the similarities and differences in age distribution of species occurring in more than one stand. This information should provide useful insight toward the analysis of other ecological parameters of the swamp forest such as primary productivity and nutrient cycling.

METHODS

The Great Dismal Swamp is an extensive swamp forest which occupies about 85,000 ha on the Coastal Plain of southeastern Virginia and northeastern North Carolina. It is delimited on the west by the "fossil dunes" of the Suffolk escarpment, a distinct Pleistocene shoreline, and on the east by the Fentress rise which is composed of interglacial and barrier sediments. Although at one time the swamp occupied about 200,000 ha between the Chesapeake Bay and Albemarle Sound, its area has been markedly decreased by lumbering operations, fire, and land reclamation for agriculture (Whitehead, 1972). These activities have also substantially altered the nature of the Swamp's vegetation. Highly organic and very acidic soils characterize most of the soil types of the Swamp. About 75% of the total Swamp area is mucky peat in which only a fraction of the vegetable materials composing it is recognizable.

The present study was conducted during the summer of 1978 on four stands in the Dismal Swamp, each representing a different community type (mixed hardwood, cedar, cypress and maple-gum). Above and below-ground biomass have been measured in these stands (Dabel and Day, 1977; Day and Dabel, 1978; Montague and Day, 1980) and nutrient cycling and leaf litter decomposition are currently being studied (Day, unpublished data). The Atlantic white cedar (*Chamaecyparis thyoides* (L.) BSP) stand is underlain by one to two meters of peat covered by standing water in the late spring to early summer. Atlantic white cedar is the major contributor to biomass, while black gum (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.) and red maple (*Acer rubrum* L.) exhibit greater density (Dabel and Day, 1977). The bald cypress site is covered by standing water

continuously from early winter to early summer. Standing water was observed in some portions of the stand during the summer of 1978. Bald cypress (*Taxodium distichum* (L.) Richard) is the dominant species based on contributions to basal area and biomass. Bald cypress is also the species with the greatest density, followed by red maple and black gum (Dabel and Day, 1977). The maple-gum community is also flooded from early winter to early summer, but usually not continuously. It is dominated by water gum (*Nyssa aquatica* L.) and red maple in both basal area and density (Dabel and Day, 1977). The mixed hardwood stand is the driest of the four sites. The dominant species include black gum and several species of oak (Dabel and Day, 1977). This site is located on remnant sand dunes from the Pleistocene shoreline located on the western boundary of the swamp. All four stands have been logged previously but precise records on when they were logged have not been located. A major impetus for this study was the need for data which could be used to determine when the last major disturbances (i.e., logging) occurred on these stands. Nomenclature follows Radford, Ahles and Bell (1968).

A 150 meter line transect was subjectively located in each of the four sites. The point-quarter method was used at points 15 meters apart on the transect to select individuals equal to or greater than 4 cm diameter breast height, and to measure basal diameter of saplings equal to or greater than 1 cm and less than 4 cm DBH. Seedlings less than 1 cm in diameter and less than 1 m high were collected and placed in a plant press for future aging. For the purposes of this study, however, they were used to estimate numbers of individuals occurring in the 0-4 year age bracket. Care was taken to insure that the seedlings collected were not sprouts from individuals that had died back. DBH was recorded for each individual cored. Increment cores were taken from the north side of each tree, 30 cm from the ground with a 12″ borer (40 cm for trees with diameters which necessitated use of the 15″ borer). Forty cores were taken from each stand, and ten additional cypress cores were taken from the cypress site, one from each point to more accurately represent the age distribution data for that stand. Cypress was not adequately represented in the original sample. The cores were placed in straws in the field and returned to the laboratory where they were placed in grooved wood strips for drying and sanding. The annual rings were enumerated and the age of each tree recorded.

A special note should be made here concerning the problems involved in aging trees by this method. Trees with ring porous wood, such as oaks and ashes, were relatively easy to age after simple sanding. Non-ring porous wood such as that of black gum and water gum required burning with an iron, sanding and coating with water to make the rings visible. An attempt was made to eliminate false, double and incomplete rings from the ring count. Douglas (1919) noted that cypress trees are prone to double rings.

