VARIATION IN GROWTH EFFICIENCY OF SELECTED WESTERN HEMLOCK (*TSUGA HETEROPHYLLA* (RAF.) SARG.) TREES

by

GARY LEE NELSON

BSc., Colorado State University

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF FORESTRY

in

THE FACULTY OF GRADUATE STUDIES

Faculty of Forestry

We accept this thesis as conforming to
the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
August, 1979

Department of Forestry

The University of British Columbia
2075 Wesbrook Place
Vancouver, Canada
V6T 1W5

Date 14 August 1979

ABSTRACT

Eighty western hemlock trees, in the age range of 15 to 48 years, were selected on three Crown Zellerbach tree farms in northwestern Oregon and southwestern Washington to sample the range of variation in growth efficiency. Growth efficiency is defined as the ability of the crown to produce the maximum amount of wood in relation to its crown surface area. Selection of the trees was based on the crown index ratio (live crown length/crown width). The objectives of the study were to estimate:

1) the range of variation in growth efficiency of individual trees,
2) how variation in growth efficiency of individual trees could be utilized to maximize volume on a unit area, and
3) the efficiency of narrow crown western hemlock trees as wood producers.

Results from regression analysis showed that there was sufficient variation in growth efficiency, with a range of the standardized residuals exceeding at least ±2.0 standard errors of the estimate for all three regression models. Based on this range it is suggested that selection of ten year basal area increment or gross stem volume for western hemlock in relation to crown surface area or sapwood basal area may be worthwhile.

The significance of the variation in growth efficiency becomes apparent when the higher growth efficiency classes are selected. It is estimated that selection of the higher growth efficiency classes rather than the average may increase ten year basal area increment/hectare by 39 to 45 percent.

It appears from the trees measured that there is little relationship between growth efficiency and the degree of slenderness of the crown.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I am very grateful to Dr. O. Sziklai, Faculty of Forestry and supervisor of my thesis committee, for assistance and encouragement in the preparation of this thesis. Thanks are also extended to Dr. D. Lester, Crown Zellerbach Corp., for his support and insight in the preparation of this thesis. Gratitude is also extended to Dr. D. Williams and Dr. J. Demaerschalk, Faculty of Forestry, for reviewing the thesis and contributing their advice.

In addition, acknowledgement and thanks are extended to Mr. M. A. El-Sharkawi, Ms. S. Phelps, and Ms. G. Ho for their assistance and time in computing.

I am greatly indebted to Crown Zellerbach Corporation and the Western Forest Genetics Association for their finicial support in the form of the Forest Genetics Research Foundation Scholarship which made this research possible.

Thanks are also extended to Mr. Y. El-Kassaby, Mrs. A. Fashler, and Mrs. M. A. DeVescovi for their support and encouragement.

Finally, my most sincere thanks to my wife, Karen, for her unfailing support and love.

VARIATION IN GROWTH EFFICIENCY OF SELECTED WESTERN HEMLOCK (TSUGA HETEROPHYLLA (RAF.) SARG.) TREES

INTRODUCTION

Western hemlock (Tsuga heterophylla (Raf.) Sarg.) is one of the most important commercial tree species in the Pacific Northwest. It is not only a primary lumber producer, but one of the major species used for pulpwood on the coast. Its occurrence ranges along the Pacific coast from southeastern Alaska to northern California, and in the Rocky Mountains from the southern half of British Columbia through northern Idaho, to northwestern Montana (Harlow and Harrar, 1969).

In the last several years, western hemlock has come into increasing demand in the planting programs of private and public agencies; and this trend is expected to continue at an accelerated rate (Piesch, 1974). However, little attention has been given to the study of western hemlock genetics (Meagher,1976), because for many years it was considered the least desirable among commercial conifer species in the Pacific Northwest. Even though its potential for management as an efficient volume producer has long been recognized (Hogue, 1929; and Dimock, 1958), it is just recently being utilized.

Forest tree improvement is a practical extension of genetics, with the objective of obtaining genetically better trees for planting (Wright, 1962). Research related to forest tree improvement and genetics has been in progress for 150 years, but only in the past 25 years has research been intensive (Wright, 1976). For western hemlock this research began about a decade ago, with studies initiated in 1968, independently by Piesch (1974) and Meagher (1976). Prior to that time a small number of plus trees had been selected in British Columbia (Walters et al., 1960).

Western hemlock appears well suited to genetic improvement efforts (Piesch, 1976). Wellwood (1960) reported variation in tracheid length, and trees having tracheids either shorter or longer than average retained that feature as they continued to grow. Appreciable variation was also reported in height of two-year-old seedlings, both within and between populations of western hemlock (Piesch, 1974). Meagher (1976) found that western hemlock populations differentiate rapidly with locality and elevation.

