AGE AND SIZE STRUCTURE OF NATURAL AND SECOND-GROWTH BLACK SPRUCE PEATLAND STANDS IN NORTH-EASTERN ONTARIO

B.J. HORTON
A. GROOT

Contracted by:
Horton Forestry Services Limited
R.R. 4, Stouffville, Ontario
L4A 7X5

ABSTRACT

Stand structure was examined in 40 natural and second growth black spruce (Picea mariana (Mill.) B.S.P.) peatland stands in northern Ontario, by means of age and diameter frequency distributions and diameter-age regressions. Three types of age structure were identified — even-aged, uneven-aged and composite. Age structure patterns were wholly or partially influenced by natural disturbances — either fire or windfall. Even-aged structure was typical of better-drained sites, uneven-aged structure of more poorly drained. All three age structure types were observed in natural stands, but purely even-aged stands were not present in the second-growth condition. In the absence of disturbance, it is hypothesized that black spruce peatland forests can achieve uneven-age equilibrium. Diameter-age relationships for trees within stands were generally weak. Diameter distributions were less useful than age distributions for understanding stand dynamics.

Key Words: age structure, Picea mariana, peatlands, northern Ontario, size structure, forest ecology, disturbance.

AGE AND SIZE STRUCTURE OF NATURAL AND SECOND-GROWTH

BLACK SPRUCE PEATLAND STANDS IN NORTH-EASTERNN ONTARIO

INTRODUCTION

Most forest ecosystems in the boreal forest region of central Canada have been dependent on natural disturbance - fire, wind, insects - for renewal. In this region the frequency of disturbance is such that succession seldom progresses through a complete generation of trees to a stable climax forest, all-aged and uneven-sized.(Dix & Swan 1971, Rowe & Scotter 1973, Carleton & Maycock 1978).

Although this view of succession is generally applicable to upland sites, some peatland forests may be less susceptible to disturbance, and thus may have had greater opportunity to follow successional pathways. In particular, the uneven size distribution, and often patchy appearance of many black spruce (Picea mariana(Mill.) B.S.P.) swamp forests suggests that they are not even-aged.

A number of characteristics of such forests make them likely candidates for escaping disturbance and developing an uneven-age structure. First, large areas of peatland forest may have much lower frequency of fire than upland forests (Vincent 1965). Second, pure stands of black spruce are relatively free of insect pests, especially the spruce budworm, which so often affects balsam fir (Abies balsamea)(L.)Mill.) and white spruce (Picea glauca(Moench)Voss). Third, the resiliency of root systems in peat and lesser stature may make peatland trees resistant to massive blowdown.(Le Barron 1945). Fourth, the incidence of butt and root rots is much less severe in black spruce on lowland sites than on upland sites. Fifth, black spruce can regenerate by layering or by seed, and is mid-tolerant, so recruitment in the understorey is possible.

In the past century, timber harvesting has created a new type of disturbance affecting succession and stand development in peatland forests. Harvesting has also resulted in the renewal of forest ecosystems in many cases. In northeastern Ontario, much of the peatland area harvested for black spruce pulpwood from 1915-35 now supports well stocked black spruce forests which are largely of advance growth origin - suppressed understorey trees left undisturbed by horse logging systems.

METHODS

STUDY AREA

Sample plots were established in black spruce peatland and transitional forests of the Northern Clay Section (Rowe 1972) of northeastern Ontario in two localities - east of Cochrane (Lat. 49, Long. 80 30') and north of Kapuskasing (lat. 49 30', Long 82 20').

This region has a continental climate. Mean annual temperature is 0.5 C. and mean annual precipitation 82 cm., half of it occurring in the growing season. It is characterized by nearly level topography underlain by Precambrian rocks with surface deposits of lacustrine clay and water-worked tills originating from glacial Lake Ojibway (Rowe 1972).

Black spruce swamp forests prevail on the lowland flats, often alternating with sedge and heath bogs and locally including tamarack (Larix laricina (DuRoi)K.Koch) or cedar (Thuja occidentalis L.) as minor companion tree species. Black spruce also occupies the gently rising uplands intermixed with balsam fir, white spruce and poplars (Populus spp.). A comprehensive forest ecosystem classification (Jones et al. 1983), available for this region, provided a primary basis for sampling. The system allocates stands to vegetation types and "operational groups" (OG's), the latter embracing a group of vegetation types and soil conditions. This study was confined to the following peatland and transitional peatland OG's in which black spruce predominates:

OG 11 - Ledum - wet organic soil 40-160 cm. deep, thick surface fibric horizon with little ground water flow.

OG 12 - Alnus - herb-poor - wet organic soil 40-160 cm. deep, thick surface fibric horizon, with moderate ground water flow.

OG 13 - Alnus - herb-rich - wet, well decomposed, organic soil 40+ cm. deep, thin surface fibric horizon, strong ground water flow.

OG 9 - Conifer-herb/moss rich - mixed conifers on moist, fine clay-loam soil 5-30 cm. organic matter, intermediate to poor drainage.

OG 8 - Feathermoss/sphagnum - moist fine clay-loam soil with 20-40 cm. organic matter, poor drainage.

OG's 9 & 13 were combined here because of the former's rarity and an apparent similarity in productivity, making four site categories in all. Within each of these sites, second growth stands (logged mainly in the 1920's & early 30's) and natural-origin stands were selected for sampling. Balsam fir and tamarack formed minor components in some of the stands sampled but overall other tree species were of negligible occurence.

METHODS cont'd

FIELD AND LABORATORY MEASUREMENTS

The study was carried out in two parts - an initial phase to establish optimum plot size and sampling intensity and a second phase incorporating the main sample. A total of 40 plots was established in the field. The distribution of sample plots by stand origin and site type is summarized in Table 1.

TABLE 1. Distribution of Sample Plots by Study Phase and Treatment

SITE TYPE/ STAND ORIGIN	PHASE 1		PHASE 2		COMBINED	
	Second Growth	Natural	Second Growth	Natural	Second Growth	Natural
OG 11 - Ledum	1	1	7	3	8	4
OG 12 - Alnus- herb poor	1	1	7	3	8	4
OG 9/13 - Conifer- herb/moss rich, Alnus- herb rich	1	1	4	2	5	3
OG 8 Feathermoss Sphagnum	1	1	4	2	5	3
TOTALS	4	4	22	10	26	14

Plots were carefully located to avoid significant transitions in stand structure, stand composition or site type. Second-growth stands were identified from aerial photographs, logging records and ground checks for stumps. Plots in second-growth stands were oriented with the long axis perpendicular to skidways as distinguished on aerial photos.

The size of plot used was 10 x 80 m. in Phase 1 and 10 x 50 m. in Phase 2. Plots were broken down into grids of 1 m. quadrats within which all trees (stems > 1.4 m. height) were tallied as to species, diameter breast height and stem form (presence of basal sweep, lean or forking). Stocking of advance growth (stems < 1.4 m. height) of relevant species was recorded for each quadrat. Dead stems were disregarded in the tally. Heights were taken for all plot trees in Phase 1 and for 30 representative trees in Phase 2. Increment cores through the pith at stump height (25 cm.) were obtained from all trees in each plot for determining age.

Ten trees representing the full diameter range in each plot were felled for detailed stem analysis. Sections were taken at ground level, stump height (.25 m.), 1 m., breast height (1.4 m.) and at every additional metre (2, 3 etc.). In Phase 1, the four largest of these trees were also sectioned 0.1, 0.2 and 0.3 m. below ground (where possible) for age determinations. (cf. McEwen 1966).

In the laboratory, annual rings were counted under a microscope on all increment cores and below-ground discs. Stem analysis was carried out on the computerized Tree Ring Increment Measurement (Fayle et al 1983) (TRIM) system which was developed by the Ontario Ministry of Natural Resources. This system provides a comprehensive analysis of height, diameter and volume growth throughout an individual tree's life history.

METHODS cont'd.

ANALYSES

For ease of presentation, two general site types were distinguished based on differences in productivity, drainage and moss thickness. Operating Groups 11 and 12 were classified as "poor swamp" sites and Groups 8, 9 and 13 were combined representing "rich swamp/transitional sites.

Percentage frequency distributions for 20-year age classes were prepared for each plot using the age at stump height (25 cm.) of all trees above breast height (1.4 m.) as determined from increment cores. Stems below 1.4 m. were assessed as to stocking per 1 m2 quadrats rather than density. An approximation of the density of stems less than 1.4 m. tall is given by:

$D = -LN (1-S)$ where D is the density (1m2 basis) and S is the stocking (1m2 basis).

This relation is valid when the number of stems on quadrats is Poisson-distributed (random). Because black spruce advance growth is usually clumped however, the calculated density is likely to be an underestimate. This estimate of density, recognized to be conservative, was added to age classes 1-20 and 20-40 years on an arbitrary 2/3, 1/3 basis thus making the age frequency distributions representative of all tree stems rather than only those above breast height.

The difference between age at stump height and the total age determined from below-ground sampling was calculated for 4 dominant and co-dominant trees from

each plot of the Phase 1 sample. Averaging the figures from both natural and second-growth plots on all site types, an overall correction factor of 12.5 years for total·age was determined. For second-growth plots, the percentage of stems of pre-harvest origin was estimated by applying this correction factor to the stump age and then comparing the total age to the harvest date.

Size class frequency distributions were prepared for all stands based on the estimate of seedling density described above and 2 cm. d.b.h. classes for stems taller than 1.4 m.

Least-squares regression analysis on d.b.h. over stump age was carried out for trees taller than 1.4 m. in all stands. The power function $y = Ax^B$ was applied as it generally gave the best fit in a sample of plots.

RESULTS

Age Structure of Natural Stands

Three general age structure patterns were recognized:

1) uneven-aged structure with stems distributed throughout many different age
   classes and with no single age class predominating

2) even-aged structure with most dominant stems in the one or two oldest age
   classes and

3) composite structure with a large even-aged component but also with some stems in
   2 or more older age classes.

Age class frequency distributions are shown in Table 2 for all stands of natural
origin, categorized by age structure pattern within the two general site types
(poor swamp or rich swamp/transitional). Of the 14 natural stands studied, 7 were
even-aged, 5 were uneven-aged and 2 were composite in structure. The age structure
of natural stands was related to site type. Uneven-aged stands predominated on the
poor swamp sites (Operating Groups 11 and 12) whereas even-aged stands were more
common on the rich swamp and transitional sites (Operating Groups 13 and 8).

The even-aged natural stands all had unimodal frequency distributions with
high relative proportions of stems in the oldest 20-year age class and very few
stems in intermediate classes (Fig.1A). Four stands showed high levels of
recruitment in the youngest age class (Stands 17, 33, 26, and 34) while the others
did not (Stands 4, 9, 31). The maximum age of the even-aged stands ranged from
80-160 years with the majority originating 101-120 years ago.

The uneven-aged natural stands generally had positively-skewed age structures overall but within that pattern the stems over 40 years old frequently followed a bell-shaped distribution with peak frequencies around the 90 and 110 year age classes (Fig.1D). The maximum age in these stands was between 210 and 310 years - significantly older than the even-aged stands. Stand 13 showed the most stable age structure (Fig.1G) with minor peaks at 110, 190 and 290 years.

The two natural stands showing composite age structure were very similar in pattern to the even-aged stands except for the presence of a few older residual stems.

Age Structure of Second-Growth Stands.

Table 3 shows age frequency distributions for the second-growth stands. Those uneven-aged stands with a consistent positive skew (negative-exponential pattern) in the age distributions were distinguished from stands with otherwise irregular distributions. None of the second-growth stands were even-aged. Uneven-aged structure prevailed in 22 stands - 16 with a positive skew and 6 with irregular distributions. The other 4 second-growth stands showed composite age distributions. The age class during which logging occurred is underlined for each stand in Table 3 and the percentages of stems of pre-harvest origin are shown to the right of the distributions.