The method described by Dapson (1971) was used to examine the age distribution of each species occurring within the four communities. Age classes of each species were arranged in descending order from oldest to youngest. The frequency of each tree was recorded as "1". The relative frequency of each age class equalled the frequency of trees in that age class divided by the total number of trees of each species sampled. Relative cumulative frequency (RCF) was calculated by accumulating these relative frequencies from oldest to youngest. This procedure is illustrated in Table 1. Relative cumulative frequencies were then plotted against age. An equation for best fit plot through these points was determined, using linear regression following a log transformation of RCF in most cases. For some species a log transformation of age was necessary to obtain the highest correlation coefficient.

The advantage of using this method lies in its utility for comparing populations of varying age structures. A median ecological longevity (MEL) can be determined for each species by substituting 0.5 for RCF in the following general equation:

$$\text{Age} = a_0 + a_1\text{RCF}$$

where RCF equals the probability of occurrence. Due to the nature of the log transformation used for most of the regression equations it was not possible to determine maximum ecological longevity (MAX), at which the RCF or probability of occurrence is nil. An alternative method was used as suggested by Spring et al. (1974). RCF was set equal to 0.01, thereby approaching the minimum probability of occurrence. Due to the non-random nature of y (age), the correlation coefficient(r) cannot be used to describe the correlation of the variables. However, according to Dapson (1971) it does define the mathematical "goodness of fit" of individual points to the line described by the regression equation.

Further analysis included constructing bar graphs of five year age class intervals plotted against relative frequency. To do this it was necessary to perform linear regressions for age and DBH correlations to place the saplings into their proper age brackets. For this purpose the average sapling diameter of 2.5 cm was chosen to estimate the age for each species which occurred as a sapling.

Table 1. Example of the preliminary steps in determining maximum and minimum ecological longevity. Frequency of each tree (in this example, *Chamaecyparis thyoides*) is "1". Relative frequency is n/N, where n is the number of trees in that age class, and N is the total number of trees sampled for each species. RCF = relative cumulative frequency, accumulated from oldest to youngest (after Dapson, 1971)

Age	*n*	*Relative Frequency*	*RCF*
113	1	0.066	0.066
102	1	0.066	0.132
101	1	0.066	0.198
94	2	0.133	0.331
91	2	0.133	0.464
86	1	0.066	0.530
85	1	0.066	0.596
81	1	0.066	0.662
75	2	0.133	0.795
74	1	0.066	0.861
70	1	0.066	0.927
55	1	0.066	1.000

RESULTS

A total of 160 trees was cored and the mean age per species recorded for each site (Table 2). The oldest individual was a 113-year-old cypress tree occurring on the cypress site. Bald cypress also exhibited the greatest mean age of all species sampled (Table 2). Median ecological longevity (MEL) was used as an indicator of the relative age structure of a population. MEL values represent the age at which there is a 50% probability of occurrence for that species; half the population should be younger, half older. The greatest MEL value occurred for bald cypress on the cypress site (Table 3). For species occurring on both the cypress site and any one of the other sites the larger MEL value occurred in the cypress stand. For example, MEL for red maple was 64 years in the cypress stand, and 36 and 34 years in the maple-gum and cedar stands respectively. The same trend occurred for water gum and black gum (Table 3). This indicated that the oldest stand of trees among the four was the cypress community. The youngest stands were the maple-gum and cedar, indicating they were the most recently logged communities.

The ecological longevity curves of the species sampled correspond closely to Dapson's four model frequency distributions typifying populations which are expanding, stationary, declining with reproduction, or declining without reproduction. Bald cypress was declining in numbers although it was still reproducing to a minimum degree, as indicated by the bar graph of relative frequency vs. age class and the ecological longevity curve (Figure 1). The ecological longevity curve is convex and skews far to the right of the y axis. The bar graph is clustered to the right in the older age classes. In contrast to the declining bald cypress population the red maple population in the cypress stand was expanding. Large numbers of individuals occurred in the 0-14 year age classes (Figure 1). The red maple population in the cypress stand was older than the red maple population in the cedar stand (Figure 2) and the maple-gum stand (Figure 3). There were many individuals occurring in age brackets over 60 in the cypress stand (Figure 1). Red maple appeared to be expanding in the cypress, cedar and maple-gum communities.

