Evaluation of Full-Sib Families of Douglas-fir in a Nelder Design.

Roy Stonecypher and Rex McCullough

ABSTRACT

Thirty Douglas-fir full-sib families and an unselected check were evaluated in a Nelder's design covering a range of densities from 735 to 26,300 trees/ha. Regression analysis resulted in good overall fits of volume and caliper to density with the power function ($y = ax^b$), and indicated differential response of families to density.

Key words: _Pseudotsuga menziesii,_ spacing, spacing x genetic interaction, heritability, juvenile-mature correlations.

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INTRODUCTION

The use of systematic designs for spacing experiments was first proposed by Nelder (1962) and later recommended by Namkoong (1966) as potentially valuable for examining genetic variation in density response in forest tree improvement research.

The sampling of an adequate range of densities in genetic studies utilizing rectangular plots, requires large areas, many trees for each genetic entry, and results in differential precision of estimates and inefficient use of genetic material and experimental area (Namkoong 1966). The systematic designs proposed by Nelder (1962) offer an alternative which effectively addresses the problems associated with multiple-tree plot spacing experiments. In using such systematic designs, however, it should be recognized that certain assumptions normally associated with traditional randomized designs are not valid and analyses must be appropriately modified.

The objectives of the Nelder planting of selected families of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) reported here were:

1. To examine genetic response to density.

2. To examine the impacts of density on genetic variances and juvenile-mature correlations over time.

3. To examine the effects of density on mensurational traits.

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4. To compare performance of genetic material grown under varying densities with performance in field tests.

This paper will report results related to the first three objectives stated above.

METHODS

Four circles of a Nelder's design were established in 1973 at the Weyerhaeuser seed orchard near Jefferson, Oregon at latitude 44°45' N and longitude 123°2' W. The site is in the central Willamette Valley of Oregon and has an elevation of approximately 61 m. The area used was formerly under agriculture and has minimum soil and topographic variation. The soils consist of sandy river alluvium and are well drained.

Four circles of the design were established utilizing full-sib families and two unselected check sources. The genetic entries were derived from 60 selected parents of Weyerhaeuser Company's low-elevation Coos Bay, Oregon breeding program. The parents are located near the central coast of Oregon and range in latitude from 43°21' N to 43°27' N and in elevation from 122 to 366 meters. The unselected control entries were derived from two seed lots which were obtained from stands of the type normally used in operational collection of seed for planting at Coos Bay.

The actual genetic material was obtained from excess seedlings of a two-parent mating design which is part of an operational genetic test for Weyerhaeuser's Coos Bay tree breeding program. There were thus 30 full-sib families and 2 unselected checks established in the four circles.

The spacings and densities used in the design are presented in Table 1. The genetic entries were randomly assigned on rays in two of the circles, and on the arcs in the other two. Thus, in circles 1 and 2 individuals are competing with their full-sibs within the ray, while in circles 3 and 4 competition is random in relation to families. Unfortunately, the need to utilize circle 1 material to replace mortality in the other circles precluded the general use of circle 1 in the analyses.

Decisions as to the range of spacings used and the physical layout were largely driven by the amount of material and experimental area available.

Table 1. Spacing and number of trees for 11 arcs used in the Nelder Design.

Arc	Spacing		Trees	
	m^2	(ft^2)	/ha	/acre
2	0.38	(4.1)	26,300	(10,625)
3	0.54	(5.8)	18,500	(7,510)
4	0.76	(8.3)	13,160	(5,248)
5	1.13	(12.0)	8,850	(3,630)
6	1.59	(17.1)	6,290	(2,547)
7	2.26	(24.4)	4,425	(1,785)
8	3.25	(35.0)	3,077	(1,245)
9	4.62	(50.0)	2,164	(871)
10	6.64	(71.5)	1,506	(609)
11	9.52	(102.5)	1,050	(425)
12	13.60	(146.4)	735	(298)

The circles thus established had 33 rays and 13 arcs (Figure 1). The first and last arcs were guard trees and one of the rays was a filler. The shape of the growing space was held constant in the design used and thus conform to type Ia of Nelder (1962).

Measurements of total height were made annually with the exception of the sixth year. Caliper at 50 cm above ground line was measured starting in the third year and continued as the height measurements. Volume was calculated using equations developed by Kovats (1977).

As indicated earlier, systematic designs are generally not suited to traditional analysis of variance techniques. Although we did use analysis of variance for satisfying one of the objectives of this study, the majority of the analyses used regression.

Increasing mortality, presumably related to competitive stress, was observed as early as the fourth year in arcs 2-4 and extended to arcs 5, 6, and 7 by the fifth year and beyond. Since analyses would be expected to be influenced by mortality, adjustments of spacing were made to account for space created by loss of competing trees.

RESULTS

Density-Growth Relationships

Plots of volume versus density by years indicate that patterns of response to density were developed as early as the fourth year and became definite and clear by the seventh year (Figures 2, 3, and 4). Caliper response was very similar to volume as would be expected, but height indicated a negative response at both the high and low densities (Figures 5 and 6). It is emphasized, however, that the range of densities examined in this study were extreme at the higher end. In using the extremely high densities of these plantings, competition becomes manifest at an early age and its influence on growth is greatly enhanced. It is tempting to speculate, however, that the responses observed at the higher densities at young ages in this study, may be representative of those at older ages with material grown under more realistic densities.

Examination of plots for volume, caliper and height of eighth year data versus density indicated that curves of the form indicated in Figures 4 through 6 would adequately describe the growth-density responses. The growth data summarized by density are presented along with the $\log_e$ transformed regression equations in Table 2.

Table 2. Means and regressions for eight-year data averaged over all families.

Trees/ha	Volume (dm^3)	Height (m)	Caliper (cm)
26300	9.2	6.7	6.3
18500	9.5	6.7	6.4
13160	12.6	6.9	7.4
8850	15.2	7.1	7.9
6290	17.8	7.1	8.7
4425	23.6	7.3	10.3
3077	27.1	7.0	11.3
2164	34.9	7.1	13.2
1506	41.7	6.9	14.5
1050	49.3	6.8	15.9
735	53.2	6.5	17.4

1. ln (volume) = 7.68 - 0.55 ln (trees/ha); r^2 = 99%

2. ln (height) =
   6.16 + 0.053 ln (trees/ha) - 8.59 x 10^{6} (trees/ha); r^2 = 70%

3. ln (caliper) = 4.95 - 0.31 ln (trees/ha); r^2 = 99%

Genetic Variation in Density Response

The major objective of this study was to determine if spacing x genotype interactions were evident. Regressions of the form

ln (volume) = a+ b ln (trees/ha)

were calculated for each of the 30 families and unselected check (Table 4). The analysis of variance of the regression coefficients over groups indicates that there are significant differences among entries in slope and/or intercept (Table 3).