Positively-skewed distributions occurred most commonly on the poor swamp sites - operating groups 11 and 12. Typically over 60 percent of all stems were in

the 3 youngest age classes - trees released or regenerated after logging. Remaining classes showed steadily declining frequency to a maximum age of 130 to 230 years (Fig. 1J). Uneven-aged stands generally showed a bell-curved distribution among the older trees with a peak period of recruitment ususally pre-dating the harvest and spanning 2 or 3 age classes. Several of these stands also showed a significant amount of recruitment in the early age classes, resulting in an overall bi-modal pattern. Overall, the uneven-aged second-growth stands had a lesser maximum age than the uneven-aged natural stands with the oldest trees being less than 240 years and generally less than 200 years.

Second-growth stands with composite age structure all occurred on transitional sites - operating groups 8 and 9. In two of the 4 composite stands, the dominant even-aged component was related to the harvest date. In the other stands the dominant component pre-dated the harvest. (Fig.1M).

The proportion of stems over breast height which pre-dated the harvest varied among stands from 50 to 100 percent, averaging 83 percent overall. Stands with positively-skewed age distributions had significantly fewer pre-harvest stems (77%) than stands with uneven and composite age structure (92%). It was determined from selected plots that this advance growth usually amounted for more than ninety percent of the current volume. Overall, second-growth stands had higher average densities of seedlings and unmerchantable stems (< 10 cm. d.b.h.) than natural stands on the same sites.

Size Structure

Tables 4 and 5 show diameter class frequency distributions for natural and second-growth stands. Three distribution patterns were recognized: normal, positively-skewed and irregular. This classification is only indicative of general trends and in some cases the distinction between patterns is not great. The pattern for each stand is indicated in the Tables and the age structure pattern is also shown for comparative purposes.

Considering only trees above breast height, most of the natural stands (Table 4) showed a normal or bell-curve, diameter distribution (Fig. 1B) with peak frequency in the 11-19 cm. range. This pattern prevailed in the stands with even-aged and composite age structure. The other natural stands had irregular diameter distributions characterized by higher relative percentages in the small size classes (1-9 cm.) and sometimes inconsistent fluctuations in the larger classes (Figs. 1E,1H). Irregular distributions occurred more commonly in the Operating Groups 11 and 12 - sites supporting more advance growth in the understorey.

Many of the second-growth stands (Table 5) exhibited a positively-skewed diameter distribution (Fig 1K). This pattern occurred most commonly on the poor swamp sites (OG 11 & 12) and in the uneven-aged condition. Other stands had normal or irregular diameter distributions (Fig. 1N). The irregular distributions were usually intermediate forms showing some characteristics of both the positively-skewed and normal distributions. This often resulted in a bi-modal pattern with one peak in the smallest size classes and a second peak in the 15 cm. range. Overall the second-growth stands had significantly higher proportions of

unmerchantable stems (<10 cm. d.b.h.) than the natural stands, although the maximum diamieters were comparable.

Size/Age Relationships

Co-efficients of determination (R2) for diameter/age regressions are shown in the right hand column of Tables 4 and 5 for all stands. Results are displayed graphically for 5 stands in Fig. 1. Overall the relationship varies erratically among stands from weak (R2 < .50) to strong (R2 .70-.80) with little pattern according to origin or site type. Interestingly both the weakest and strongest correlations occurred in natural stands with even-aged structure.

DISCUSSION

Black spruce is adapted to survive wildfire, historically the foremost factor conditioning the boreal forest. Its semi-serotinous cones can remain closed on the tree tops for many years, accumulating a large supply of seed ready for dissemination following a fire of less than all-consuming intensity. Therefore, like the serotinous-coned jack pine (Pinus banksiana Lamb.) and lodgepole pine (Pinus contorta Dougl.var.latifolia Engelm.), black spruce frequently has a seral role in the forest mosaic, forming even-aged stands of unimodal age distribution which, failing disturbance, gradually succeed to climax spruce-fir. This is the conventional natural scenario for upland and swamp-transitional sites where black spruce occurs (Horton & Lees, 1961, Vincent, 1965). The even-aged and composite natural stands identified in this study presumably originated by wildfire. It is noteworthy that these fire origin stands were most frequent on the rich swamp and transitional peatland sites which would be more prone to burning than the poor swamp sites. Recruitment was generally rapid for about the first 20 years following the fire and gradually suppressed thereafter. Lieffers (1986) found a similar 20-year recruitment period for black spruce following fire in Alberta. In most stands recruitment levels began to increase again 80 to 100 years after the initial disturbance. This could be attributed to layerings or seedlings which are able to develop as the canopy matures and more light reaches the ground. Harcombe (1986) observed a very similar 80 to 100 year cycle following fire of rapid invasion, suppression and recruitment re-initiation in an Oregon spruce-hemlock forest. He suggested that the re-initiation of recruitment was the result of natural thinning in the stand and not disturbance.

The natural fire-origin stands showed widely variable amounts of advance growth in the understorey depending on site and stand conditions. For the same peatland forests Groot (1984) found that the abundance of black spruce advance growth could be positively correlated with maximum stand age, the thickness of the fibric moss layer and the amount of sphagnum moss cover and negatively correlated with stand basal area, herbaceous cover, crown cover, dominant height and alder cover (Alnus rugosa). Most of the variability observed in this study can be explained on the basis of these correlations.

The oldest trees in the uneven-aged natural stands were from 200 to 300 years old and there was no evidence of a primary even-aged cohort which would mark stand initiation by disturbance. Disturbances did however affect the age structure of these stands, as evinced by a consistent wave of recruitment peaking in the 90 and 110 year age classes and accounting for up to 60 percent of stems older than 40 years. This could have resulted from a partial disturbance - either fire or windfall - which removed part of the main canopy, thereby releasing advance growth and initiating new regeneration. As this phase of recruitment coincided with the time of origin of most of the even-aged stands, it appears likely that some of the uneven-aged stands were partially affected by fire some 120 years ago. Because of the wetness of these sites, fire may have been unable to spread at ground level and was confined to the upper canopy.

Only Stand 13 appeared to be unaffected by any significant disturbance in the last 300 years. There were minor peaks in the age frequency distribution which occurred 80 to 100 years apart caused by minor disturbances which each probably removed less than 20 percent of the canopy. This cycle may reflect the frequency of wildfire in the region. The age structure of Stand 13 generally conformed to a

power function survivorship model characterized by a sustained input of seedlings and a decreasing mortality rate with age. It could be argued that disturbances in the other uneven-aged stands caused a departure from this model. Leak (1975) and Hett and Loucks (1976) found that this form of survivorship best described the age structure of other long-lived uneven-aged forests. In any case, as Harcombe (1985) has pointed out, mathematical modelling of stand development may be an over-simplification; localized conditions and small events as well as catastrophic occurrences can shape the patterns, resulting in considerable diversity. It is hypothesized that in the absence of disturbance, black spruce peatland forests can achieve uneven-aged equilibrium.

A similar subclimax situation has been described by Despain (1983) and Parker (1986) for certain lodgepole pine communities which formed pure, uneven-aged stands in the absence of fire. Both black spruce and lodgepole pine are generally considered to be colonizing, shade-intolerant species yet in some cases they are able to regenerate in the understorey and persist as suppressed advance growth until released through mortality or disturbance.

Stand structure comparison with other spruce species is complicated by the fact that most uneven-aged forests are composed of two or more genera and succession can alter the composition over time. Within one stand, different species can have very different age structure patterns. This was observed by Stewart (1986) for old growth montane conifer forest in Oregon. Knowles and Grant (1983) found that Engelmann spruce (Picea engelmannii (Parry) Engelm.) was a climax component in an old uneven-aged spruce-fir stand in Colorado and exhibited a markedly decreased mortality rate after 200 years. Similarly red spruce (Picea rubens SArg.) and white spruce (Picea glauca (Moench) Voss) were stationary components in New Hampshire and

Ontario spruce-fir associations respectively. (Leak 1975, Hett and Loucks 1976).

The effect of harvesting was to maintain or introduce uneven-age structure into the stands. No second-growth stand was even-aged, although several were composite in structure. Some of these stands may have had an even-aged component at one time that was removed by the harvest. The second-growth sample generally represented areas that were mostly unaffected by the fires which were common in the region some 120 years ago. Manual cutting and horse skidding methods used in the early logging preserved much of the advance growth in these forests. At the time of release the unmerchantable residuals varied in size and age to a maximum of about 8 metres in height and 160 years old. In most stands, the existing advance growth responded well to release and went on to dominate the canopy. It is expected in monocultures developed after disturbance that the first recruits would express dominance over later ones (Ross and Harper 1972). The amount of post-harvest recruitment varied among stands and was apparently related to the site type and the size and extent of the established residuals. Positively-skewed age structures were observed mostly on the poor swamp sites where regeneration by layering in the thick moss was prevalent. Since these sites were slow-growing and often erratically stocked, there could have been a prolonged recruitment period following logging. The higher growth rate in the rich swamp and transitional site types likely resulted in more rapid crown closure and inhibition of later recruitment.

Age structure patterns in the rich swamp and transitional second-growth stands were more typically bimodal or bell-curved. This resulted from peak periods of recruitment, mostly in the 90 and 110 year age classes, implying partial disturbances in these stands 40 to 60 years before they were harvested, which produced considerable restocking of trees. Their presence as that of

well-established residuals would have precluded or greatly reduced the recruitment after logging of younger trees either through release or regeneration. In some cases the harvesting initiated a second phase of recruitment in the younger age classes, creating an overall bi-modal pattern. Bi-modal age distribution usually implies two stand disturbances, each incurring subsequent recruitment. Harcombe (1985) attributed bimodal size distribution in Sitka spruce (Picea sitkensis (Bong.) Carr.) to the incidence of blowdown. Vincent (1965) recorded major windfall damage in 1959 affecting large areas in our study region. During our sample we noticed localized partial stand disturbance from recent windfall in mature stands.

In any case, extensive severe windfall would have much the same effect as non-mechanized clearcutting in setting the scene for subsequent natural regeneration and stand development. Similarly, partial windfall would be akin to partial cutting. In either context, as well as that of wildfire, black spruce appears to be capable of maintaining its subclimax status in these swamp sites. As Lorrimer (1980) suggested, such consdiderations are very pertinent in shaping management policies.

In the second-growth stands with composite structure, the even-aged component was attributed to a pre-harvest disturbance in Stands 12 and 35. In stands 19 and 30, the dominant component coincided with the time of harvest and was formed from released advanced growth or seedlings established after the harvest.

The bell-curve diameter distribution observed for even-aged stands in this study is typical of even-aged stands in general. Conversely the positively skewed (negative exponential) diameter distribution that characterized many second-growth stands in this study is typical of uneven-aged stands in general. Many of the

uneven-aged natural and second-growth stands with irregular diameter distributions represent departures from the negative exponential model caused by partial disturbance. Although some of the tree size/age relationships were moderately strong, generally they were not sufficiently strong that diameter could be used as a surrogate for age in the analysis of age structure. This reaffirms Harper's (1977) contention that it is dangerous to assume that size reflects age. Black spruce trees of the same age may vary widely in growth depending on the degree of suppression or response to release. Because of the ability of black spruce to survive for long periods of time in a suppressed state, disturbances of the main canopy can release advance growth which varies considerably in age, thereby contributing to an all-aged structure.

REFERENCES

Carleton, T.J. and Maycock, P.F. 1978. Dynamics of the boreal forest south of James Bay. Can.J.Bot. 56:1157-1173.

Despain, D.G. 1983. Nonpyrogenous climax lodgepole pine communities in Yellowstone National Park. Ecology 64(2):231-234.

Dix, R.L. & Swan, J.M.A. 1971. The roles of disturbance and succession in upland forests at Candle Lake, Saskatchewan. Can.J.Bot. 49: 647-676.