In the cedar stand many individuals were standing dead, or had already fallen, as the stand was reaching senescence. The

Table 2. Range of ages for individual species in four plant communities in the Great Dismal Swamp, Virginia

Species	*Range of Age in Years*	*Maximum Age*	*Mean Age ± SE*
MIXED HARDWOODS STAND			
Quercus alba	41-109	109	77.6 ± 13
Quercus laurifolia	96	—	—
Quercus nigra	43-65	65	54.3 ± 6.3
Quercus michauxii	57-75	75	66.0 ± 8.5
Acer rubrum	36-50	50	41.3 ± 4.0
Ilex opaca	25-86	86	46.3 ± 5.4
Ostrya virginiana	38-40	40	39.0 ± 0.7
Nyssa sylvatica	30-60	60	45.0 ± 14.8
Liquidambar styraciflua	23-49	49	35.3 ± 5.5
Magnolia virginiana	36-47	47	41.5 ± 4.9
Liriodendron tulipifera	40-49	49	44.5 ± 4.2
Oxydendrum arboreum	29-39	39	33.6 ± 2.9
Pinus taeda	52	—	—
Carpinus caroliniana	12	—	—
BALD CYPRESS STAND			
Acer rubrum	26-101	101	66.8 ± 8.8
Nyssa aquatica	17-97	97	59.3 ± 9.9
Taxodium distichum	55-113	113	85.8 ± 3.6
Nyssa sylvatica	48-101	101	78.0 ± 8.3
Fraxinus caroliniana	20-47	47	30.3 ± 2.6
MAPLE-GUM STAND			
Acer rubrum	25-69	69	37.7 ± 4.7
Nyssa sylvatica	24-47	47	34.6 ± 6.4
Liquidambar styraciflua	28-59	59	43.5 ± 14.8
Fraxinus americana	42-52	52	47.0 ± 4.9
Nyssa aquatica	20-103	103	51.8 ± 5.5
Ostrya virginiana	24-38	38	32.1 ± 2.5
ATLANTIC WHITE CEDAR STAND			
Chamaecyparis thyoides	36-101	101	56.5 ± 3.3
Acer rubrum	23-56	56	34.8 ± 3.9
Magnolia virginiana	18-33	33	25.5 ± 7.1
Nyssa sylvatica	22-55	55	36.3 ± 3.9

Table 3. Ages at which probability of occurrence (RCF) is 0.5 (MEL) and 0.01 (approaching MAX) for species occurring in mixed hardwood (MH), cedar (CE), maple-gum (M-G) and cypress (CY) stands

Species	*Stand*	*Age at Which Probability of Occurrence =* 0.5 (MEL)	0.01
Taxodium distichum	CY	86	115
Chamaecyparis thyoides	CE	53	122
Acer rubrum	CE	34	96
A. rubrum	M-G	36	115
A. rubrum	CY	64	198
Nyssa aquatica	CY	57	205
N. aquatica	M-G	47	161
Nyssa sylvatica	CE	35	96
N. sylvatica	CY	80	128
Ilex opaca	MH	44	133
Quercus spp.	MH	65	180
Mixed canopy spp.	MH	38	92
Mixed sub-canopy spp.	MH	35	59
Fraxinus caroliniana	CY	30	73

community was undergoing a transition from cedar to red maple and black gum. Atlantic white cedar was a declining population which was not reproducing as indicated by a complete absence of trees in the younger age classes (Figure 2). Red maple was rapidly expanding in the cedar site. A steep ecological longevity curve and concave aspect of the bar graph demonstrate this trend in Figure 2. Black gum was also an expanding population in the cedar site as it exhibited a similar curve.

Water gum had achieved a relatively stable age distribution in both the cypress and maple-gum sites. The even age distribution of this species exhibited in Figure 3 corresponded closely to the water gum community in the cypress stand. In the mixed hardwood stand all of the species appeared to have