Table 3. Analysis of variance of regression coefficients over groups.

Source	DF	Mean square	F
Groups	61	1.366	4.24**
Within groups	901	0.322	

** Significant at 0.01 level

An examination of Table 4 indicates large differences among families in volume and in slope or response to density. Plots of selected entries are presented in Figure 7. Family 1 is an extremely fast growing family with a response slope equal to the population average while family 30 is a relatively high performing family with a slope well below the average. It appears that family 30 is performing relatively poorly at the lower densities. Note also that the unselected check has a steeper slope than average and is performing very poorly at the higher densities.

Particularly strong evidence for spacing x density interaction is presented in Figure 8. Although families 102 and 57 had rather similar performance in average volume at 8 years, family 57 is performing much better at higher densities.

Density-Genetics Variance Relationships

Recently, information has been published that indicates that onset of inter-tree competition in genetic tests results in changes in genetic variances of growth traits and in juvenile-mature correlations (Franklin 1979). Insofar as the extremely high densities of this study may represent onset of competition in older, more conventionally spaced tests, it was felt that an examination of heritabilities at contrasting densities over time would be useful. Separate analyses of variance and cross products were, therefore, carried out for the three growth traits for each of two classes of density, three circles, thirty full-sib families, and the five measurement years. Density classes were divided into high and low using the curves of Figures 2 and 3 as guides. Arc 6 (see Table 1) was used as the division point. The high density class was thus represented by densities of 6,290 to 26,300 trees/ha and the low density class by 735 to 4425 trees/ha. Estimates of the full-sib family components and heritability by spacing class for the three growth traits were then developed (Table 5). Comparisons of heritability for the high and low density classes indicate a decrease with increasing age for the lower density class. There is thus an indication that as the material in the lower density comes under competition heritability decreases. However, Table 6 indicates little evidence for change in genetic correlations related to density classes.

CONCLUSIONS

Relationships between density and average tree volume and caliper were well defined by the seventh year of the test (Table 2 and Figure 3). The estimated response slopes for volume and caliper were -0.55 and -0.31 respectively.

Regression analyses of the response of individual families to density indicated the presence of family x density interactions (Table 4 and Figures 7 and 8). There did not appear to be a correlation between family mean growth performance and response to density (Table 4). Whether such interaction would occur at older ages under more realistic densities is conjectural. If such is the case, however, the implications for breeding programs designed to increase yield per unit area in Douglas-fir would be significant. We plan to continue to examine this planting, and to initiate new Nelder plantings using a more realistic range of densities with genetic material of specific interest to our breeding program.

An examination of the effect of onset of inter-tree competition on heritability estimates indicated slight impact in this study. While there was a tendency for estimates of heritability to decrease with age, there was no evidence that increasing competition changed juvenile-mature correlations (Table 5 and Figures 9 and 10).

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Table 4. Regressions for eight-year volume by family.

Family	a	b	S(b)	Mean dm^3	S.E.	Rank
Check	8.44	-0.71	0.07	19.3	1.19	29
1	7.71	-0.50	0.07	44.7	3.03	1
3	7.39	-0.50	0.07	31.9	2.44	9
5	6.64	-0.46	0.12	22.9	1.14	24
7	7.76	-0.58	0.07	23.0	1.63	23
9	8.14	-0.65	0.08	22.6	1.47	26
14	8.35	-0.62	0.08	32.4	2.18	8
16	7.63	-0.54	0.11	33.1	2.27	5
20	6.86	-0.45	0.08	28.4	1.94	14
22	8.07	-0.62	0.08	24.7	1.76	20
23	8.07	-0.68	0.09	16.7	1.31	31
28	7.61	-0.55	0.12	28.8	1.93	15
30	5.98	-0.32	0.09	32.7	1.97	6
44	8.70	-0.70	0.10	27.8	2.53	18
46	6.64	-0.42	0.10	28.8	2.25	16
47	6.18	-0.39	0.14	24.7	1.77	21
48	7.35	-0.51	0.14	30.5	2.25	12
53	7.84	-0.56	0.08	32.5	2.39	7
57	5.72	-0.34	0.10	22.4	1.31	27
58	8.09	-0.60	0.09	30.9	2.33	11
59	8.12	-0.63	0.10	26.1	2.13	19
60	8.32	-0.62	0.09	31.3	2.40	10
61	8.54	-0.62	0.08	37.6	2.62	3
62	8.72	-0.67	0.08	33.3	2.42	4
68	7.96	-0.64	0.07	18.4	1.18	30
70	7.58	-0.61	0.14	20.0	1.74	28
72	6.93	-0.48	0.12	28.2	2.33	17
75	8.56	-0.66	0.08	30.5	1.96	13
83	8.60	-0.62	0.08	40.3	3.00	2
101	7.97	-0.61	0.06	22.8	1.44	25
102	9.03	-0.75	0.10	24.4	1.95	22

Table 5. Heritability estimates for two spacing classes by years.

	High Density			Low Density		
Year	$\sigma^2 f$	$S(\sigma^2 f)$	h^2	$\sigma^2 f$	$S(\sigma^2 f)$	h^2
			VOLUME			
3	0.034	0.012	0.36	0.070	0.020	0.60
4	0.204	0.071	0.43	0.336	0.108	0.47
5	1.125	0.461	0.34	2.106	0.844	0.30
7	4.124	1.770	0.28	17.002	6.009	0.28
8	8.971	4.237	0.25	60.945	20.818	0.25

	High Density			Low Density		
Year	$\hat{\sigma}^2 f$	$S(\hat{\sigma}^2 f)$	h^2	$\hat{\sigma}^2 f$	$S(\hat{\sigma}^2 f)$	h^2
			HEIGHT			
3	282.62	119.49	0.24	450.95	145.70	0.40
4	305.36	177.91	0.13	608.24	193.48	0.36
5	568.80	227.57	0.30	488.08	194.70	0.26
7	731.40	354.32	0.21	337.60	239.67	0.08
8	1364.93	584.07	0.29	827.97	368.08	0.18

	High Density			Low Density		
Year	$\sigma^2 f$	$S(\sigma^2 f)$	h^2	$\sigma^2 f$	$S(\sigma^2 f)$	h^2
			CALIPER			
3	0.040	0.016	0.27	0.076	0.023	0.47
4	0.156	0.059	0.35	0.242	0.077	0.45
5	0.347	0.154	0.28	0.489	0.194	0.24
7	0.623	0.273	0.26	1.401	0.456	0.27
8	0.685	0.354	0.23	3.473	1.030	0.33

Table 6. Juvenile-mature correlations for two spacing classes.