This investigation deals with the variation and selection of growth efficiency of individual western hemlock trees. The objectives of the study were to estimate:

1) the range of variation in growth efficiency of individual trees:
   a) relating gross stem volume/crown surface area to age,
   b) relating ten year basal area increment to crown surface area, and
   c) relating ten year basal area increment to sapwood basal area,
2) how variation in growth efficiency of individual trees could be utilized to maximize volume per unit area, and
3) the efficiency of narrow-crown western hemlock trees as wood producers.

LITERATURE REVIEW

The importance of crown variation in relation to wood quality and quantity has long been recognized by forest geneticists. Emphasis is usually placed on variation in the branching characteristics such as branch angle and branch diameter (Barber and Reines, 1956; Rudolph, 1956; Campbell, 1961; Stephenson and Snyder, 1969; and Dorman, 1976), that is, characteristics affecting wood quality.

The primary objectives of a tree improvement program in most countries, is to select and breed trees with increased growth rates, desirable stem form, and increased resistance to insects and diseases. For western hemlock, volume superiority is the single most important trait among stem straightness, spiral grain, branch size considerations, specific gravity, and cellulose content (Thomas and Stevens, 1977).

There are many factors which influence the growth of individual trees on a given site, however, competition is probably the single most important factor (Brown and Goddard, 1961). Competition is defined as the active demand by two or more organisms for a common resource. Therefore, if trees are selected for superior growth rate or volume without consideration of the degree of competition to which they have been subjected, it may be found that they are growing no more than should be expected with the growing space available to them (Brown and Goddard, 1961).

It seems logical to assume that the size of the crown should be an indication of the competition a tree has undergone. Brown and Goddard stated that:

> "the search for plus phenotypes centers around the premise that certain trees are inherently more effi-

cient than others in the manufacture and utilization of photosynthates. Stated somewhat differently, a plus tree by *a priori* reasoning possesses the potentiality of producing more increment per unit crown size and growing space than competing neighboring trees of the same age."

The importance of leafiness in dry-matter production has led to the assumption that crown dimensions should be related to increment (Matthews, 1963). There are many examples of the positive relationship between crown width and stem diameter (Holsoe, 1948; Minor, 1951; Toda, 1954; Berlyn, 1962; and Vezina, 1962), and crown width and basal area increment (Weck, 1944; and Holsoe, 1948).

The closeness of the relation between crown diameter and stem diameter or basal area increment in many species does not preclude the existence of trees that have crowns smaller or larger than average for a given stem diameter or basal area increment (Matthews, 1963). Studies of Moller (1945) in Denmark with beech and spruce showed that the same quantity of foliage can produce different quantities of stem volume. Therefore, if the converse statement is true, that the same quantity of stem volume can be produced by different quantities of foliage, there are obvious advantages to be gained from identifying those trees which are efficient wood producers in relation to the quantity of foliage and the size of their crown diameters (Matthews, 1963). At the same time, quality characteristics such as specific gravity, cellulose content, straightness, spiral grain, and branch size should be considered for the selected tree.

Though trees with small crown diameters may not produce stem volumes equal to wide-crown trees, their efficiency may be greater. Assman (1970) found that in trees of the same species and dbh, individuals having slender crowns or a low crown fullness ratio (crown width/crown length) were more productive on a land area basis than trees having wide crowns.

In order to ascertain the shape and size of crown most conducive to a high rate of growth, the best plan is to relate the capacities of individual trees to their respective crown surface area (Assman, 1970). Matthews (1963) and others (Rudolph, 1956; Campbell and Rediske, 1966; and Morgenstern <u>et al</u>., 1975) have expressed the similar idea that selection for growth rate should be directed toward finding not the largest tree, but the tree that has utilized growing space, light, and nutrients most efficiently. This requires finding the tree with the best growth in relation to its leaf surface area (Morgenstern <u>et al</u>., 1975).

Though two trees may have the same quantity of foliage or crown surface area, the efficiency of the needles to convert carbon dioxide and water in the presense of chlorophyll and sunlight into photosynthates may differ greatly due to different morphological crown forms.

Differences in efficiency of the needles may be directly due to the capabilities of a tree's genome to synthesize photosynthates, or indirectly as a consequence of a tree's morphological crown form, where one form may be more advantageous because of the orientation of the needles to the suns rays.

Alexandrov (1971) observed four basic morphological forms of Norway spruce with 24 transitional forms. The four forms, comb, brush, compact, and flat-branched, are made apparent by the branching characteristics and reflect the ecological conditions.

The comb spruce received its name because of the structure of the second-order branches, which hang down in a comb-like curtain. The name brush spruce is given because of the brush-like structure of the second-order branches which grow in all directions. The compact spruce is similiar to the brush spruce, but the second-order branches remain horizontal because of their short length, considerable thickness, and sturdiness to form a compact mass. The flat-branched form receives its name because the first-, second-, and third-order branches develop in the same horizontal plane.

Alexandrov (1971) made no attempt in his study to determine the growth efficiency within and between the four forms. However, it is likely that each form may have the same quantity of foliage or crown surface area, but differ in their efficiency to synthesize photosynthates because of the ecological conditions, the orientation of the needles on the second-order branches, or the genetic ability of the tree itself to synthesize photosynthates even under optimum conditions.