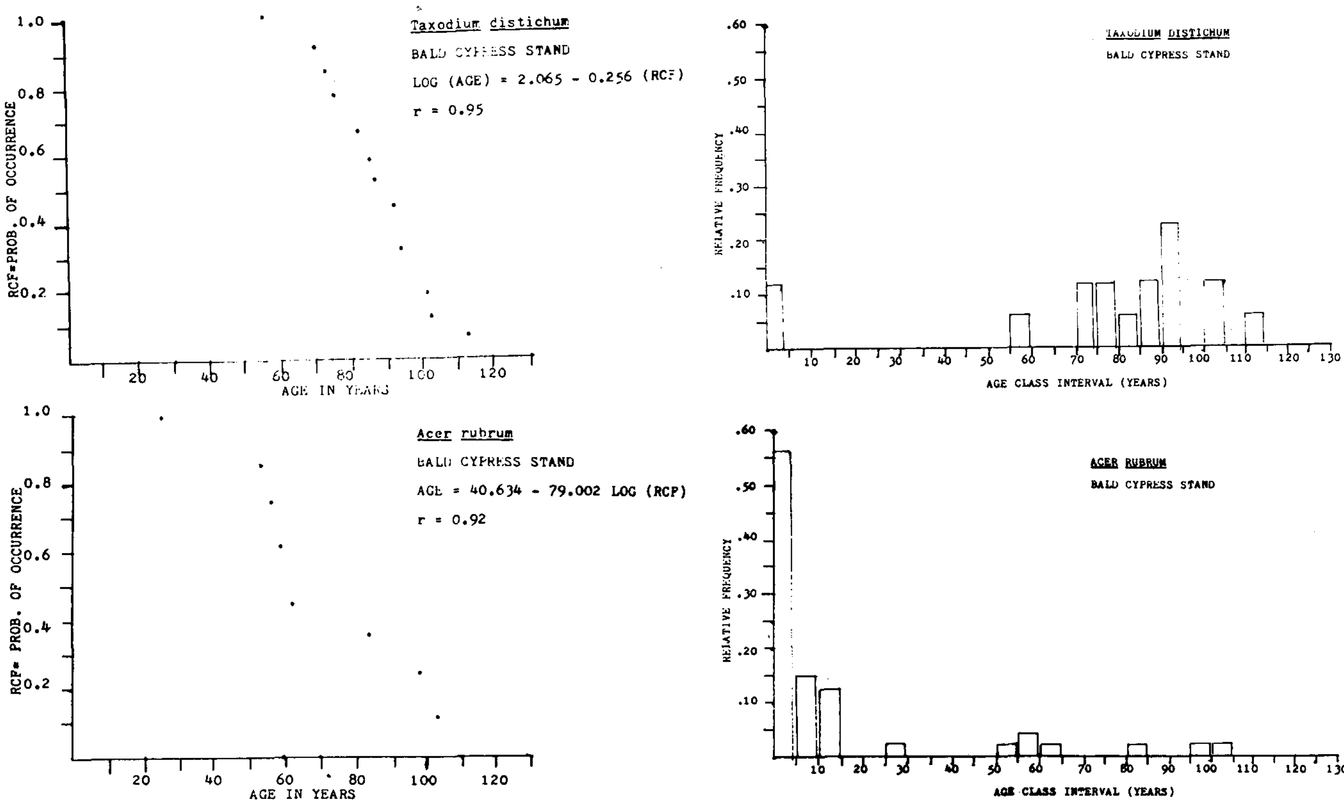


Figure 1. RCF (relative cumulative frequency) plotted against age, and relative frequency plotted against five year age class intervals for *Taxodium distichum* and *Acer rubrum* in the bald cypress site.