Fayle, D.C.F., MacIver, D. and Bentley, C.V. 1983. Computer-graphing of annual ring widths during measurement. For.Chron. 59(6): 291-293.

Groot, A. 1984. Stand and site conditions associated with abundance of black spruce advance growth in the northern clay section of Ontario. Dep. Environ., Can.For.Serv., Great Lakes For.Res.Cent. Info.Rept. 0-X-181.

Harcombe, P.A. 1986. Stand development in a 130-year-old spruce-hemlock forest based on age structure and 50 years of mortality data. For. Ecol. & Mgmt. 14:41-58. Elsevier Science Publishers, Amsterdam.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York, New York, U.S.A.

Hett, J.M. and O.L. Loucks, 1976. Age structure models of balsam fir and eastern hemlock. J. Ecol. 64:1029-44.

Horton, K.W. and J.C. Lees. 1961. Black spruce in the foothills of Alberta. Can.Dept.Forestry, For.Res.Br. Tech. Note No. 110.

Jones, R.K. et al. 1983. Field guide to forest ecosystem classification for the Clay belt. Ont.Min.Nat.Resources.

Knowles, P. and M.C. Grant. 1983. Age and size structure analyses of Engelmann spruce, ponderosa pine, lodgepole pine and limber pine in Colorado. Ecology 64(1):1-9.

Leak, W.B. 1975. Age distribution in virgin red spruce and northern hardwoods. Ecology 56:1451-54.

Le Barron, R.K. 1945. Light cutting in black spruce is practicable. J.For.
        43:486-489.

Lieffers, V.J. 1986. Stand structure, variability in growth and intraspecific
        competition in a peatland stand of black spruce Picea mariana. Holarctic
        Ecology 9:d58-64. Copenhagen.
        .

Lorrimer, C.G. 1980 Age Structure and disturbance history of a southern Appalachian
        virgin forest. Ecology. 61(5):1169-84.

Parker, A.J. 1986. Persistence of lodgepole pine forests in the central Sierra
        Nevada. Ecology 67(6):1560-67.

Ross, M.A. and Harper, J.L. 1972. Occupation of biological space during seedling
        establishment. J. Ecol. 60:77-88.

Rowe, J.S. 1972. Forest regions of Canada. Can.Dept.Nth.Aff. & Nat.Res.
        For.Br.Bull.123.

Rowe, J.S. and Scotter, G.W> 1973. Fire in the boreal forest. J.Quat Res.
        3:444-464.

Stewart, G.H. 1986. Population dynamics of a Montana conifer forest. Western
        Cascade Range, Oregon, U.S.A. Ecology 67(2):534-44.

Vincent, A.B. 1965. Black spruce. A review of the silvics, ecology & silviculture.
        Can.Dept.For. Publ. 1100.

TABLE 2 - AGE FREQUENCY DISTRIBUTIONS - % - NATURAL STANDS

SITE TYPE	OG	STAND	10	30	50	70	90	110	130	150	170	190	210	230	250	270	290	310	AGE STRUCTURE PATTERN
POOR	11	3	55.5	27.9	2.6	1.5	4.0	3.6	1.6	1.4	1.1	0.6	0	0.2					U
SWAMP	11	10	26.9	13.7	3.6	4.9	8.8	15.3	8.5	7.5	2.6	1.6	1.6	2.3	1.6	0.6			U
	12	2	28.2	14.2	2.8	4.0	9.3	22.6	9.7	4.0	2.0	2.4	0.4	0	0	0	0	0.4	U
	12	28	35.7	18.0	2.0	3.5	13.1	12.6	8.1	2.5	2.0	1.5	0	0.5	0.5				U
	12	13	36.1	18.5	5.3	3.3	4.0	5.3	3.3	2.0	4.0	5.3	4.7	2.7	2.0	0.7	2.7		U
	11	17	50.5	25.5	1.3	0.8	0.5	1.0	1.8	18.4									E
	11	33	29.4	14.7	4.4	4.4	18.2	28.9											E
	12	5	35.9	18.0	1.2	2.2	2.8	5.0	2.8	3.4	24.4	3.1	0	0	0.3	0.3	0.3		C
RICH	8	4	4.0	2.8	12.4	80.8													E
SWAMP &	8	26	37.8	19.0	0.6	2.4	7.3	32.9											E
TRANSI-	8	34	29.7	14.8	0.7	1.1	9.2	44.4											E
TIONAL	13	9	7.4	4.5	0	2.0	16.0	55.4	14.7										E
	13	31	9.0	4.5	1.1	0	2.2	82.1	0	0	1.1								E
	13	36	24.6	12.6	0.6	5.0	26.1	28.3	0	2.2	0.5								C

* U = uneven-aged   E = even-aged   C = composite

TABLE 3 - AGE FREQUENCY DISTRIBUTIONS - % - SECOND GROWTH STANDS

SITE TYPE	OG	STAND	10	30	50	70	90	110	130	150	170	190	210	230	AGE STRUCT. PATTERN *	PRE-LOG ORIGIN % **
POOR	11	1	33.2	17.4	17.6	14.8	14.0	2.2	0.6	0.2					U-P	64
SWAMP	11	11	37.4	19.1	17.2	9.7	6.3	7.2	3.1						U-P	88
	11	20	34.2	17.3	23.0	18.3	4.3	1.7	1.3						U-P	83
	11	22	41.6	20.9	5.6	12.7	7.5	5.8	2.4	0.9	0.9	0.6	0.6	0.2	U-P	85
	11	25	32.4	17.3	24.7	7.8	7.0	5.5	4.4	0.6					U-P	87
	11	29	37.7	19.3	22.2	12.1	7.0	1.1	0.1	0.1	0.1	0	0.1		U-P	87
	11	39	40.4	21.3	18.7	6.7	3.6	3.3	2.2	2.2	1.1	0.2	0.4		U-P	78
	12	8	37.1	20.6	29.8	4.5	4.1	2.4	1.0	0.5					U-P	49
	12	15	38.2	20.3	25.6	3.1	1.5	2.2	1.3	2.4	4.8	0.2			U-P	66
	12	21	34.0	17.8	29.9	7.6	3.8	4.9	1.9						U-P	65
	12	37	40.4	21.0	17.9	7.0	3.7	4.2	3.0	1.5	0.2	0.7	0.2		U-P	78
	12	38	40.8	20.9	22.2	8.0	4.0	3.1	1.0						U-P	82
	12	40	43.0	22.2	7.3	9.4	8.8	6.1	1.5	1.8					U-P	95
	11	14	35.4	17.8	3.3	4.9	9.3	17.3	6.3	3.3	1.9	0.3			U	98
	12	23	40.7	20.6	4.0	7.8	16.8	6.2	1.5	1.5	0.9				U	93
	12	27	13.5	7.3	13.5	43.3	10.1	5.4	2.0	2.7	1.3	0.7			U	82
RICH	8	24	24.1	13.1	22.3	18.2	16.5	5.4	0	0	0.4				U-P	83
SWAMP &	8	32	37.0	18.6	9.0	10.5	12.3	9.0	2.5	0.7	0.4				U-P	94
TRANSI-TIONAL	9	6	39.3	20.5	19.1	9.9	8.1	1.8	0.7	0	0.1	0.1	0.3		U-P	51
	8	7	13.1	6.7	5.7	33.0	29.7	9.4	1.9	0.5					U	98
	13	16	27.3	13.6	5.4	4.7	15.5	21.8	6.2	3.1	1.5	0	0.8		U	94
	13	18	5.0	2.5	0	1.5	1.5	13.6	19.7	25.8	15.1	7.6	3.0	4.5	U	100
	8	19	18.2	10.1	61.0	5.0	2.8	1.9	0.7	0.2					C	86
	8	30	15.1	9.8	54.3	9.6	4.8	4.4	1.6	0	0.4				C	75
	9	12	11.4	6.4	6.1	5.2	64.7	3.5	1.7	0.9					C	95
	9	35	29.2	14.6	1.8	6.3	39.0	9.1							C	98

* U-P = uneven-aged, positively skewed. U = uneven-aged. C = composite
** percentage of stems > 1.4 m. tall predating harvest
Note: Age class during which harvesting occurred is underlined

TABLE 4. DIAMETER CLASS FREQUENCY DISTRIBUTIONS - % NATURAL STANDS

O.G	STAND	S*	1	3	5	7	9	11	13	15	17	19	21	23	25	>26	DIAM PATTERN **	AGE STRUCTURE ***	R2 DIAM/ AGE
11	33	44.0	5.0	2.2	2.2	1.1	3.1	6.7	11.2	9.2	9.0	4.5	1.4	0.8			NOR	E	.82
12	2	41.9	1.7	4.6	1.2	3.5	3.5	5.8	5.8	11.0	8.7	8.1	3.5	0.6	0	0.6	NOR	U	.58
12	5	53.6	4.2	2.3	2.8	2.8	4.2	8.3	7.9	8.3	4.2	0.9	0	0.5			NOR	C	.71
11	3	82.7	2.6	1.5	1.4	1.4	1.2	1.9	2.4	2.1	1.4	1.0	0.3	0.2			IRR	U	.47
11	10	39.7	7.2	8.4	4.8	6.6	6.0	9.0	6.0	6.6	3.0	1.8	0.6				IRR	U	.59
11	17	75.2	2.8	1.7	1.7	1.5	2.2	5.0	3.3	4.5	1.5	0.2	0.2				IRR	E	.79
12	13	52.6	2.4	4.7	0.5	2.8	4.3	1.9	5.7	4.3	4.3	4.7	4.3	2.8	2.8	1.9	IRR	U	.69
12	28	53.1	2.3	4.9	2.3	3.3	1.4	0.9	5.9	7.7	5.9	4.4	3.7	1.9	1.4	0.5	IRR	U	.47
8	4	3.6	0	3.9	8.7	7.7	19.3	20.2	17.3	11.6	6.7	1.0	0	1.0			NOR	E	.25
8	26	56.5	1.7	2.2	2.2	2.2	2.4	4.8	5.4	8.3	7.8	4.3	1.5	0.6			NOR	E	.67
8	34	44.5	0.5	2.2	2.8	3.9	3.9	7.2	11.7	11.6	5.5	3.9	1.7	0	0	0.5	NOR	E	.71
13	31	13.5	0.9	0	0	3.5	0	8.7	9.5	20.8	15.1	16.4	6.5	0	4.3	0.9	NOR	E	.45
13	36	36.1	1.3	2.6	1.9	4.5	5.1	8.3	7.0	7.0	8.3	7.0	6.7	2.2	0.6	1.3	NOR	C	.67
13	9	8.6	0	0.9	2.7	3.2	3.2	12.8	9.1	17.4	11.0	17.4	11.0	1.8	0	0.9	IRR	E	.12

* Seedlings < 1.4 m. tall
** NOR = Normal distribution   IRR = Irregular distribution
*** E = even   U = uneven   C = composite