VOLUME

	High Density					Low Density			
Year	4	5	7	8	Year	4	5	7	8
3	1.00	1.00	0.90	0.96	3	0.98	0.88	0.84	0.86
4		0.96	0.80	0.88	4		0.99	0.93	0.88
5			0.95	1.00	5			0.98	1.00
7				0.97	7				0.99

HEIGHT

	High Density					Low Density			
Year	4	5	7	8	Year	4	5	7	8
3	0.93	0.79	0.85	0.78	3	0.98	0.88	1.00	0.73
4		0.75	0.60	0.70	4		0.98	1.00	0.82
5			0.81	0.98	5			1.00	1.00
7				0.86	7				0.96

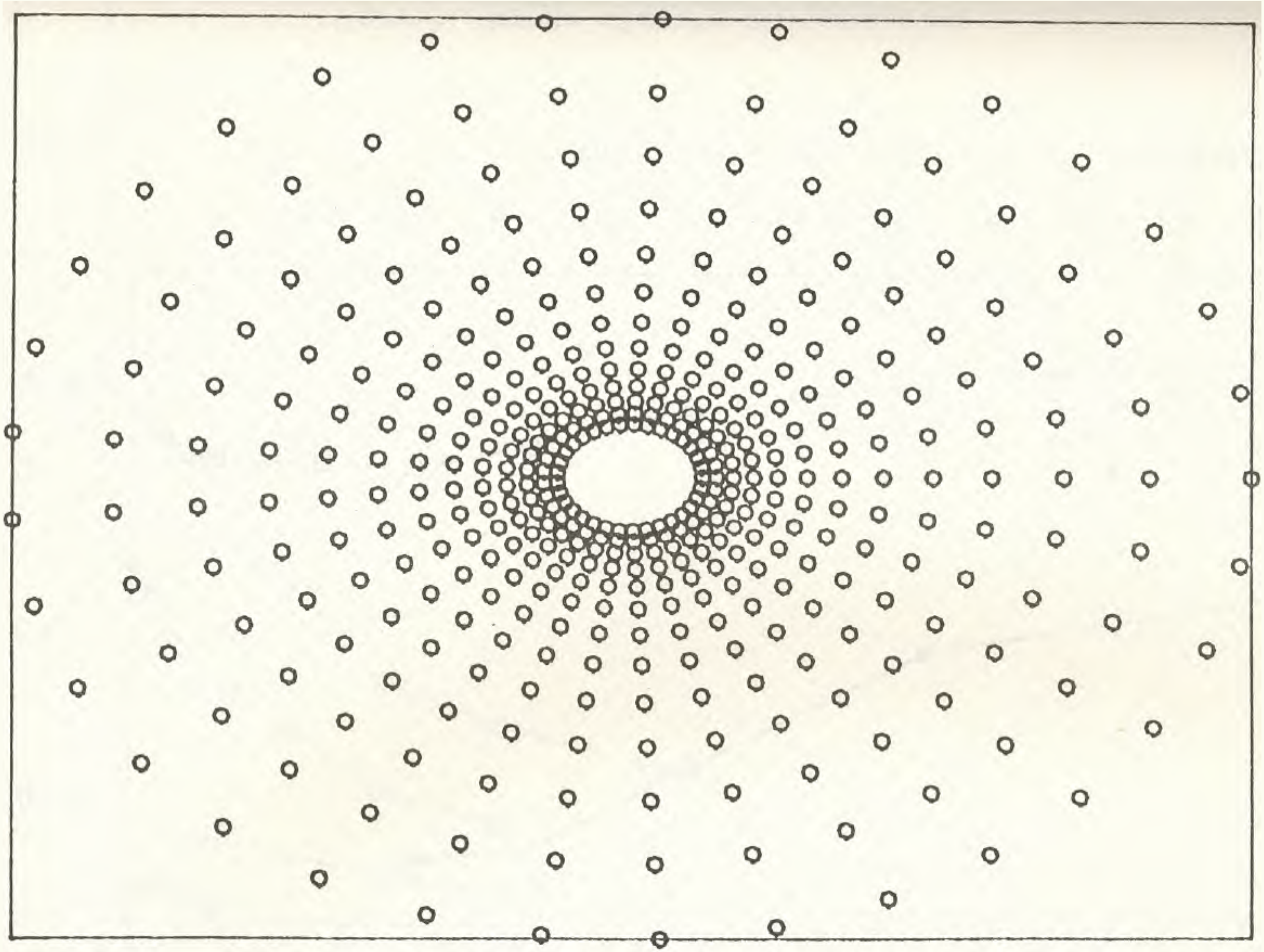

Figure 1: Diagrammatic representation of the Nelder's design used.
There are 33 rays and 13 arcs in the circle