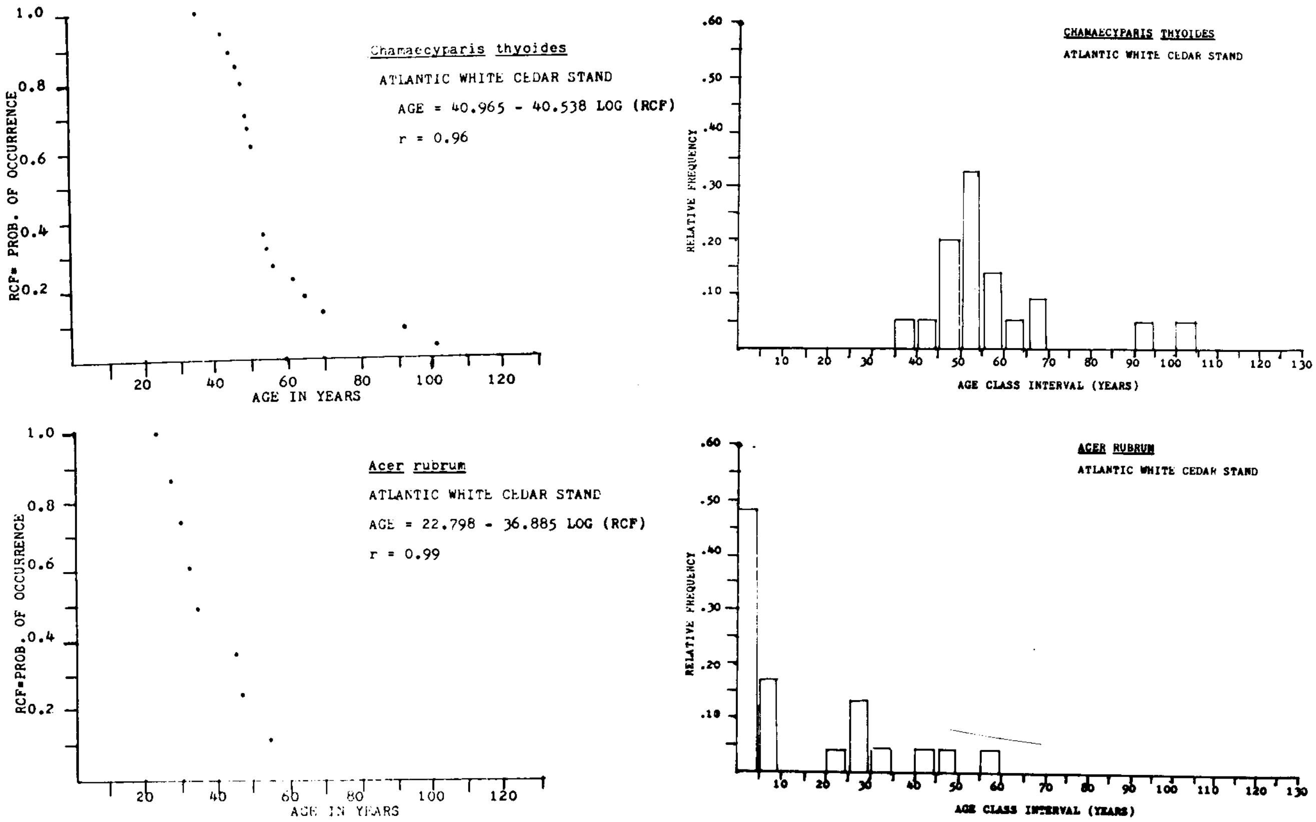


Figure 2. RCF (relative cumulative frequency) plotted against age, and relative frequency plotted against five year age class intervals for *Chamaecyparis thyoides* and *Acer rubrum* in the cedar site.