TABLE 5 - DIAMETER CLASS FREQUENCY DISTRIBUTIONS - % SECOND-GROWTH STANDS

O.G.	STAND	S*	1	3	5	7	9	11	13	15	17	19	21	23	25	>26	DIAM PATTERN **	AGE STRUCTURE ***	R2 DIAM/AGE
11	25	47.2	9.5	7.1	6.3	4.5	4.5	4.7	5.8	4.5	2.1	1.6	1.1	0	0.8		POS	U-P	.52
11	29	55.4	9.4	10.7	6.7	5.1	3.3	3.6	2.4	0.9	1.8	0.2	0.2	0.2			POS	U-P	.44
11	39	57.3	10.0	7.7	5.5	3.4	4.3	3.0	3.0	2.6	1.5	1.3	0.4				POS	U-P	.58
11	11	55.1	10.3	12.1	4.9	3.6	2.7	3.6	3.1	1.8	1.8	0.9					POS	U-P	.53
12	8	49.4	8.6	7.3	6.6	6.6	4.0	3.8	3.5	3.5	2.0	1.5	0.5	2.0	0.25	0.25	POS	U-P	.52
12	15	53.7	7.4	7.4	6.0	6.0	4.4	4.6	4.6	2.8	2.3	0.5	0	0.2			POS	U-P	.33
12	21	48.5	8.8	8.7	7.7	5.1	3.6	5.1	3.6	3.1	1.8	1.8	1.8	0.3			POS	U-P	.52
12	37	57.9	6.7	7.6	5.5	4.4	4.0	3.2	2.9	2.5	3.8	1.5	0.2				POS	U-P	.52
12	38	59.6	8.7	7.3	6.7	3.6	3.2	3.0	3.0	2.0	0.8	0.8	0.8	0.2			POS	U-P	.55
12	40	62.4	5.6	6.6	4.1	3.8	2.6	3.6	2.6	3.0	1.9	1.5	1.1	0.7	0.4		POS	U-P	.50
11	20	50.7	1.5	2.0	3.9	2.5	4.4	6.4	8.4	4.4	6.9	3.4	2.5	1.5	1.0	0.5	NOR	U-P	.41
12	23	60.3	2.4	3.2	3.2	4.0	3.2	5.8	4.6	6.7	3.6	1.6	0	1.2	0.4		NOR	U	.36
11	1	47.2	7.9	8.4	6.9	3.7	3.7	6.3	4.7	4.7	3.7	1.1	0.5	0.5			IRR	U-P	.57
11	14	52.9	4.7	6.1	3.5	4.2	5.4	5.6	5.2	4.2	5.2	0.9	1.9				IRR	U	.59
11	22	62.2	8.5	4.2	4.2	3.4	3.8	4.2	5.3	2.3	1.1	0.9					IRR	U-P	.54
12	27	18.8	4.1	9.7	9.3	5.7	5.7	6.5	6.1	15.4	10.6	3.2	2.4	0.8	1.6		IRR	U	.49
8	19	24.3	10.6	12.9	10.6	11.3	9.1	8.7	4.5	4.5	1.5	0.8	0.8	0.4			POS	C	.30
8	7	19.4	3.2	4.8	0.8	2.0	4.0	4.0	10.5	14.5	15.3	9.7	4.8	4.0	2.0	0.8	NOR	U	.36
13	18	7.5	0	2.8	2.8	1.4	1.4	2.8	10.2	10.2	8.3	25.9	13.9	5.5	7.4		NOR	U	.34
8	24	33.1	10.0	7.7	5.7	5.4	5.3	4.7	5.7	6.7	6.0	4.7	2.0	2.3	0	0.7	IRR	U-P	.63
8	30	15.8	5.0	13.5	7.6	9.3	10.1	10.1	7.6	9.7	5.0	2.5	1.7	1.7	0.4		IRR	C	.53
8	32	55.3	5.6	7.4	3.1	0.9	2.2	4.0	4.0	3.1	5.8	3.6	3.1	1.8			IRR	U-P	.55
9	6	56.6	8.0	7.4	3.9	2.6	5.0	4.6	3.0	3.9	1.7	1.3	0.9	0.4	0.4	.02	IRR	U-P	.51
9	12	15.1	2.5	0.8	4.2	5.9	5.9	4.2	10.6	5.1	9.8	13.2	9.8	6.8	2.5	2.5	IRR	C	.67
13	16	40.9	3.0	6.2	3.0	2.4	1.8	3.0	5.3	10.6	6.2	10.6	4.1	1.8	0.6	0.6	IRR	U	.56
9	35	43.8	1.1	1.7	1.7	1.7	2.8	5.6	5.6	6.2	3.6	4.5	11.8	4.5	1.7	3.6	IRR	C	.56

*   Seedlings < 1.4 m. tall
**   POS = positively skewed distribution   NOR = normal distribution   IRR = irregular distribution
***   U-P = uneven-positive   U = uneven   C = composite

FIGURE I

Age and size class frequency distributions and diameter/age relationships for 5
black spruce stands

A,B,C — Stand 26, natural origin, even-age structure, normal diameter distribution

D,E,F — Stand 29, natural origin, uneven-age structure, irregular diameter
distribution

G,A,I — Stand 13, natural origin, uneven-age structure, irregular diameter
distribution

J,K,L — Stand 38, second-growth origin, uneven-age/positive skew age structure,
positive skew diameter distribution

M,N,O — Stand 12, second-growth origin, composite age structure, irregular diameter
distribution

S refers to seedlings under 1.4 m. tall
n = number of trees aged

B.

D.

H.

G.

J.

70

60

50

40

30

FREQUENCY %

20

10

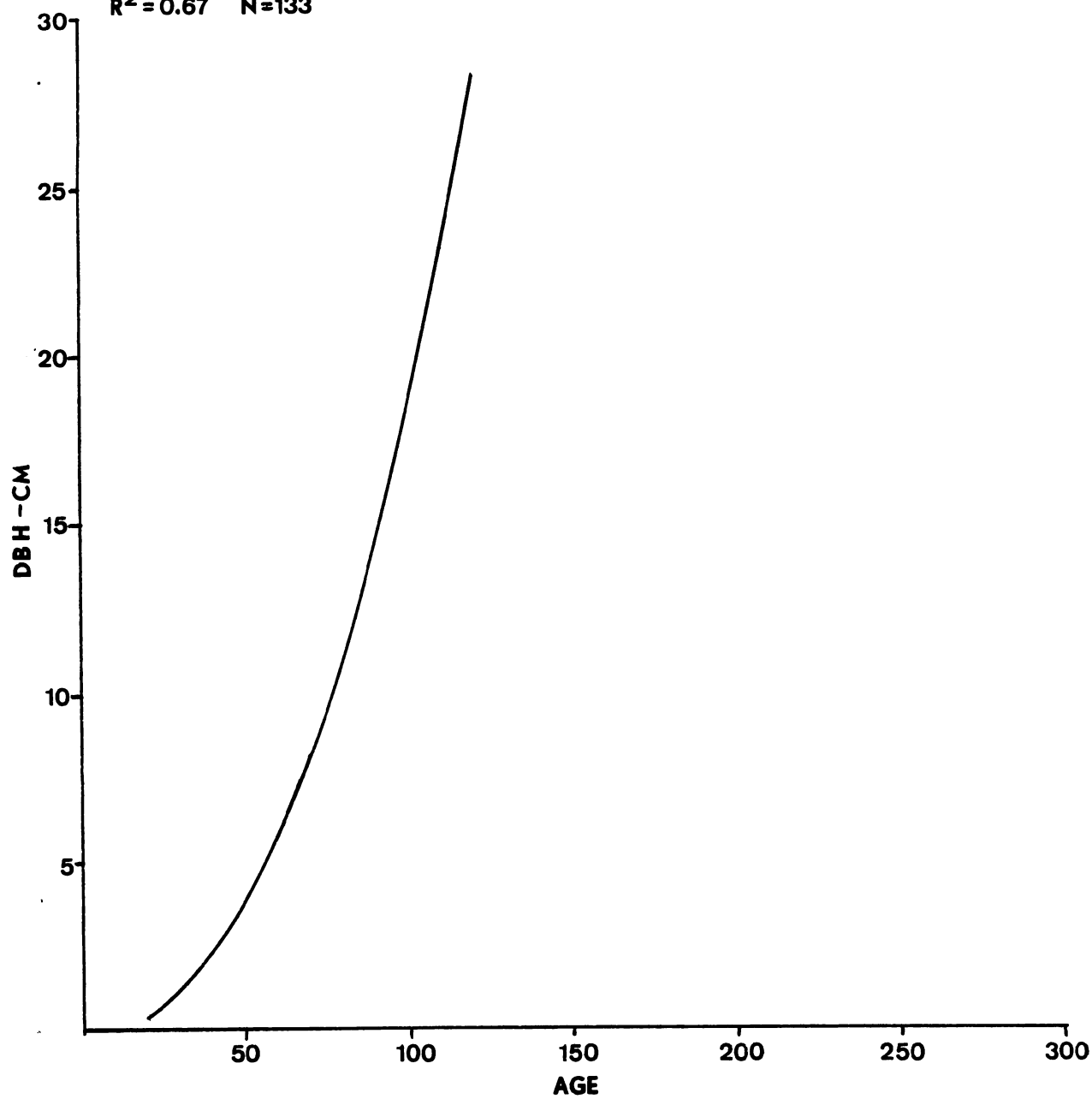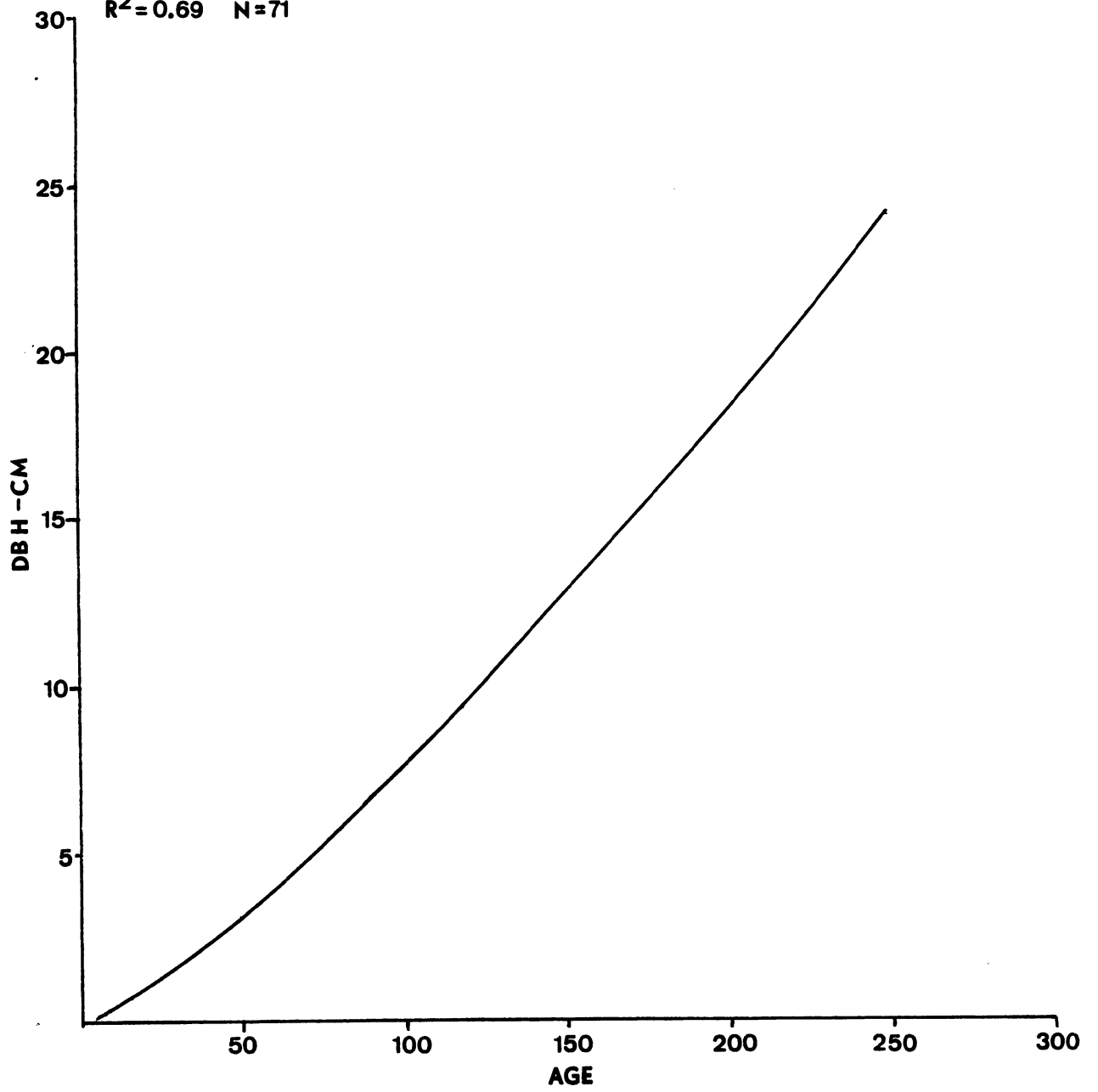10   50   90   130   170   210   250   290