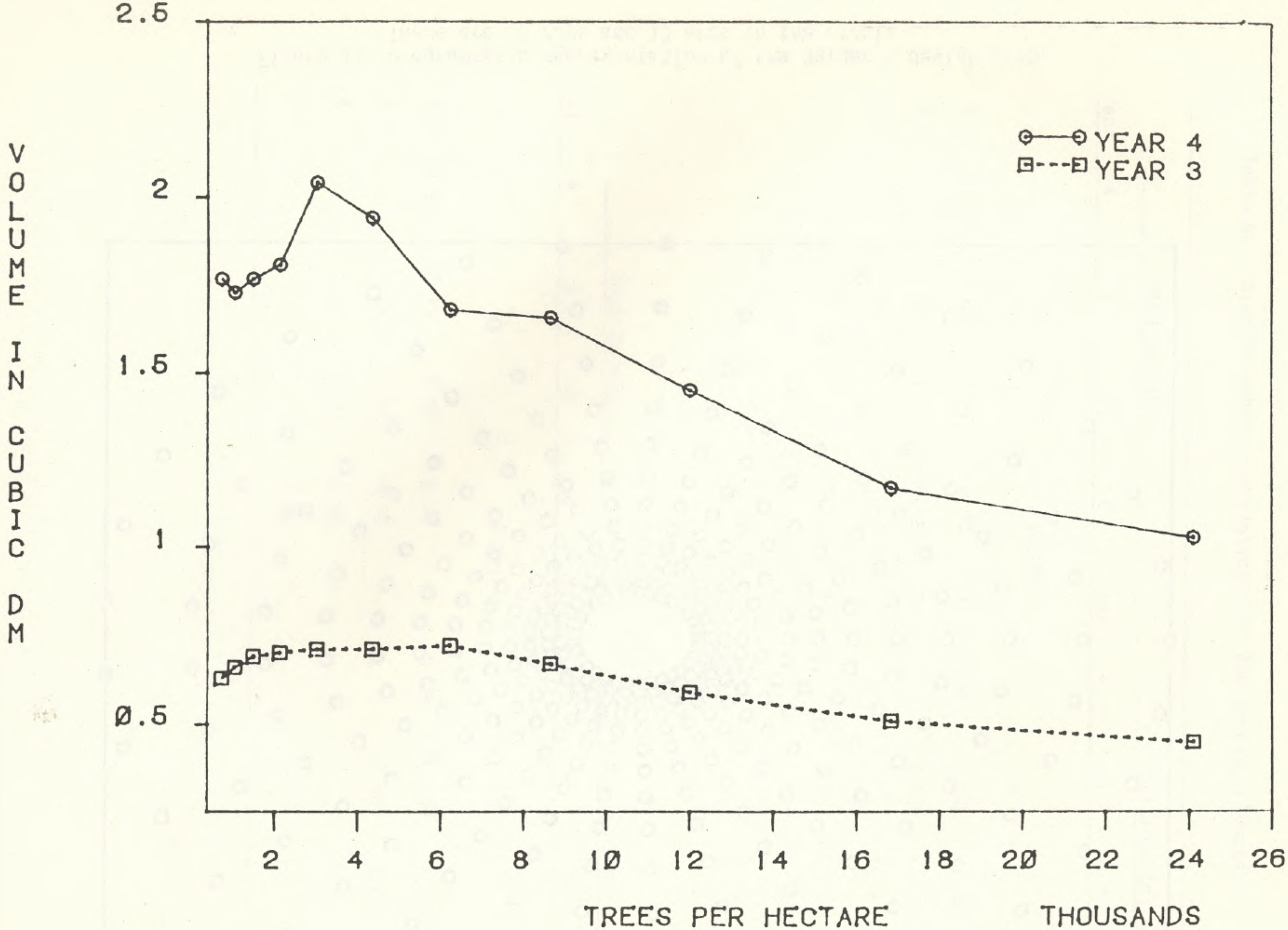

Figure 2: Average volume for all spacings and families for years 3 and 4.

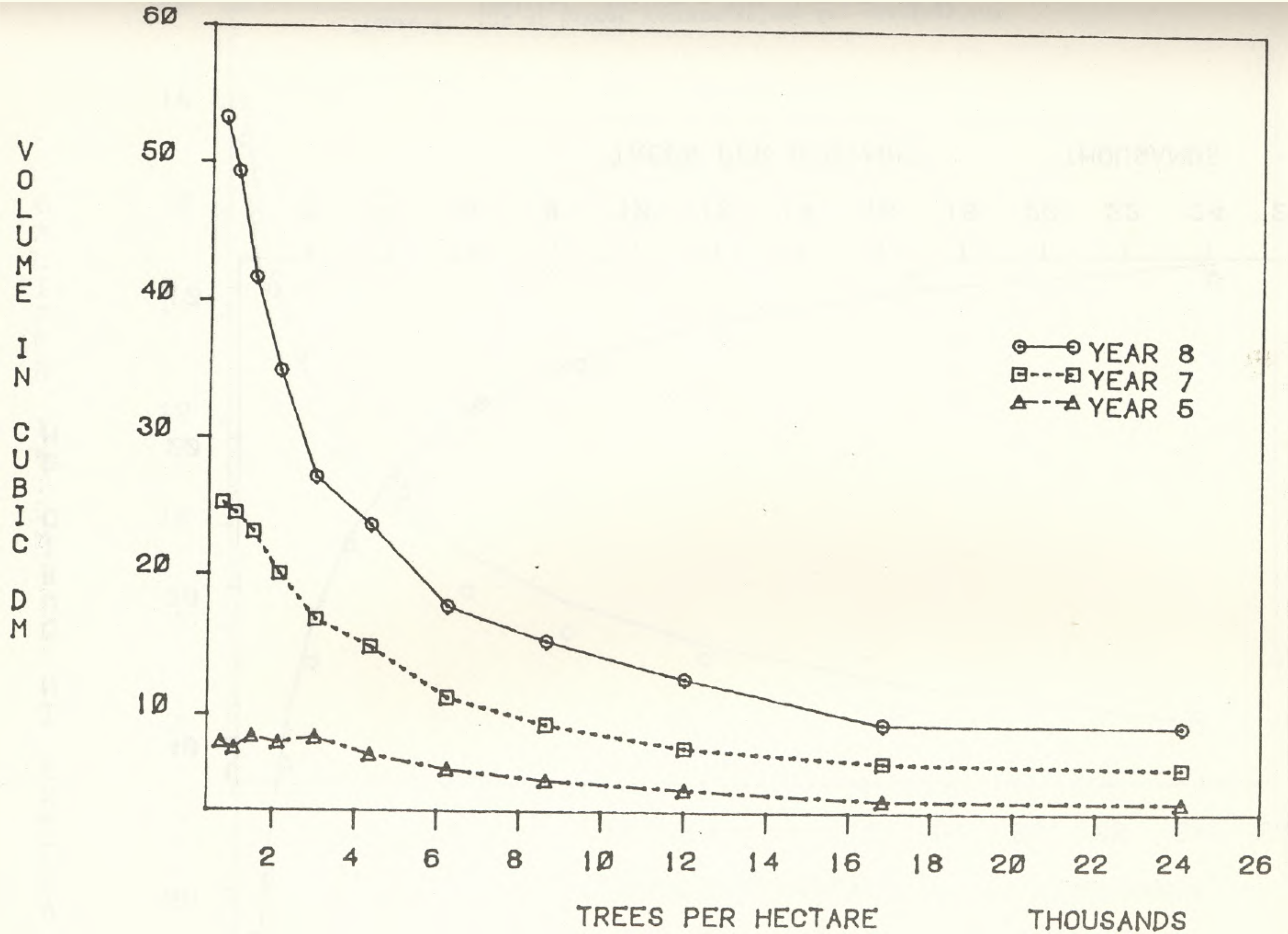

Figure 3: Average volume for all spacings and families
for years 5, 7 and 8.