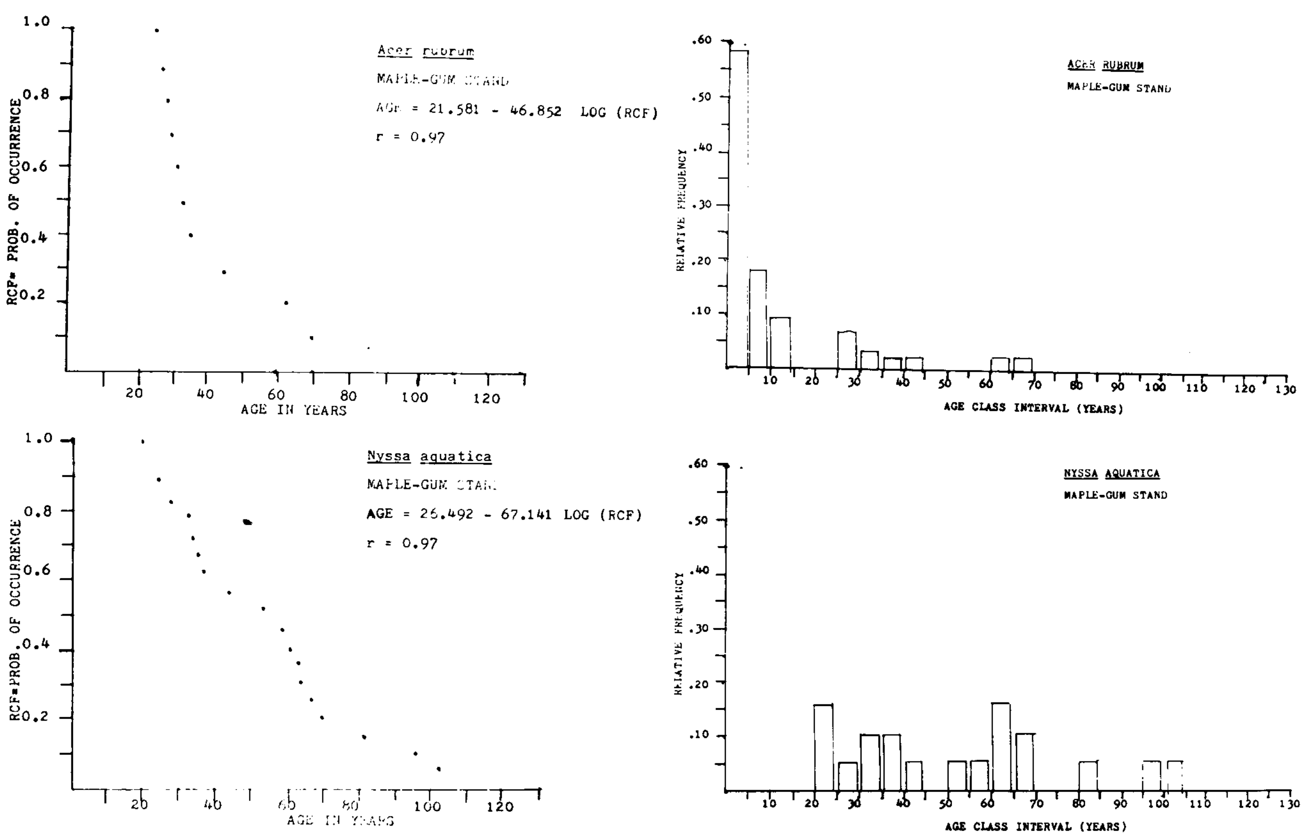
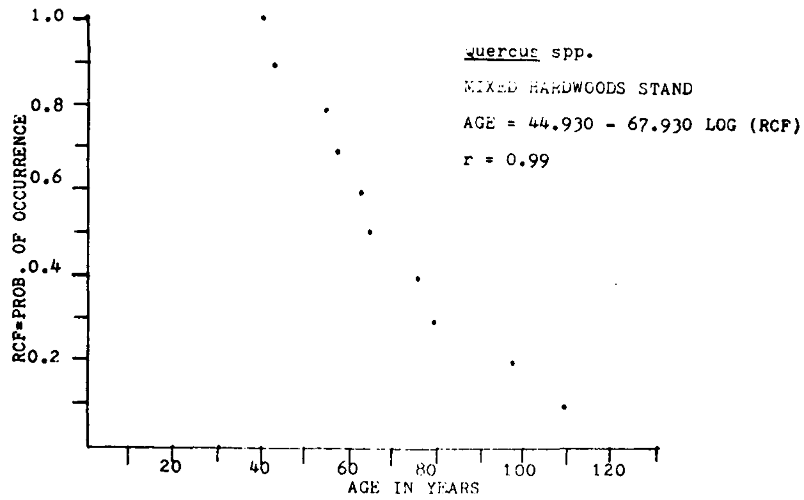


Figure 3. RCF (relative cumulative frequency) plotted against age, and relative frequency plotted against five year age class intervals for *Acer rubrum* and *Nyssa aquatica* in the maple-gum site.



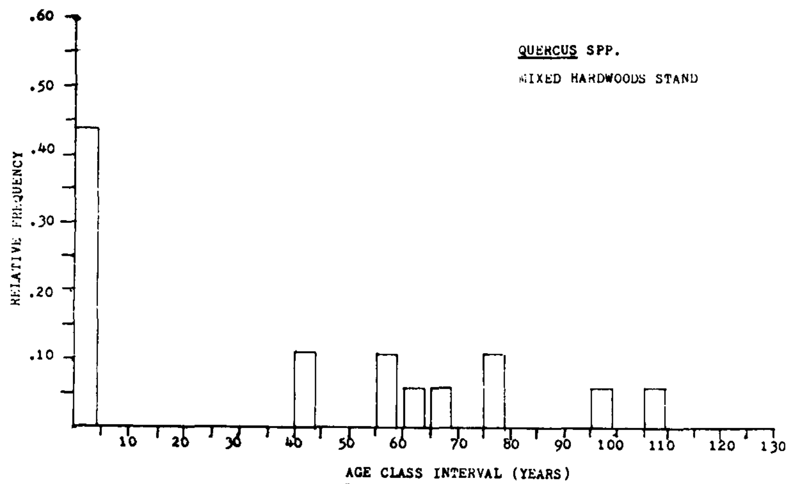


Figure 4. RCF (relative cumulative frequency) plotted against age, and relative frequency plotted against five year age class intervals for *Quercus* species in the mixed hardwood stand.

achieved a stable age distribution. Several species of oaks comprised the largest proportion of the sample and were neither expanding nor declining in numbers (Figure 4).