Measurements of foliage mass or leaf surface area for forest trees are often used by foresters, ecologists, physiologists, and others interested in tree growth to estimate photosynthetic potential. Such measurements are important as well in studies of evaporation, transpiration, and interception of precipitation.

Generally, the leaf surface area or foliage mass is the preferred measurement, and methods have been developed to estimate these for some species. By using regression analysis, Cable (1958) found a relationship between leaf surface area and ovendry weight of individual ponderosa pine fascicles. For several hardwoods and shortleaf pine, total quantity of foliage was found by estimating equations for the number of leaves by both tree and branch diameter (Rothatcher et al., 1954).

Many of these estimates are time-consuming, hence for some studies other indicators of photosynthetic area are used. Among these, crown radius X crown length, crown diameter X crown length, and crown surface area have been found to be highly correlated with tree growth.

One approach in selecting for growth efficiency is to determine in each stand the regression of breast-height diameter squared X height <u>on</u> crown diameter X crown length (Rudolph, 1956). Trees above the regression line reflect special vigor and can be selected.

A similar procedure used by Brown and Goddard (1961) for loblolly pine, is to measure basal area increment during the last ten years, and relate this to the product of crown length X crown radius. They found a correlation coefficient of basal area increase <u>on</u> crown length X crown radius to be 0.83. Again, trees above the general regression line are candidates for selection.

A more reliable indication of growth capabilities would be the use of crown surface area (Brown and Goddard, 1961). Holsoe (1948) found that the regression of ten year basal area increment <u>on</u> crown surface area in red oak and white ash gave correlation coefficients of 0.962 and 0.899, respectively.

Since crown diameter measurements are laborious and time-consuming, they are only made if the candidate tree meets minimum requirements in crown and branch characteristics and is free of damage from insects and diseases (Brown and Goddard, 1961).

Recently, conifer foliage mass was found to be highly correlated with the cross-sectional area of conducting tissue (sapwood) measured at 1.3 m above ground for Douglas-fir, noble fir, and ponderosa pine (Grier and Waring, 1974). The sapwood basal area and foliage area are related since water transport to the foliage within the tree stem is confined to the sapwood (Whitehead, 1978).

Therefore, it may be worthwhile to relate basal area increment to sapwood basal area, which would be a direct measurement of a tree's leaf area. Trees above the regression line represent efficient wood producers and are candidates for selection.

For selection, the approaches mentioned above are applications of a method called base-line selection (Einspahr et al., 1964; and Morgenstern et al., 1975). To evaluate the growth of an individual tree adequately, it is necessary not only to have information on age, stem diameter at breast height, crown length, crown width, and sapwood basal area, but there must be standards or base-lines with which to compare the growth rates of individual trees.

The regression of the dependent variable (stem volume or basal area increment) on the independent variable (crown surface area, crown length X crown radius, or sapwood basal area) determines the base-line. Candidate trees must exceed the mean of the base population by a certain amount, for example, by two standard deviations (Morgenstern et al., 1975).

There is limited information of this subject pertaining to western hemlock. A positive relationship was found between crown width and stem diameter (Smith and Ker, 1960). Variation in efficiency of bole volume/crown volume was reported between the species western hemlock, Douglas-fir, and western red cedar, with hemlock superior to both in terms of average efficiency of wood production (Smith et al., 1961). Thomas and Stevens (1977) evaluated growth efficiency in western hemlock by relating five year basal area increment to crown area. They used base-line selection techniques with selection of plus trees based directly on the size of the residual.

MATERIALS AND METHODS

Eighty western hemlock trees were selected along logging roads on Crown Zellerbach tree farms in Oregon and Washington. The location of the tree farms Clatsop, Cathlamet, and Tillamook, and the 80 selected trees, are shown in Figures 1-4.

The trees were selected to sample the range of variation in growth efficiency of individual trees in the age range of 15 to 40 years. Initial selection was based on the live crown length/crown width ratio termed crown index (Assman, 1970). This ratio gives an indication of the slenderness or roundness of tree crowns. A high ratio indicates a slender crown. For western hemlock, an average ratio was determined to be 2.5 (Walkup, 1978).

The objective was to get a range of crown index ratios as wide as possible. By using the crown index ratio, it was possible to sample the range of variation in growth efficiency, and also to determine the efficiency of narrow crown western hemlock trees as wood producers.

The characters measured on each tree were total height[1] (m), stem diameter (cm) at 1.3 m above ground (dbh), three to five upper stem diameters (cm) at their respective stem heights, bark thickness (mm) at dbh, age, live crown length (m), crown widths (m) at three different individual tree heights, ten year radial increment (cm) at dbh, sapwood radial length (cm) at dbh, and total radial length (cm) at dbh.