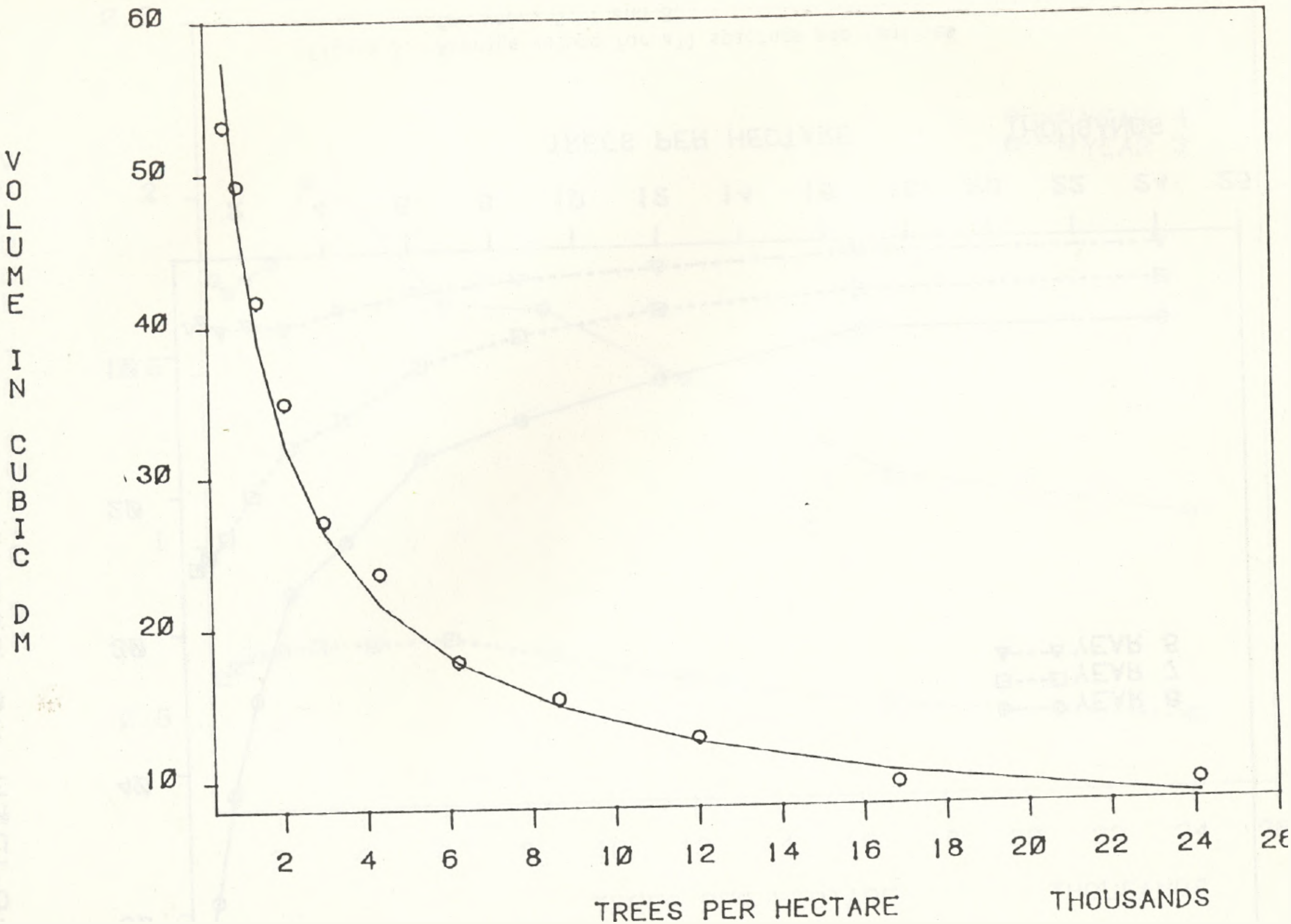

Figure 4: Fit of 8-year average volume for spacings and families. (Volume = 2165 (trees/ha)-0.55

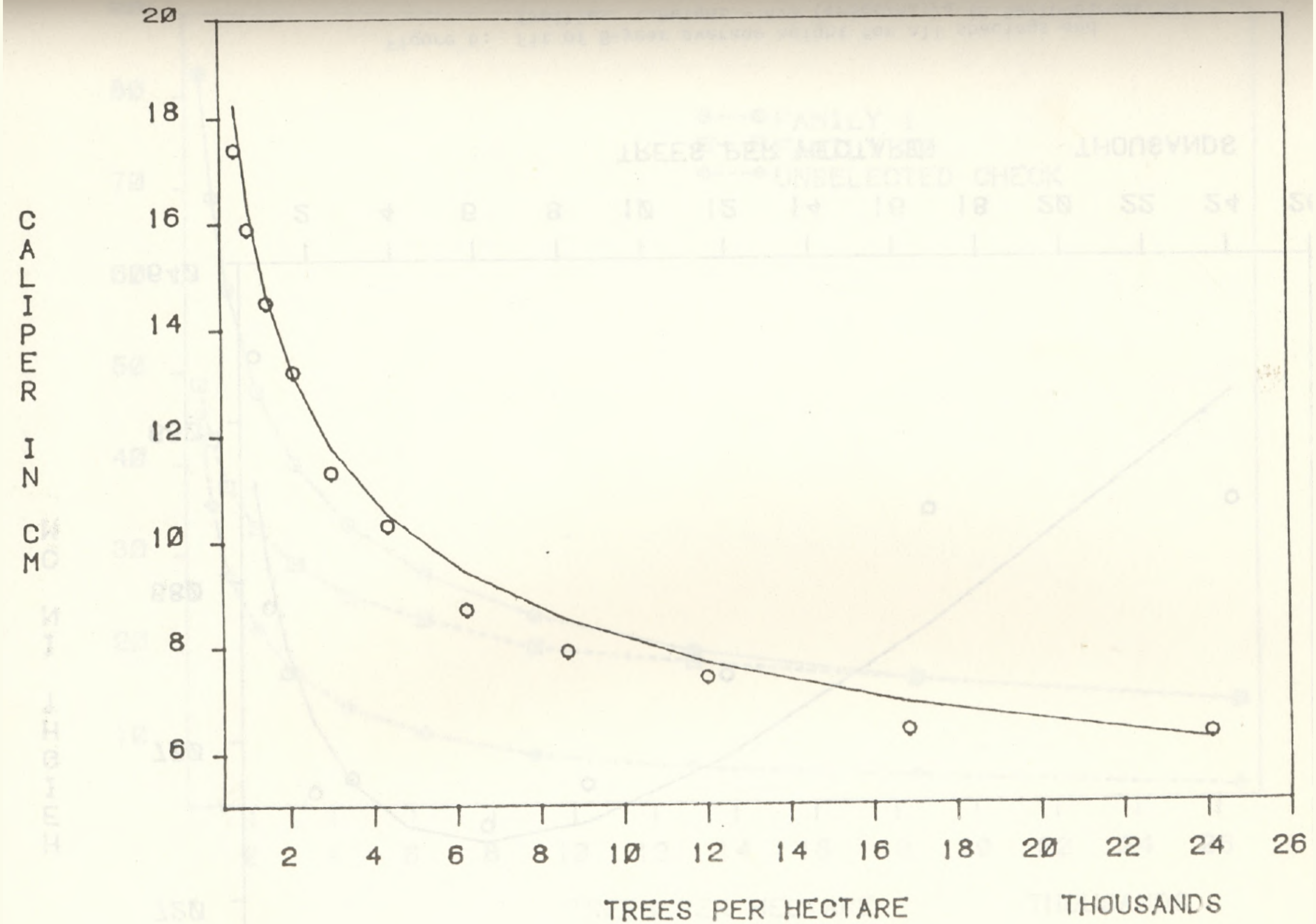

Figure 5: Fit of 8-year average caliper for spacings and families. Caliper = 141 (trees/ha)-0.31