AGE CLASS
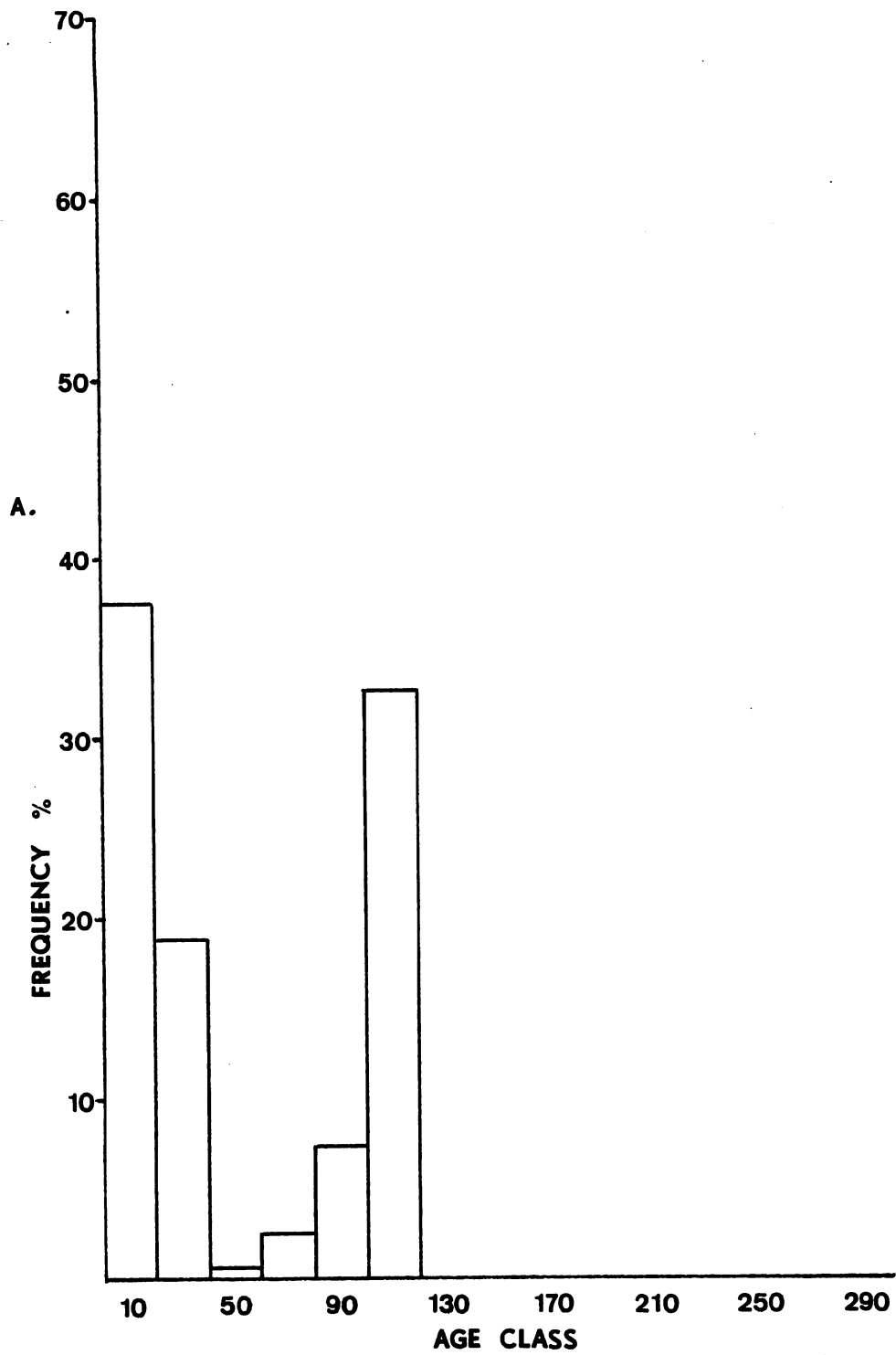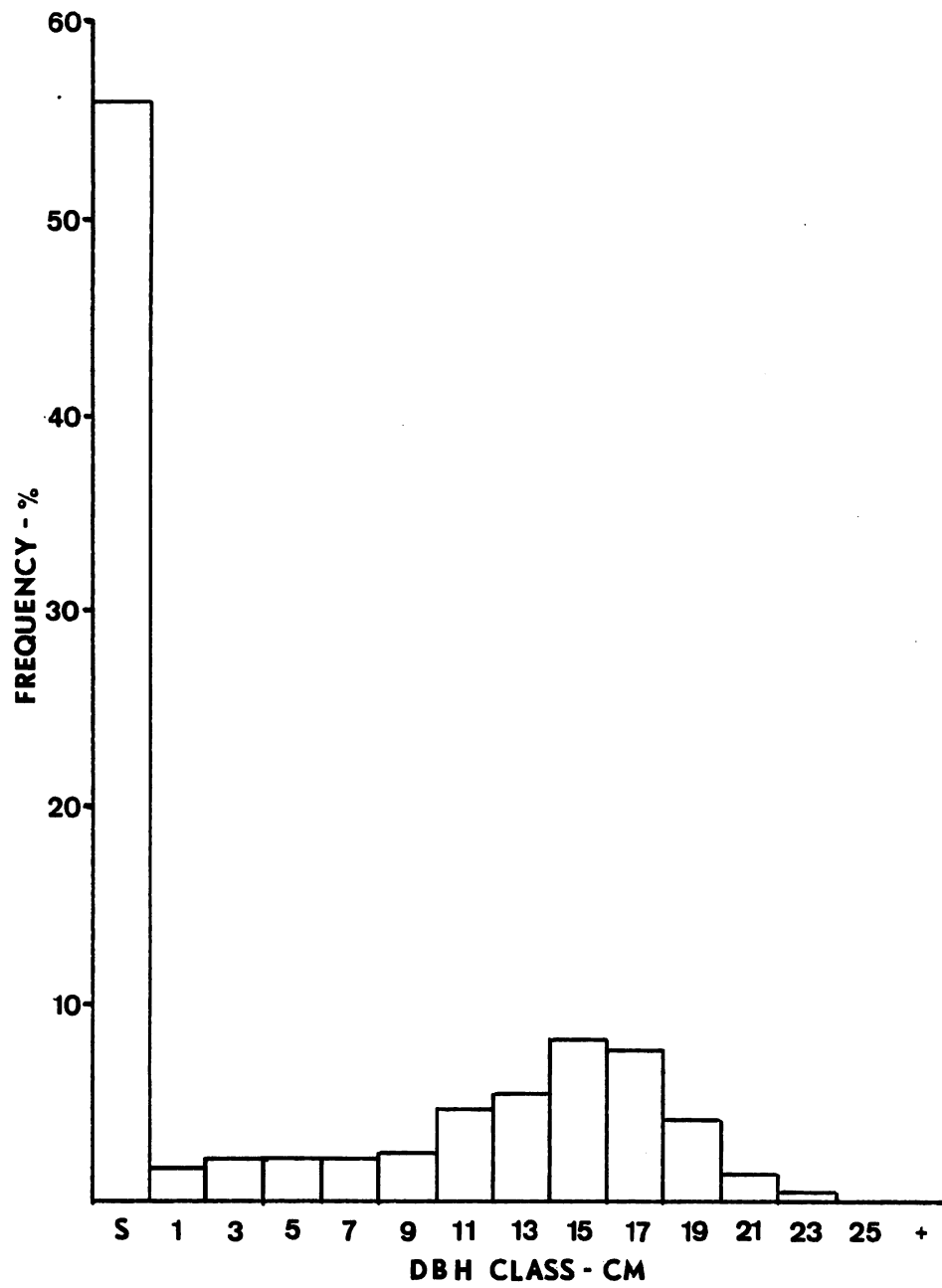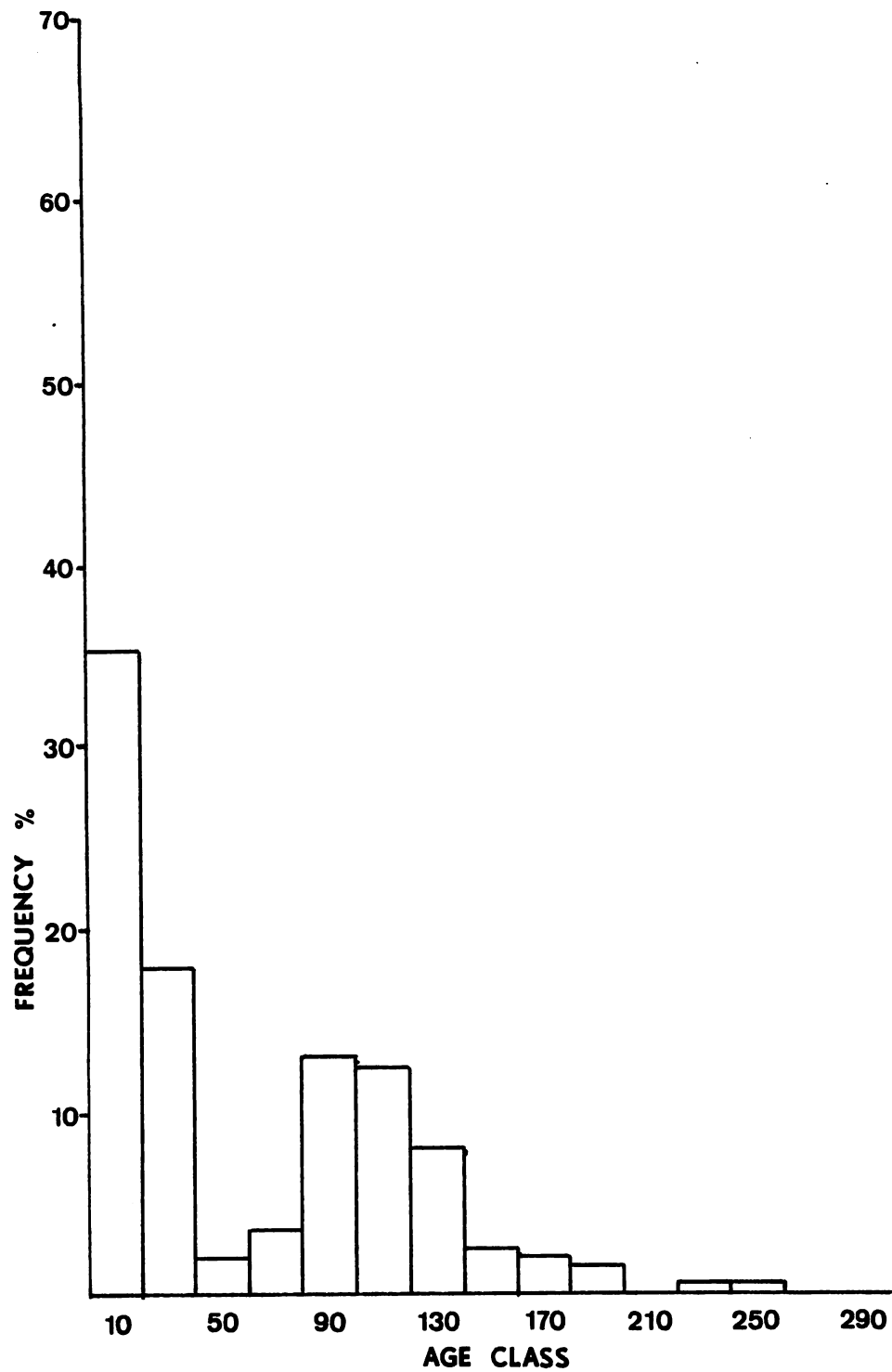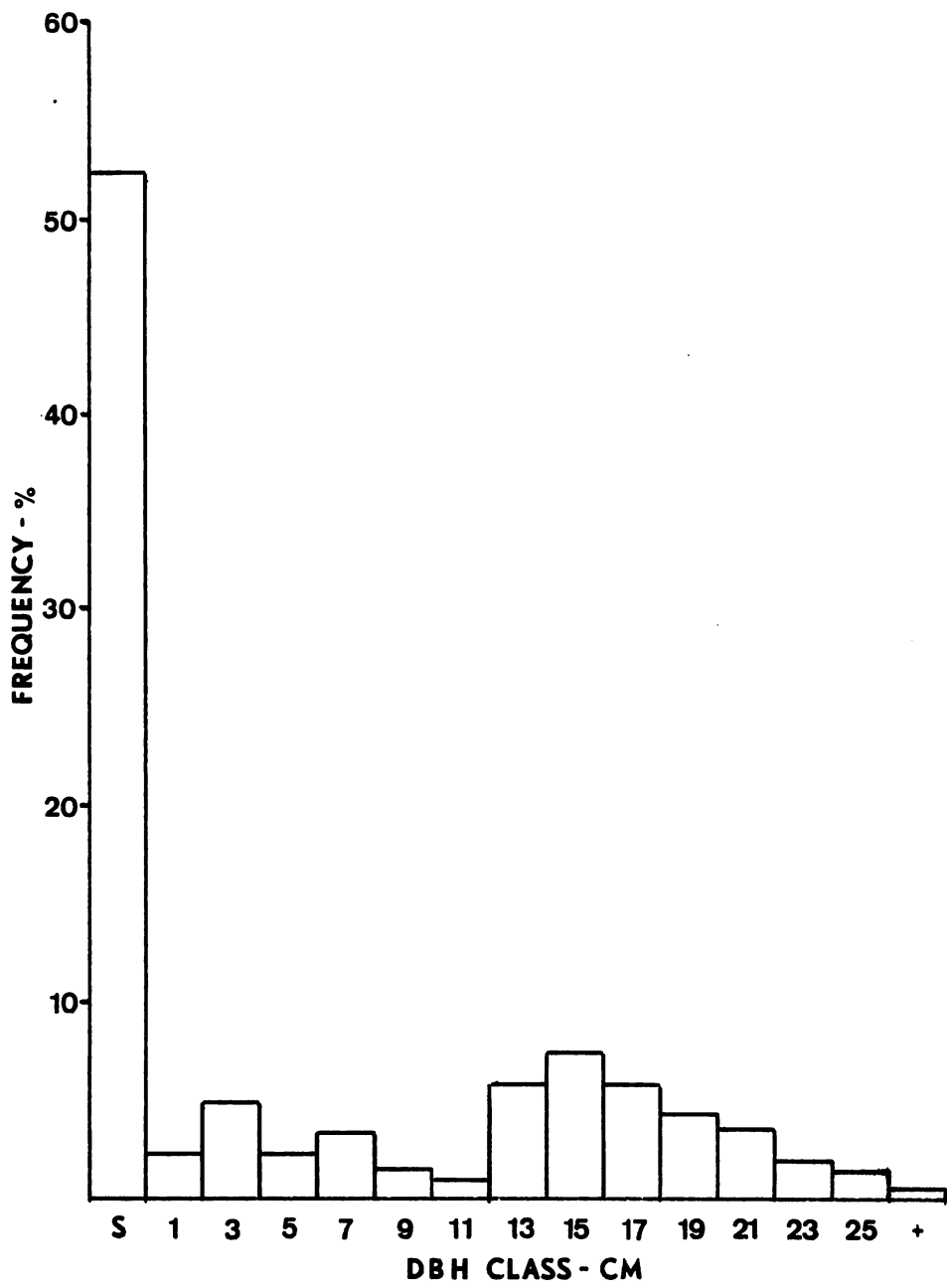