Total height, upper stem diameters, and live crown length were

[1] total height was measured to the nearest centimeter as if the drooping leader were straight

measured by a Spiegel-Relaskop. The live crown length is defined as the distance from the tip of the terminal leader to the lowest live branches of a full whorl. Diameter at stump height and dbh were measured by a diameter tape.

Crown widths were determined by measuring four radii and dividing by two. Measurements were made from the center of the stem to right angles of branch tips. Three crown widths were measured at various heights on the tree. The first crown width measured was always the base crown width. The base crown width was determined by the width of the lowest live branches of a full whorl of the tree crown. The remaining two crown widths were arbitrarily chosen at different heights where the tree crown would vary in shape, that is, deviate from a conical shape.

Crown widths were determined as follows: the radius at the widest part of the live crown base was measured, then three crown radii were measured at 90 degree intervals around the stem. The four radii were averaged to give a crown width.

Measurements of the other two crown widths was not necessarily at its widest point, but made directly above or parallel to its base crown radii. Again, four radii were measured for each of the two crown widths and averaged.

Ten year radial increment was determined by taking the average 10 year radial increment of three cores extracted at 120 degree angles at dbh. If only two cores were taken, they were extracted at 90 degree angles at dbh.

After ten year radial increment was determined for each core, they were stained to determine the radial sapwood thickness. Since western hemlock does not have a visible sapwood-heartwood boundry, a staining solution of 40 ml glycerin:30 ml methyl alcohol:60 ml concentrated hydrochloric acid was used to determine the radial sapwood thickness. The stain reacts with leucoanthocyanidins, which are present in the sapwood, resulting in a pink-to-mauve color sapwood and a greenish heartwood (Barton, 1973).

Age was determined by taking an increment core at stump height, and bark thickness at dbh was determined by a bark meter taking the average of three readings at 120 degree angles.

Total height, diameter at stump height, dbh, three to five upper stem diameters, and bark thickness were used in calculating total gross stem volume inside bark. Therefore, the stem was divided into five, six, or seven sections, and the volume for each section was calculated by Smalian's formula and summed.

The live crown length and crown widths were used in calculating crown surface area for each individual tree. The crown was divided into three sections and the surface area for each section was computed and summed as seen in Figure 5.

Ten year radial increment and total radial length were used in calculating ten year basal area increment. Likewise, radial sapwood thickness and total radial length were used in calculating sapwood basal area.

Three models were employed using least square regression techniques to determine the range of variation in growth efficiency of individual western hemlock trees. They are in order:

1) gross stem volume/crown surface area = a + b(age),
2) ten year basal area increment = a + b(crown surface area), and
3) ten year basal area increment = a + b(sapwood basal area).

Scatter diagrams of ten year basal area increment on crown surface area and ten year basal area increment on sapwood basal area, showed V-shaped distributions in both cases with the variances increasing linearly with the independent variable. Therefore, weighted least square regression techniques were used in the second and third models.

The measurement of growth efficiency was based on the deviation of an observation from the regression line, that is, the size of the residuals. Baseline selection with two selection intensities of 1/50 and 1/100 were employed to select for superior individuals for growth efficiency for all three regression models. Therefore, only those individuals whose standardized residual exceeded 2.054 (1/50) or 2.33 (1/100) were selected.

Ten year basal area increment/hectare for various sapwood basal areas was estimated from the product of ten year basal area increment/tree and the number of trees/hectare for the corresponding sapwood basal area. By relating the base crown width to sapwood basal area the number of trees/hectare can be estimated.

To determine the efficiency of narrow crown western hemlock trees as wood producers, the standardized residual (measure of growth efficiency) for all three regression models was related to the crown index ratio.