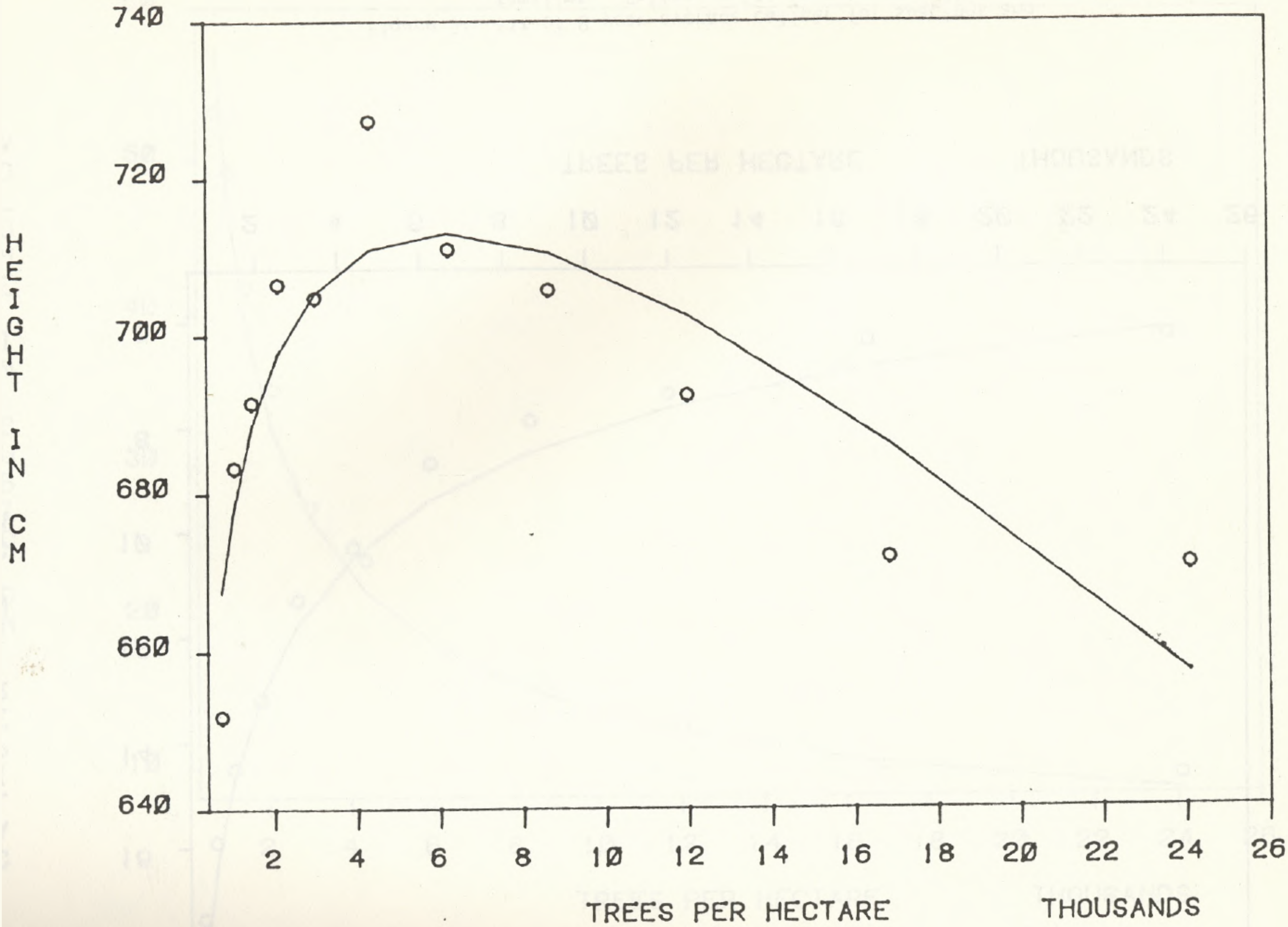

Figure 6: Fit of 8-year average height for all spacings and families. Height = 473 (trees/ha) /e (8.59x10-6trees/ha)