Maximum ecological longevity (MAX) could not be determined due to the log transformation of RCF used for the linear regressions. However, an RCF value of 0.01 was used as it promised to provide a good indicator of environmental favorability. The largest value for RCF = 0.01 occurred in the cypress site for bald cypress, maple and gum species (Table 3). As with MEL, the larger values occurred in the cypress stand for species occurring in more than one site. The order of environmental favorability can be established based on species occurring in more than one stand. Individuals in the cypress stand had the greatest age potential followed by the maple-gum and cedar stands respectively.

DISCUSSION

Age structure of a population is a function of fertility and mortality. The longevity of a species is determined by certain genetic and environmental factors (competitive ability, temperature, moisture, catastrophic winds, fire, and disease, to name a few). The average longevity for any real population will be below the potential physiological longevity. Certain environmental factors in addition to density, and other population parameters affect an individual's chance of survival. The population of Atlantic white cedar in the cedar community is declining due to natural senescence, as evidenced by the presence of heart rot. The most limiting environmental factor affecting tree growth is water supply (Zimmerman and Brown, 1971). This is reflected in the average ring size of the individual (Douglas, 1919). The values derived by substituting 0.01 for RCF reflect this aspect of environmental limitations on survival. The greatest values occurred for species within the cypress community. This was the wettest site of the four, possibly indicating a greater environmental favorability.

Analysis of growth data is expected to support the contention that greater water supply results in greater amount of growth in diameter. For example, trees growing in the cypress site are expected to show a larger growth increment per annum than those growing in the other sites because this stand is subjected to the most flooding. Growth would likely be inhibited by continuous flooding as a result of anaerobic conditions. However, such conditions do not appear to exist in the Dismal Swamp during the growing season. Because of this influence of water supply on growth it is difficult to make a strong correlation between age and diameter of a tree species.

Another aspect of population dynamics in swamp forests which is influenced by fluctuations in water level and other environmental factors, is reproduction (Braun, 1964). Cypress seeds can only germinate where standing water has disappeared and adequate aeration of the soil takes place, in addition to having a sufficient amount of sunlight. Red maple has a wide span of tolerance for varying amounts of sunlight and different amounts of soil moisture, and germinates readily in many circumstances. This coincides with Iglich's (1975) findings concerning red maple's status as an r- strategist. The species produces a large number of offspring, saturating the environment with seedlings, pouring much energy into reproduction rather than into producing fewer, stronger individuals which have a higher chance of survival. This explains the large numbers of red maple in the 0-4 year age class. The red maple population is expanding in the cedar, cypress and maple-gum stands. The failure of cedar to produce offspring was probably due to the lack of recent fire or mechanical scarification. White cedar is known as a fire dependent species, relying on short hot fires to clear the forest floor so that seeds may germinate. The replacement of bald cypress by hardwoods is probably the result of a closed canopy which limits seed germination and decreases the species ability to compete successfully with hardwoods.

The stable age structure of the mixed hardwood stand was probably due to the mesic nature of the site which was demonstrated by well developed herb, shrub and canopy layers, and increased diversity over the other stands. The dominant oaks are long lived and also have successful replacement occurring. The oak seed source is variable from year to year but the seeds germinate in ample numbers in the litter of the mature community.

Odum (1971) states that greatest accumulation of standing

crop biomass occurs in areas which have remained undisturbed for longer periods. The cypress site had the most standing crop biomass (Dabel and Day, 1977) of the four communities. This coincides with the findings in this study which show the dominant member of the tree stratum, bald cypress, as the oldest species occurring in all four sites, i.e., the highest mean age. This was further supported by the MEL values derived for species within this stand. As the age of a population increases, MEL shows a progressive upward trend (Dapson, 1971).

The data obtained in this study should be useful for making further correlations between age structure of these tree communities and other ecological parameters. Iglich (1975) found in her study of the Coweeta watershed that net primary productivity, nutrient composition and biomass of the vegetation vary according to stand age and distribution of tree sizes. When the age data from this study is collated with the other ecological information gathered from these four plant communities, the role of each species can be evaluated.

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