FIGURE 1 LOCATION OF CLATSOP, CATHLAMET, AND TILLAMOOK TREE FARMS IN OREGON AND WASHINGTON

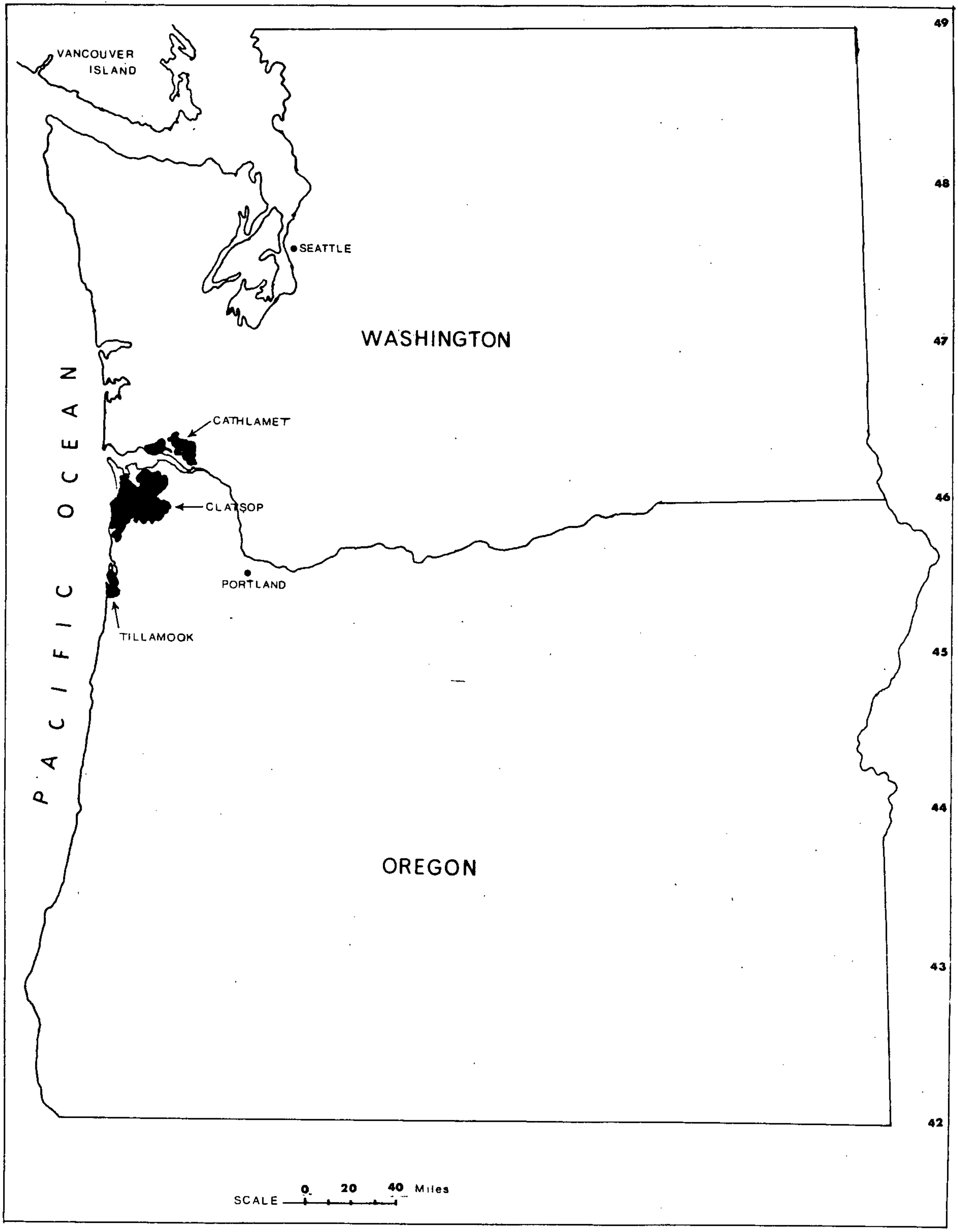