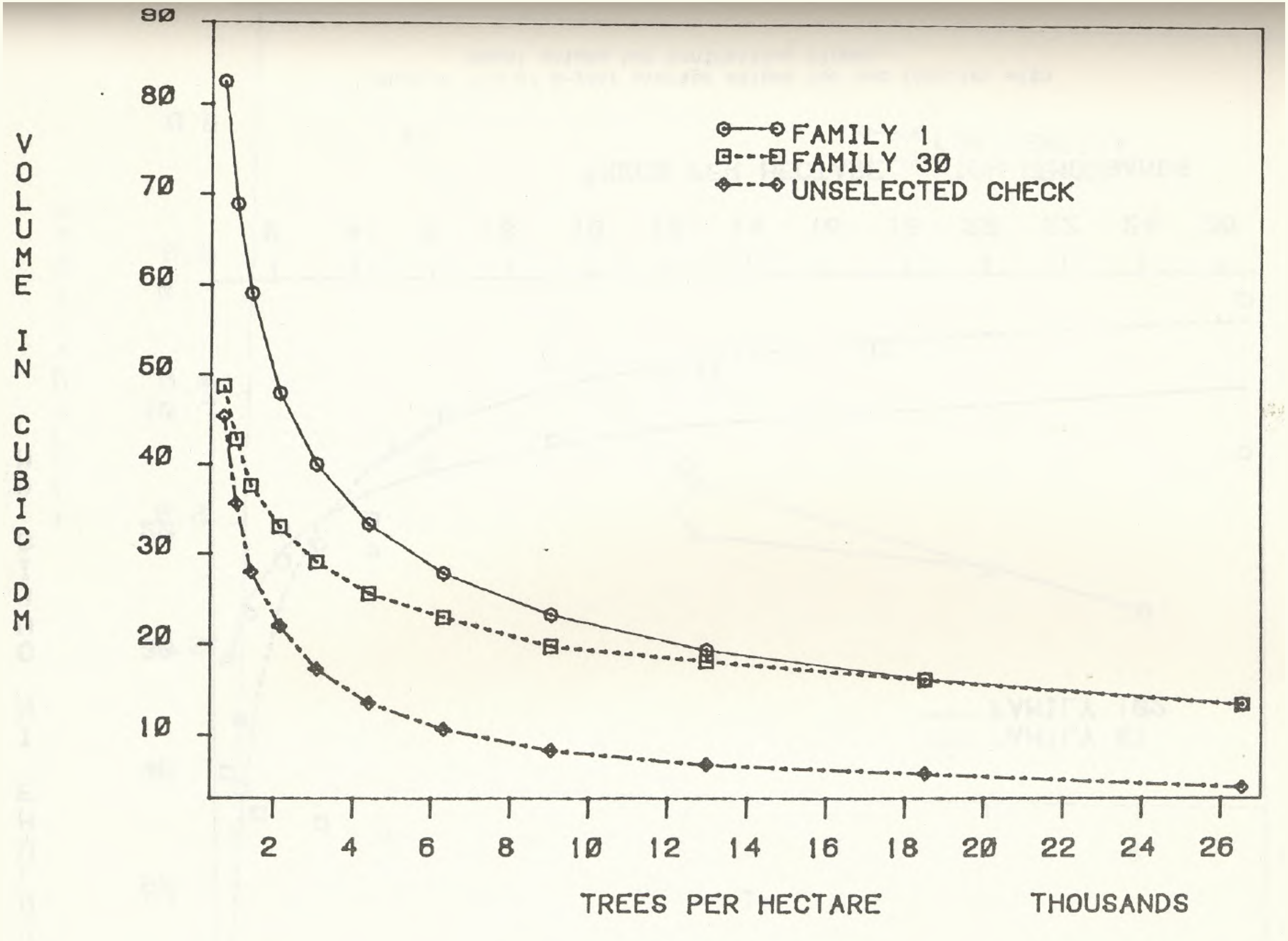

Figure 7: Fit of 8-year average volume for two families and unselected check.

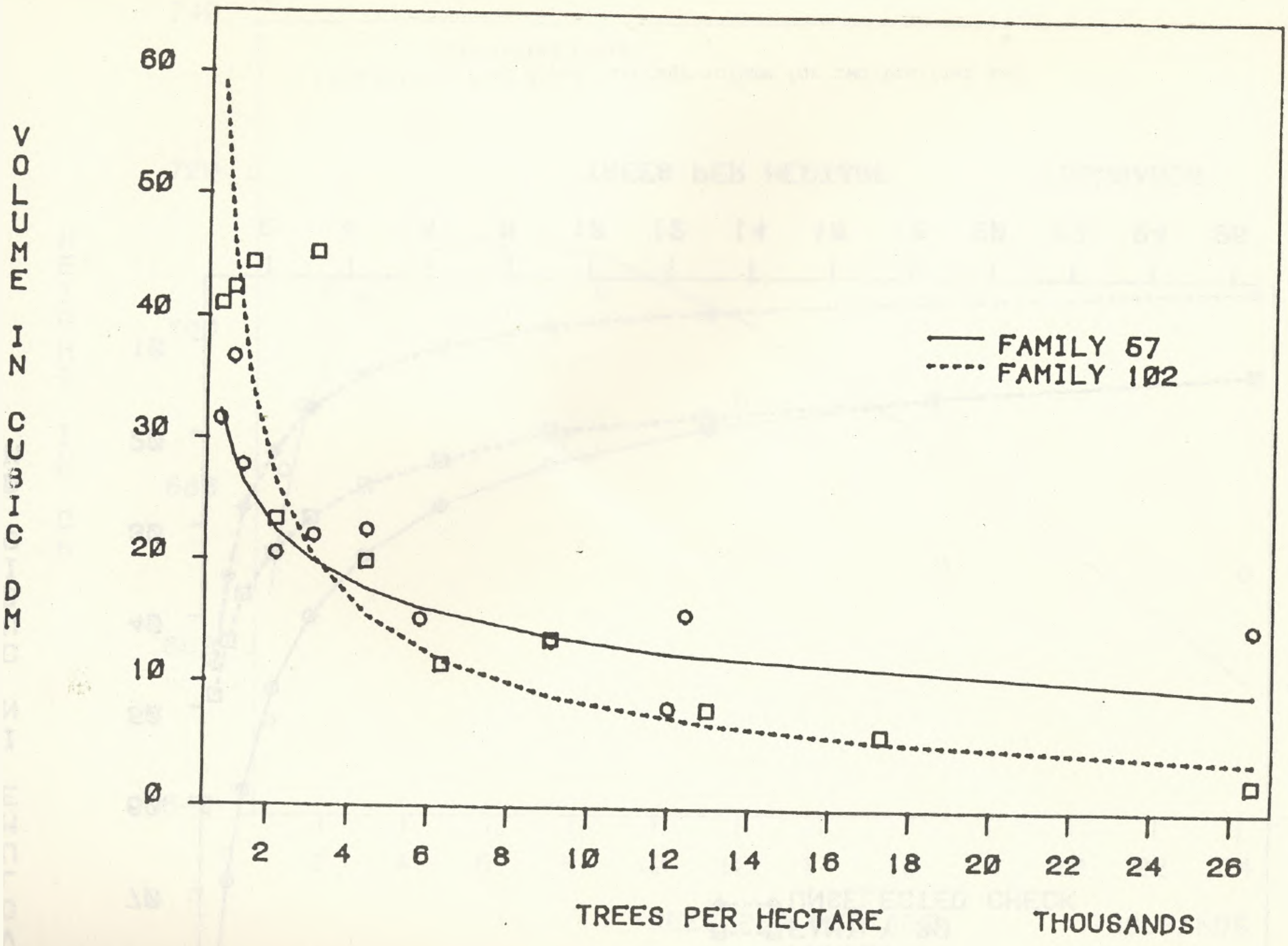

Figure 8: Fit of 8-year average volume for two families with equal volume but contrasting slopes.