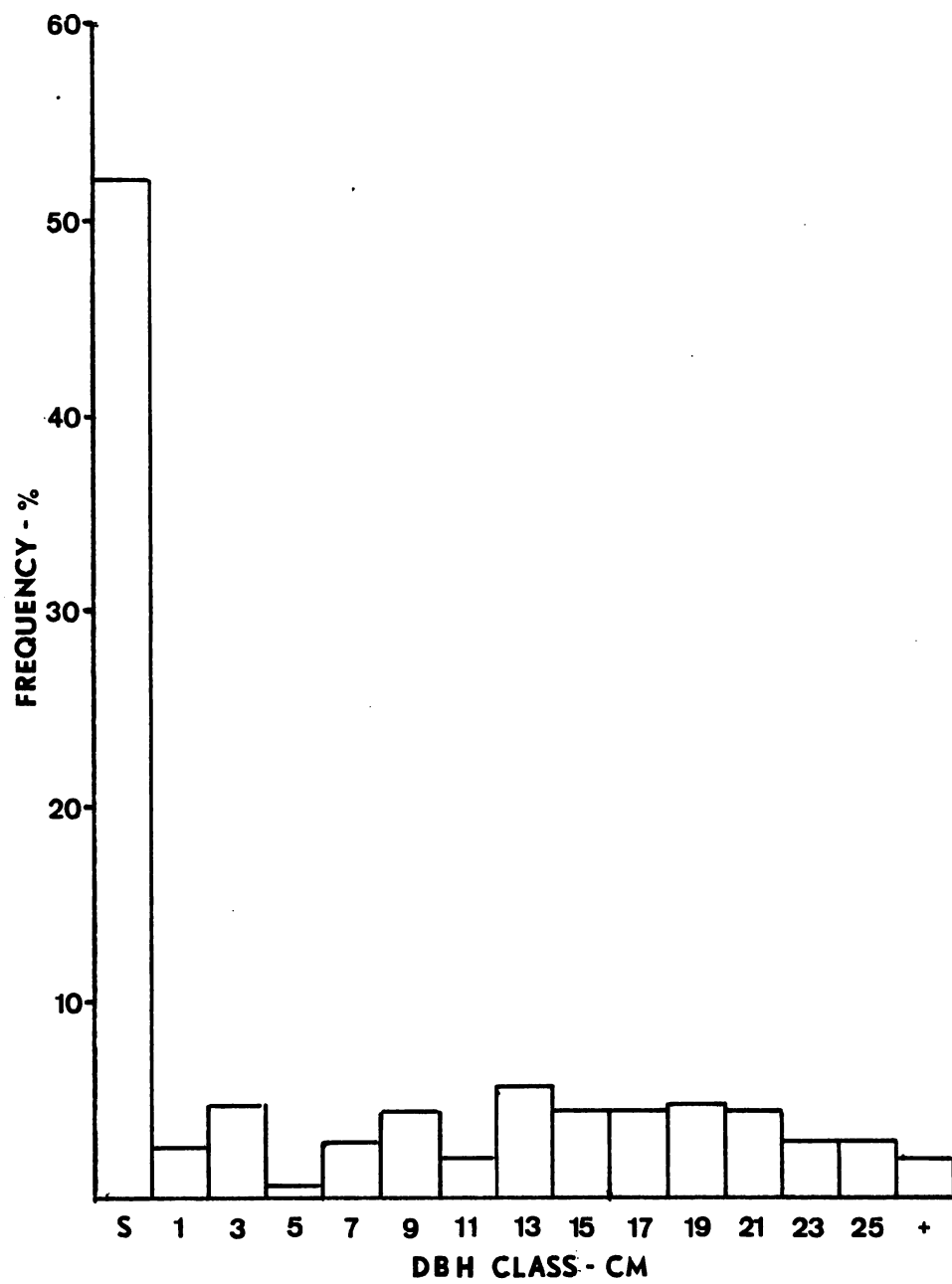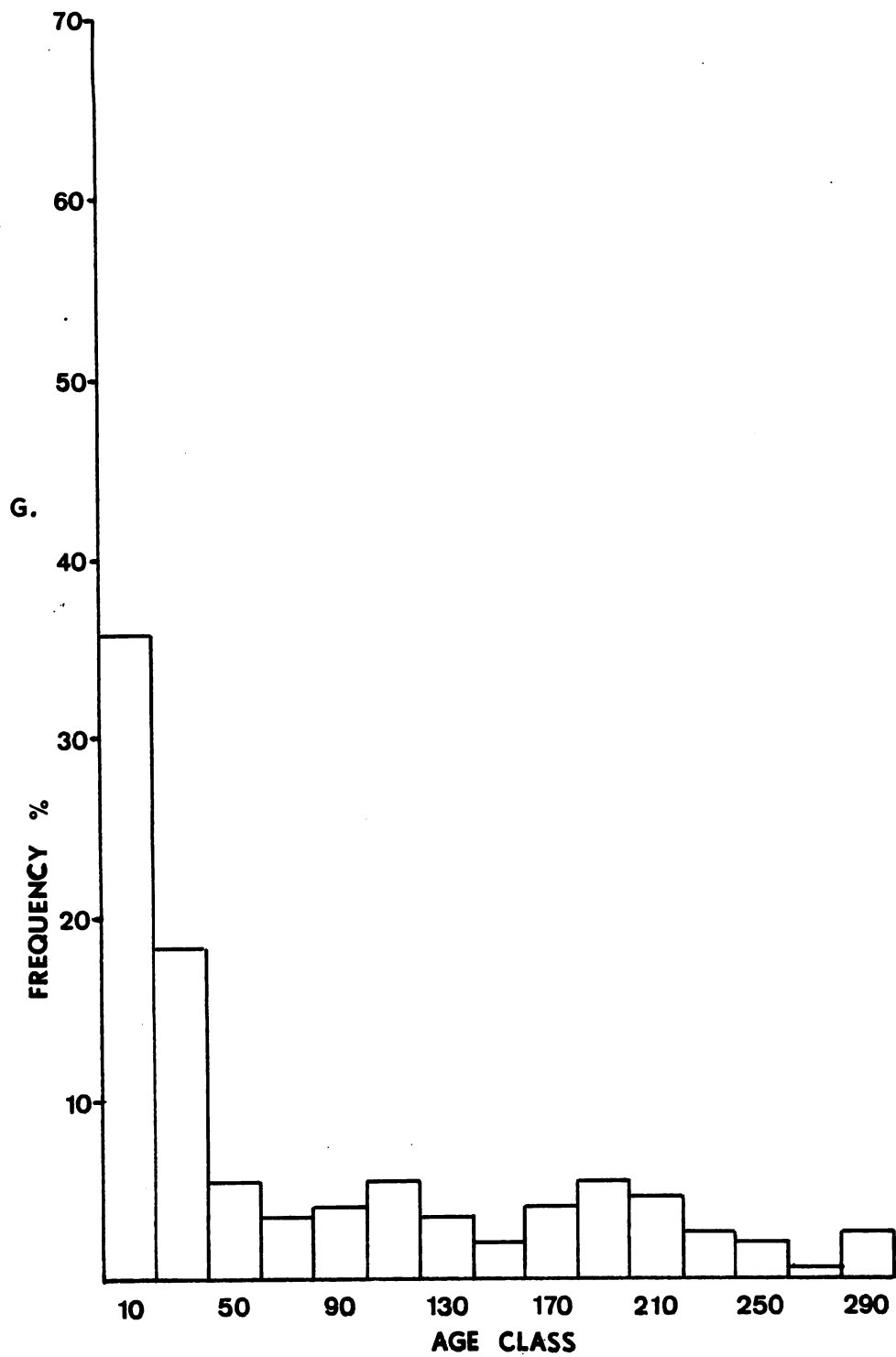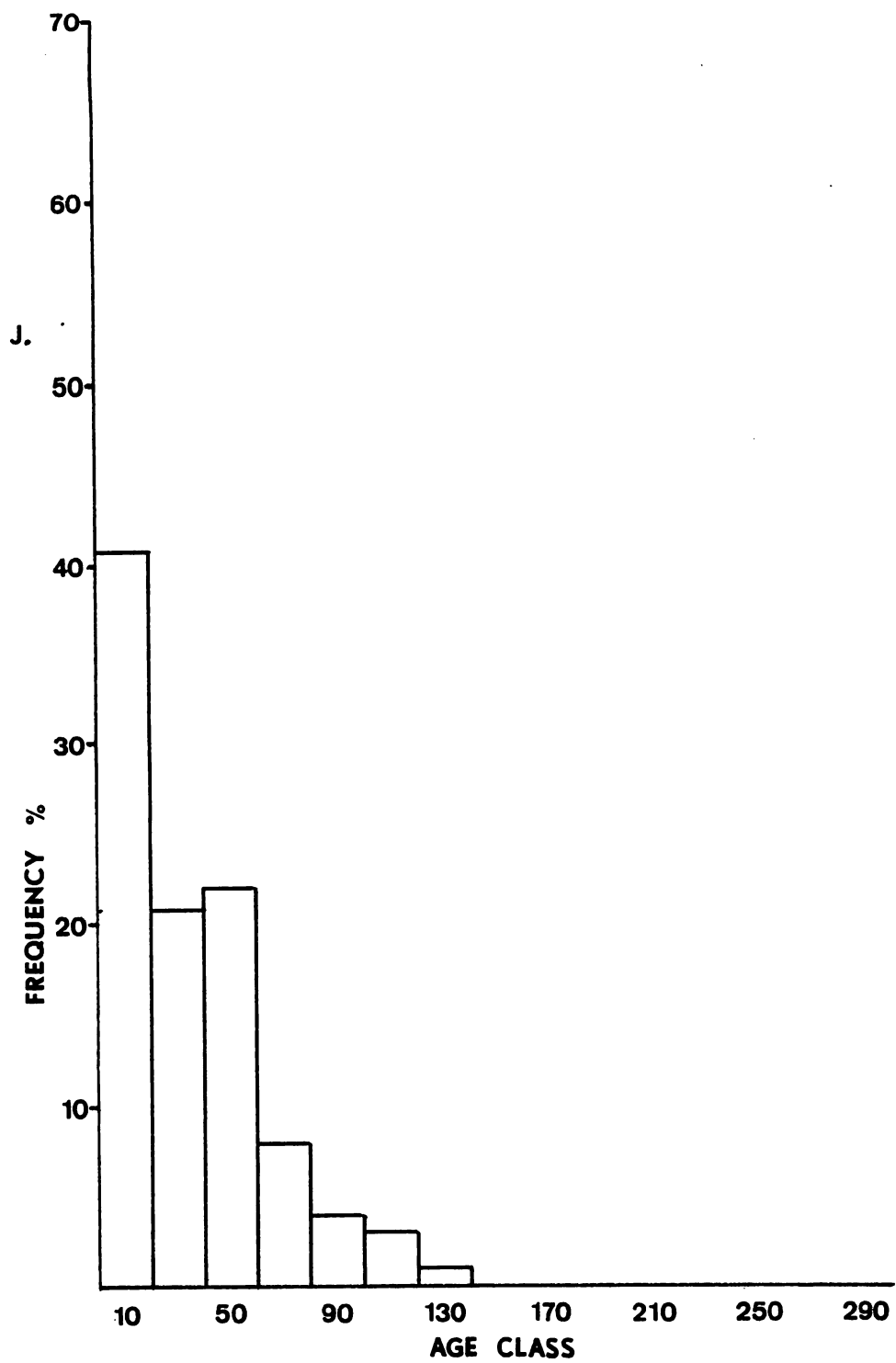
K.