FIGURE 2 CLATSOP TREE FARM

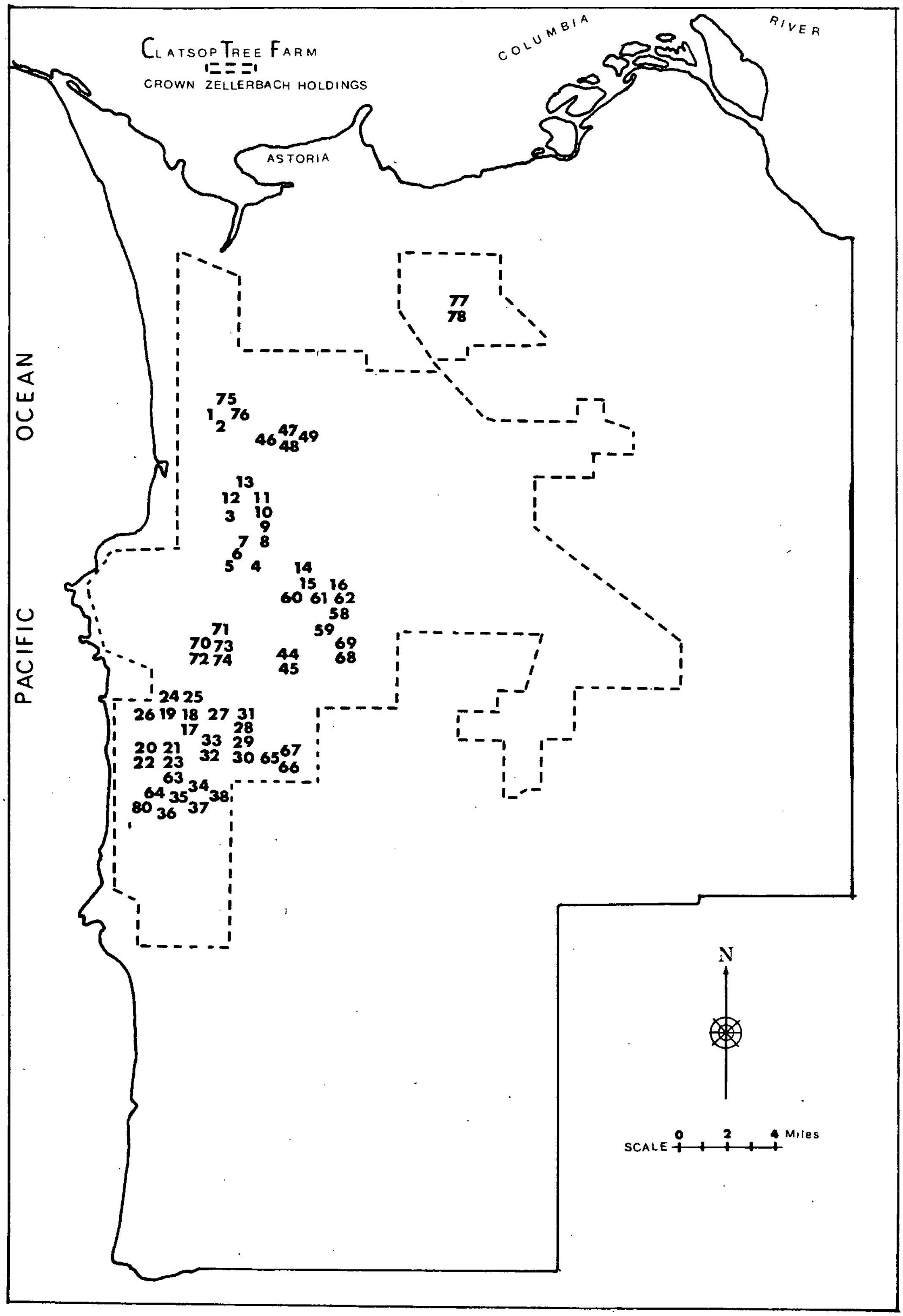


FIGURE 3 TILLAMOOK TREE FARM

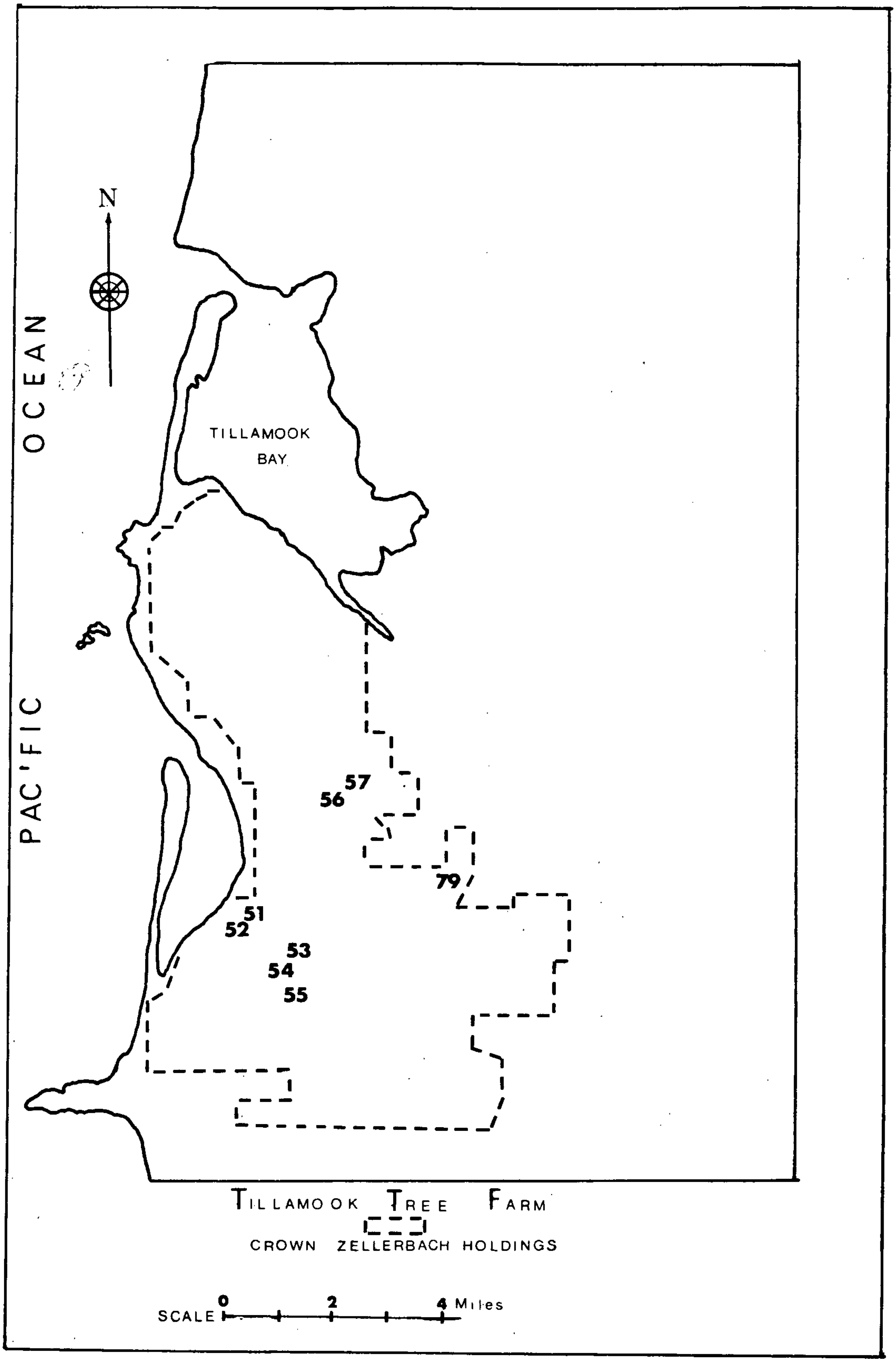