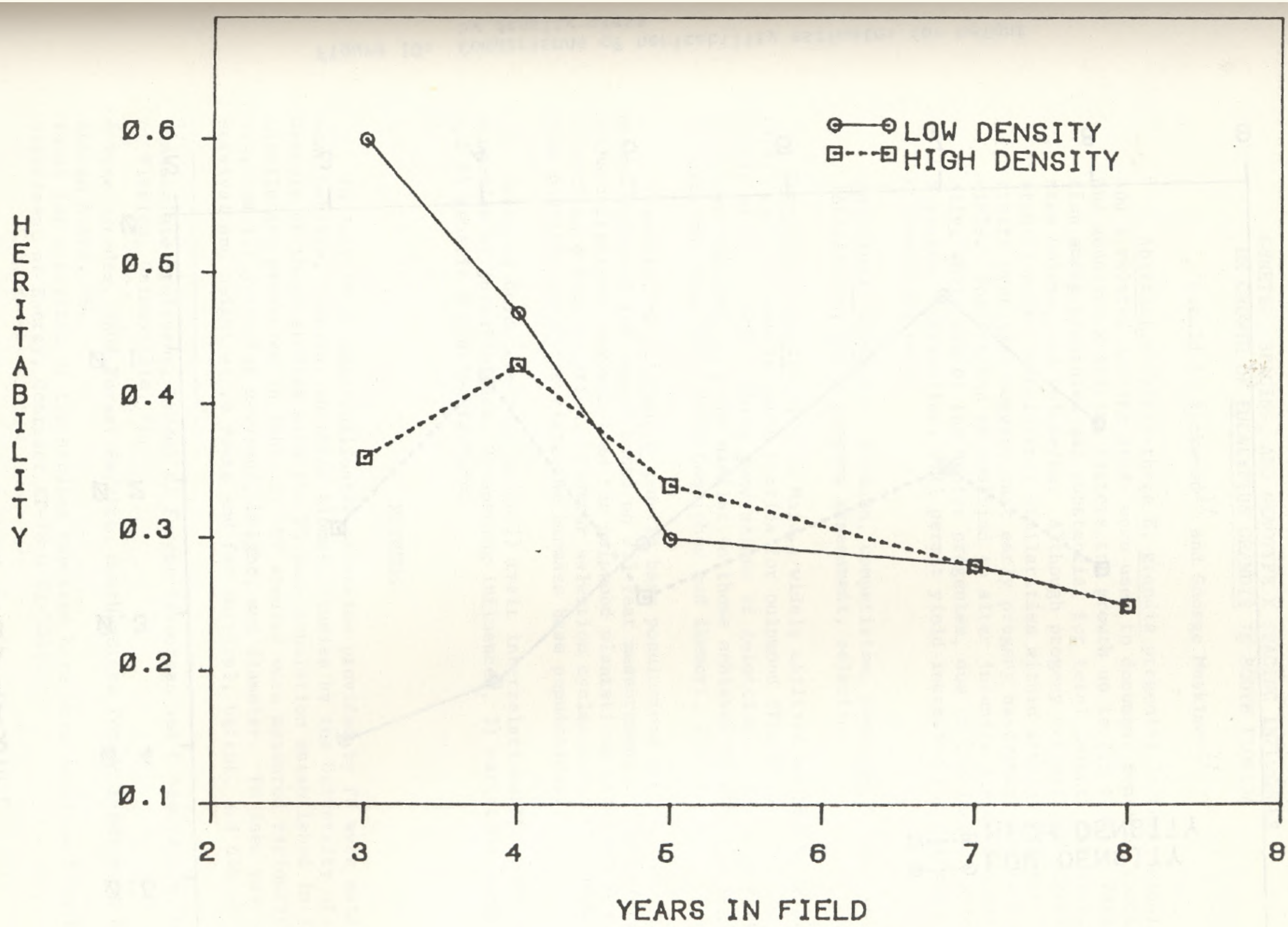

Figure 9: Comparisons of heritability estimates for volume
by density class.

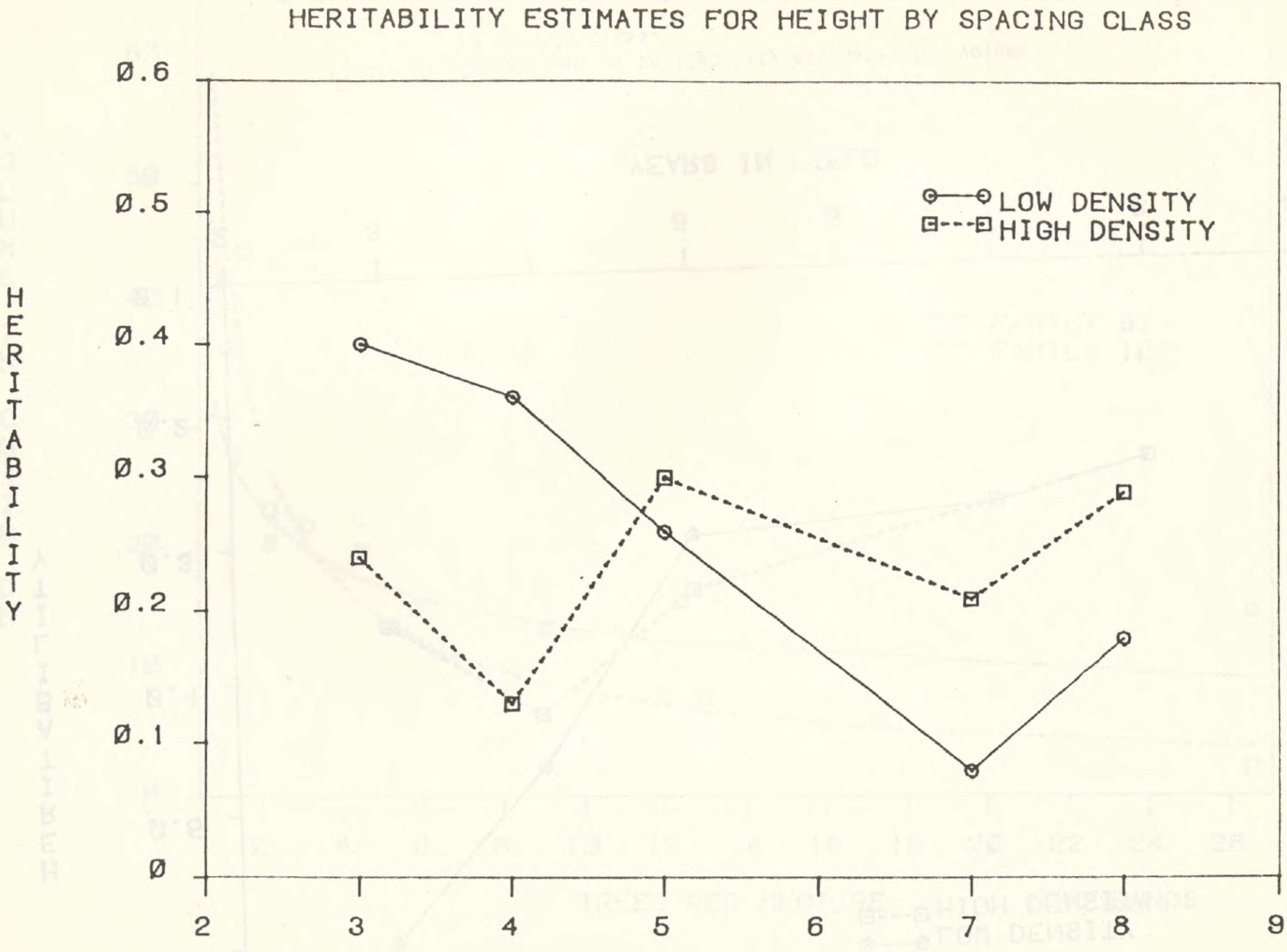

Figure 10: Comparisons of heritability estimates for height by density class.