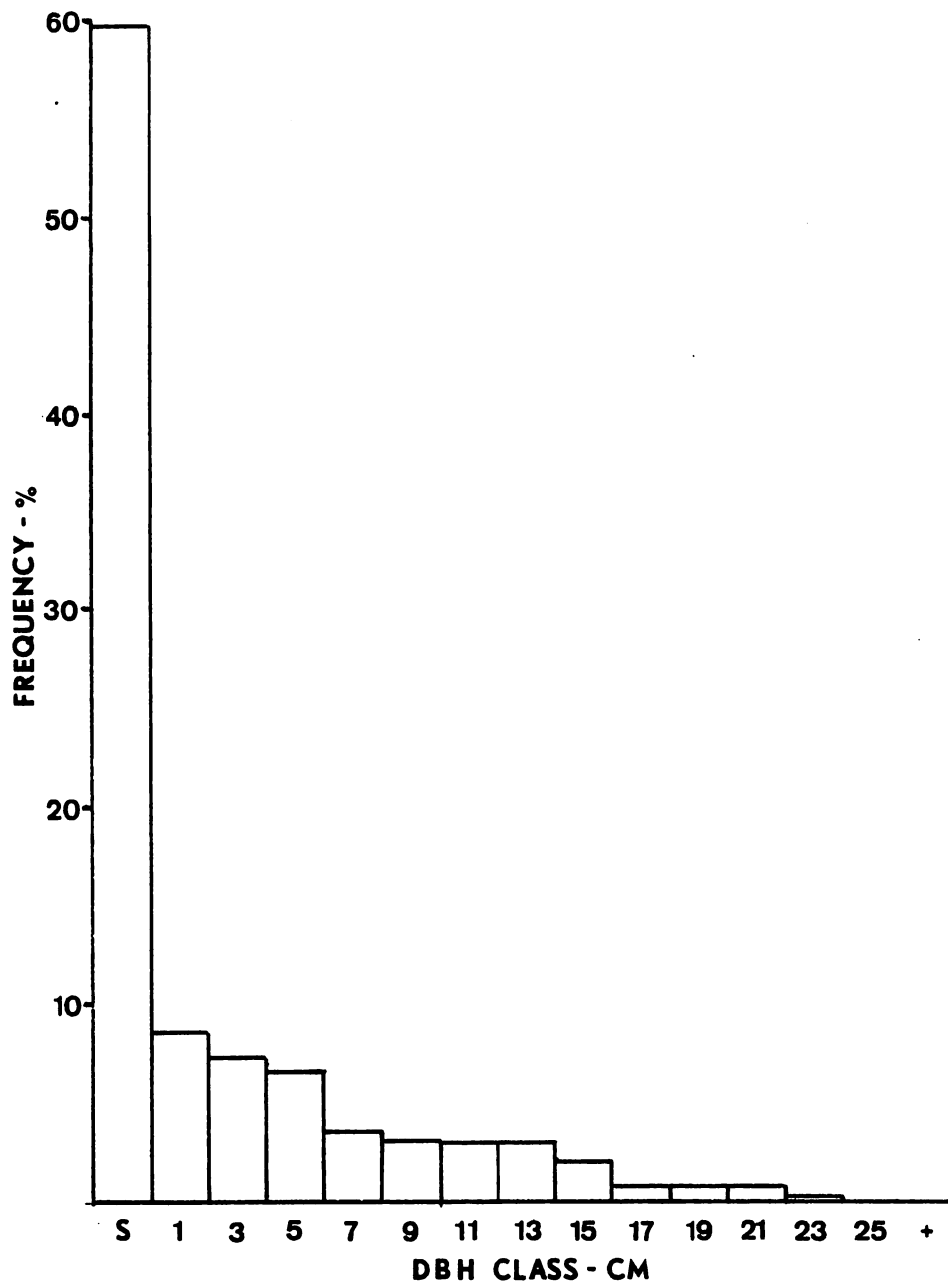
M.
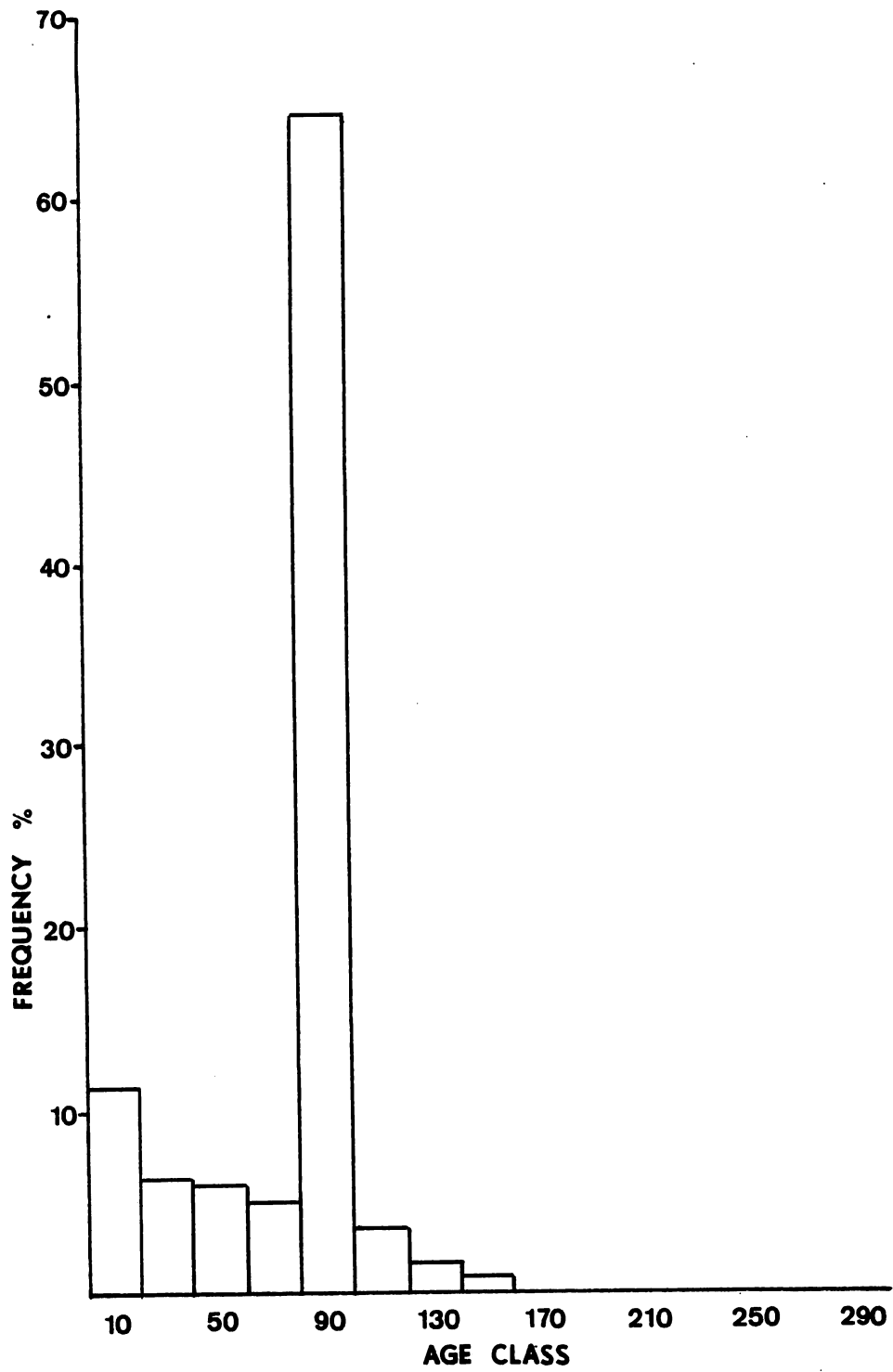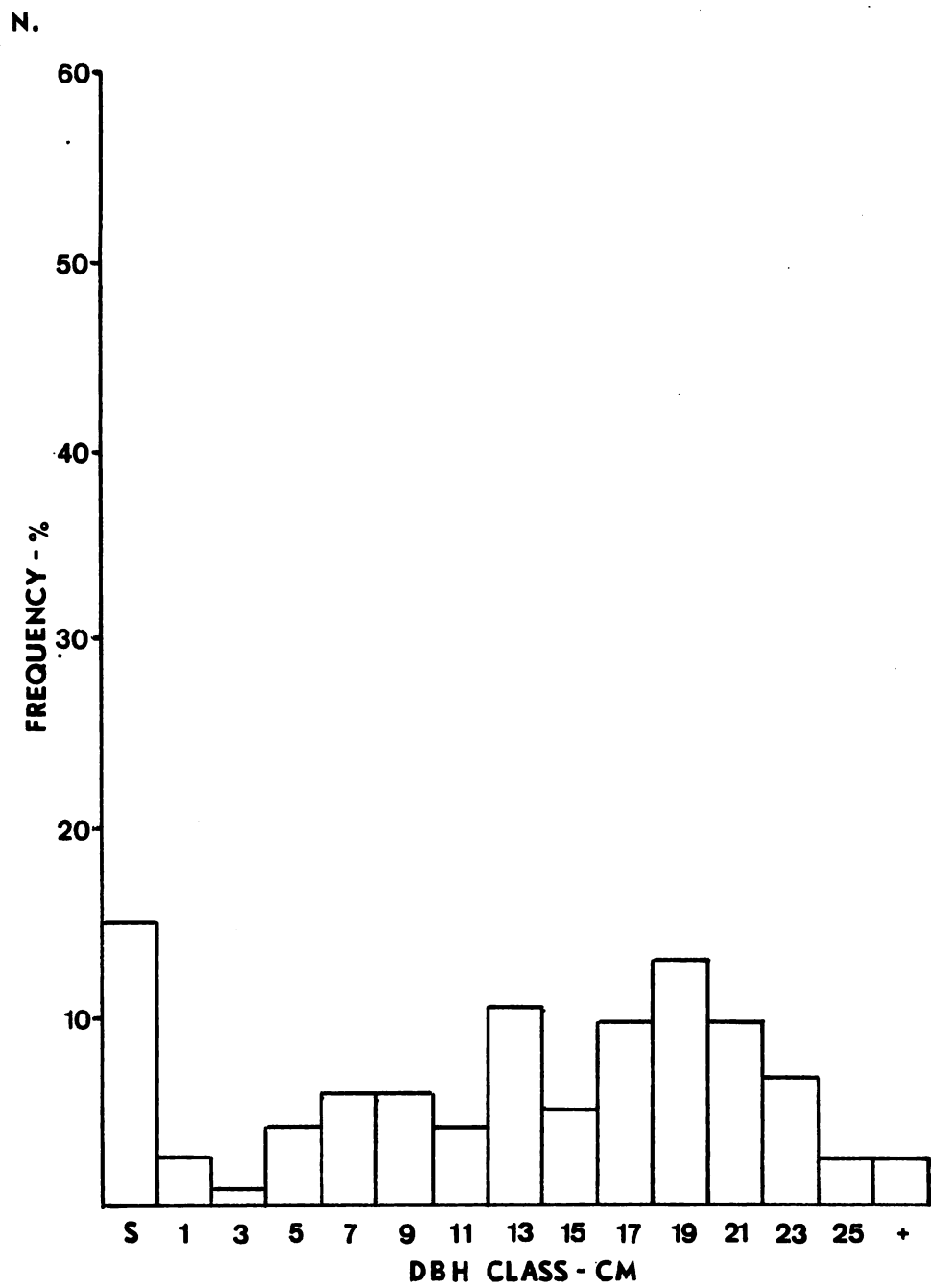
O. $\log Y = -3.3789 + 2.3260 \log X$