FIGURE 4 CATHLAMET TREE FARM

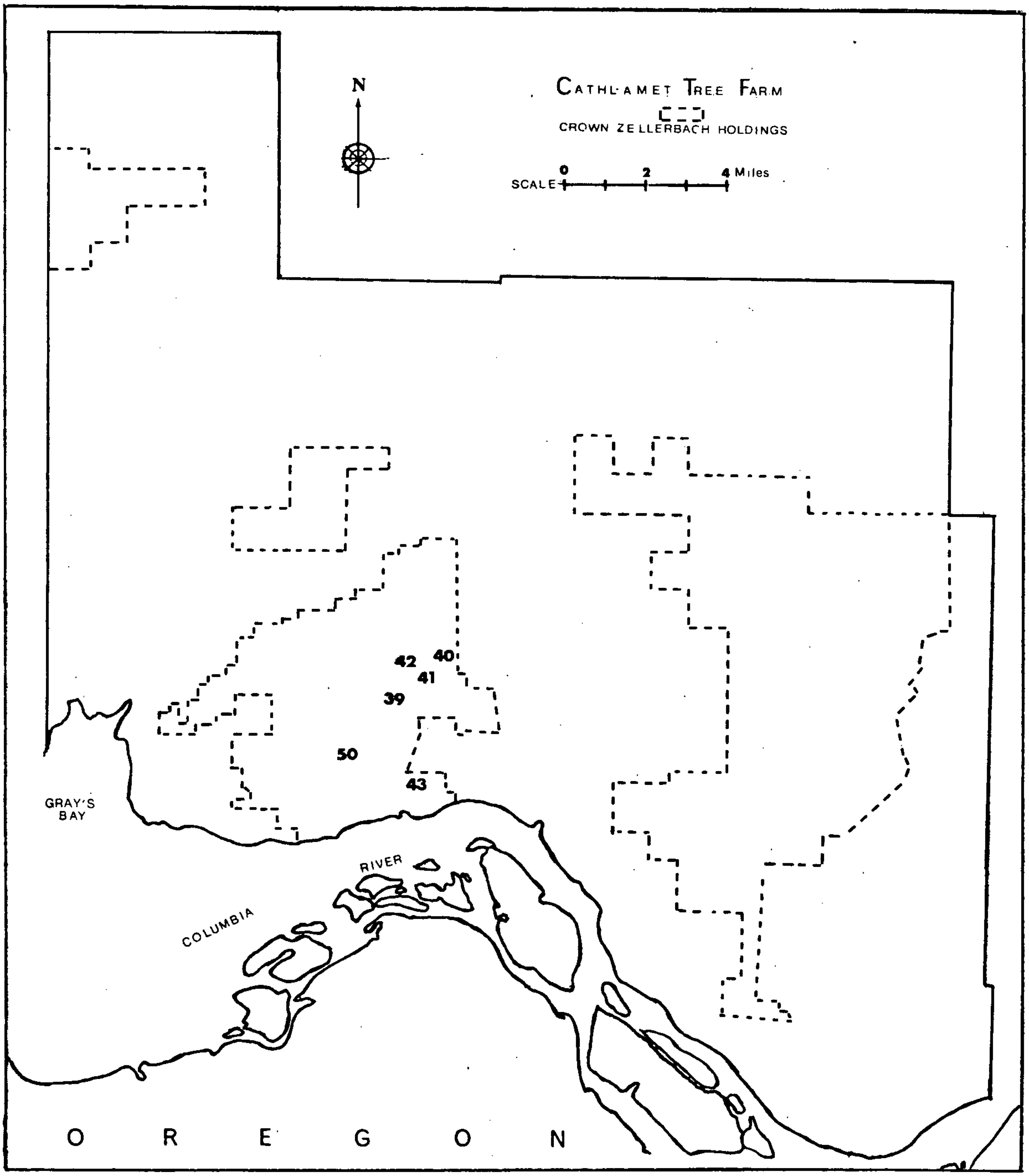
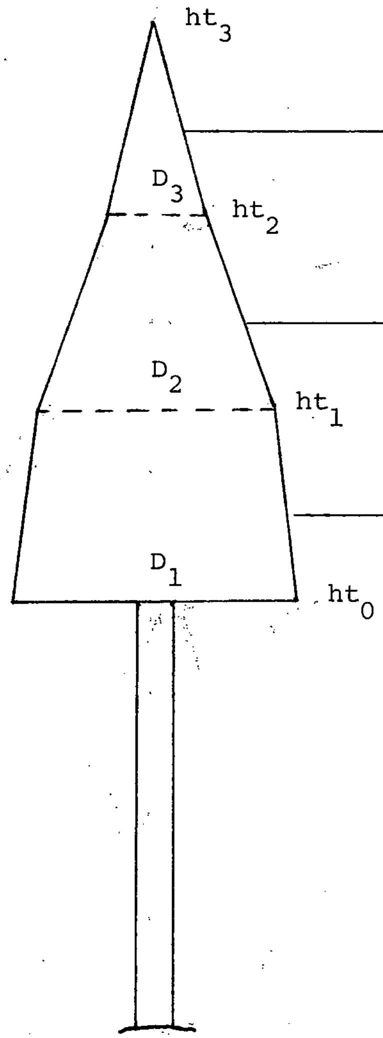