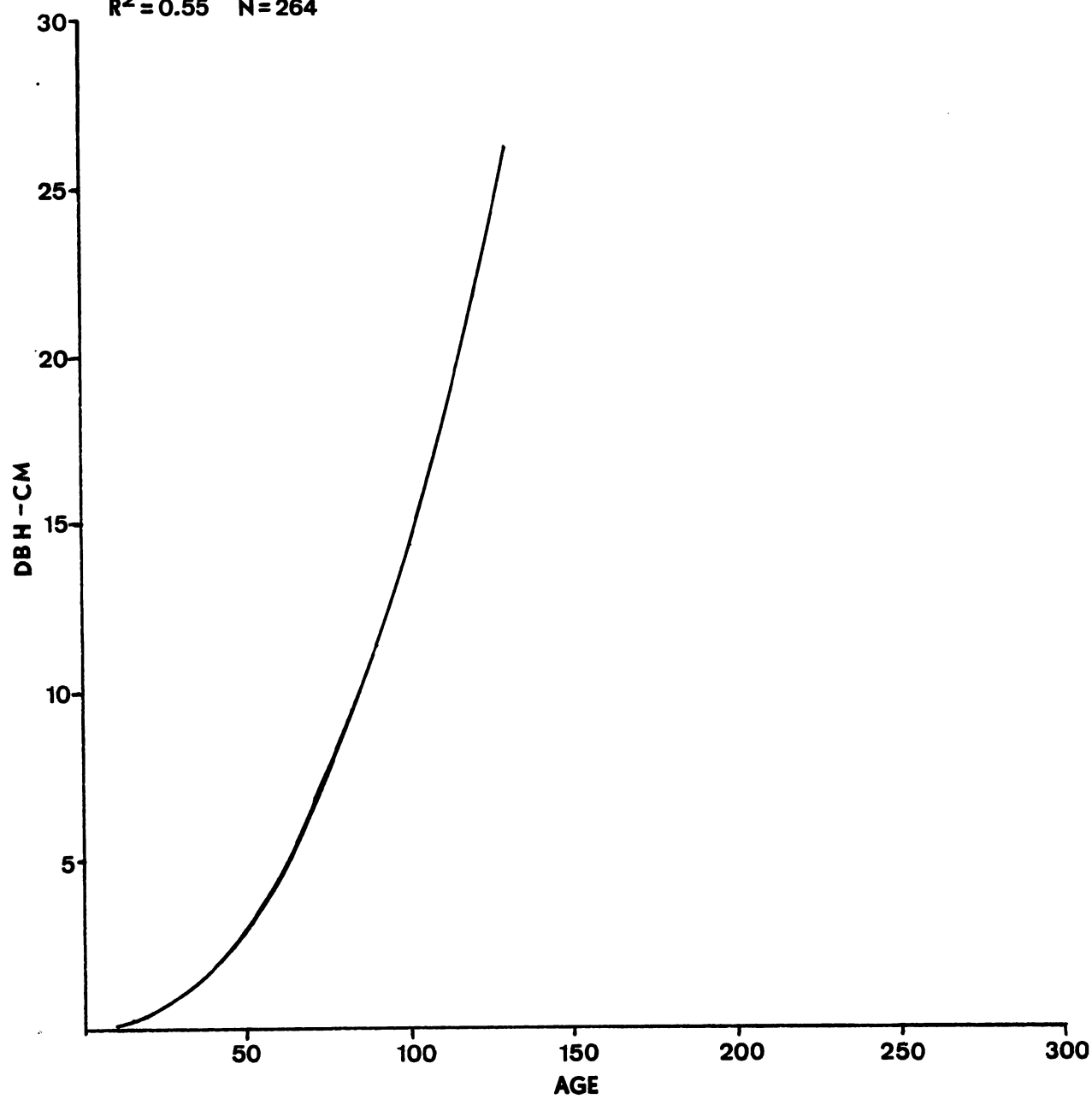$R^2 = 0.67 \quad N = 133$

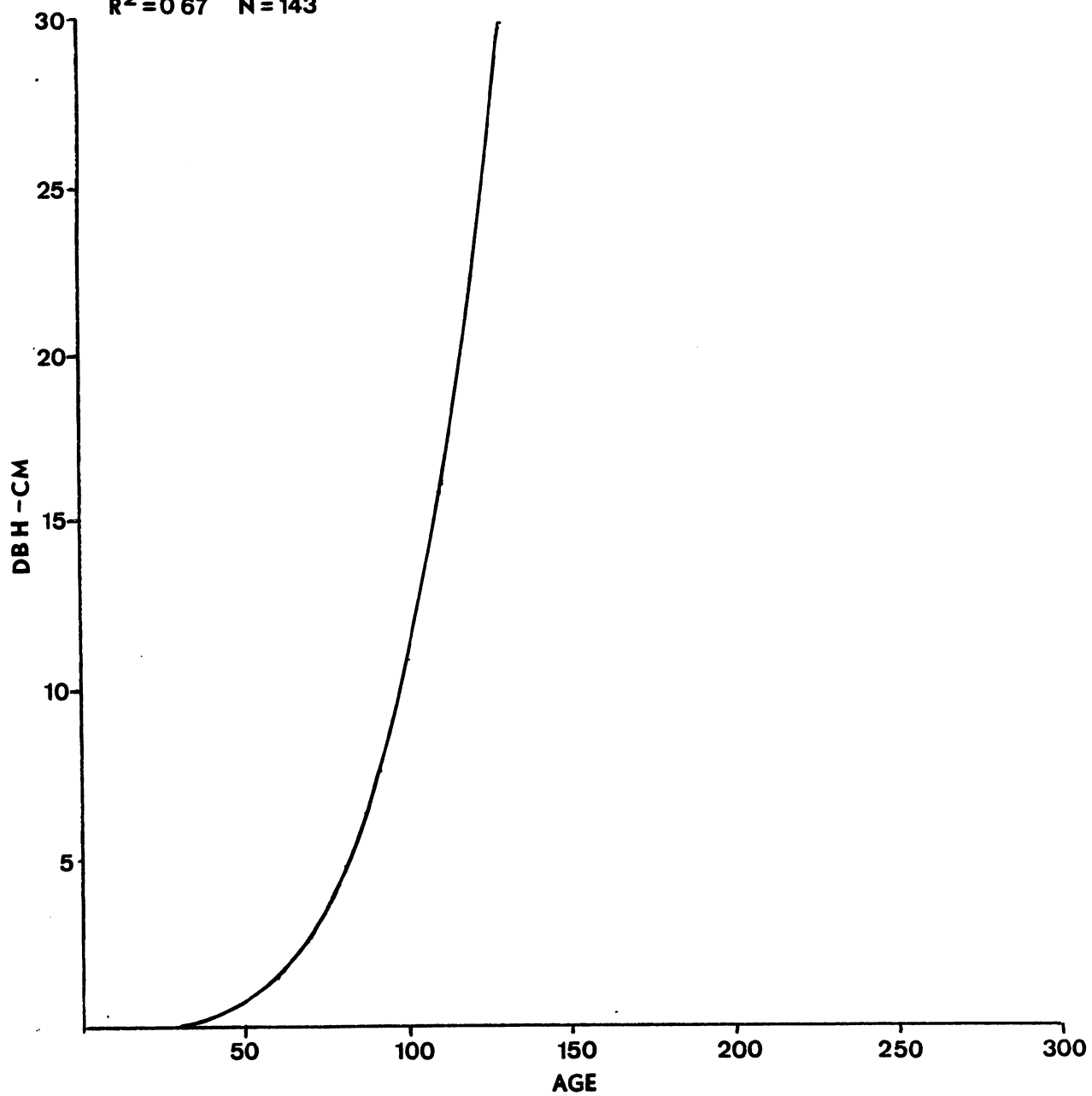I. $\log Y = -1.6370 + 1.2628 \log X$

$R^2 = 0.69 \quad N = 71$

L. $\log Y = -3.4458 + 2.3034 \log X$

$R^2 = 0.55 \quad N = 264$

C. log Y = −6.8332 + 3.9379 logX

$R^2 = 0.67$ N = 143

F. log Y = −2.9637 + 1.9575 log X

$R^2 = 0.47$ N = 93