FIGURE 5: METHOD OF CALCULATING CROWN SURFACE AREA/TREE



$$\frac{\pi D_3}{2}\sqrt{\frac{D_3^2}{4} + (ht_3 - ht_2)^2} = z_1$$

$$\frac{\pi (D_3 + D_2)}{2}\sqrt{\frac{(D_2 - D_3)^2}{4} + (ht_2 - ht_1)^2} = z_2$$

$$\frac{\pi (D_2 + D_1)}{2}\sqrt{\frac{(D_1 - D_2)^2}{4} + (ht_1 - ht_0)^2} = z_3$$

where $z_1 + z_2 + z_3$ = crown surface area (m^2)

$D_{1,2,3}$ = crown widths

$ht_{0,1,2,3}$ = tree heights within crown

RESULTS AND DISCUSSION

1. Range of Variation in Growth Efficiency

The three methods employed using least square regression techniques determined the range of variation in growth efficiency of individual western hemlock trees. Growth efficiency is defined as the ability of the crown to produce the maximum amount of wood in relation to its crown surface area. The measurement of growth efficiency was based on the deviation of an observation from the regression line, that is, the size of the residual. Therefore, the range of variation in growth efficiency is determined from the upper and lower values of the residuals or the standardized residuals.

The measurements taken on the 80 individual observations with computations of gross stem volume, crown surface area, etc., are shown in Table 1. It is apparent from Table 1 that for nearly the same basal area increment or the same age and nearly the same gross stem volume, there exists large differences in crown surface area. Therefore, simple regression techniques were used to rank the trees according to the size of their residual, most productive in volume growth or ten year basal area increment, and then later select efficiently growing individuals by base-line selection. Selection of efficiently growing individuals is based on the assumption that all trees measured are equal in other phenotypic traits of interest. An additional assumption is that there is no major variation in climatic and edaphic influences between the 80 observations.

The differences in gross stem volume or ten year basal area increment for individuals with nearly the same crown surface area may be due to differences in crown shape or form; thereby causing differences in the efficiency

TABLE 1: MEASUREMENTS AND ESTIMATIONS OF VARIOUS PARAMETERS ON THE 80 SELECTED TREES

TREE NO.	CROWN INDEX RATIO	TEN YEAR BASAL AREA INCREMENT (cm^2)	GROSS STEM VOLUME (m^3)	CROWN SURFACE AREA (m^2)	TEN YEAR BASAL AREA INCREMENT* (cm^2)	SAPWOOD BASAL AREA (cm^2)	AGE
1	2.97	270.98	0.3654	127.261	270.98	299.43	24
2	4.11	244.53	0.1565	56.304	284.24	318.14	19
3	1.59	154.12	0.0441	53.598	154.12	113.62	15
4	2.58	323.54	0.2259	153.203	323.54	362.58	21
5	2.68	460.79	0.8203	123.514	460.79	603.58	30
6	3.83	144.76	0.0824	45.896	144.76	133.94	24
7	2.66	115.07	0.0530	33.153	115.07	114.78	20
8	1.75	417.93	0.3174	148.593	417.93	414.26	21
9	2.55	219.02	0.1309	42.142	219.02	216.20	19
10	1.92	487.75	0.3794	103.917	487.75	426.33	18
11	3.24	329.93	0.1259	51.910	329.93	325.24	19
12	2.66	309.57	0.1292	63.070	309.57	277.76	21
13	2.12	207.93	0.0892	84.191	207.93	198.06	19
14	3.92	214.36	0.2013	64.205	214.36	258.82	27
15	1.92	439.48	0.2259	92.758	439.48	484.61	21
16	2.08	178.04	0.0793	83.191	178.04	179.97	20
17	2.44	319.10	0.1840	44.535	319.10	397.73	22
18	2.57	156.35	0.1029	30.563	164.03	206.75	22
19	3.57	245.46	0.1743	43.295	245.46	335.75	27
20	2.42	168.89	0.3005	50.506	168.89	351.96	27

* Occasionally some increment cores did not stain to determine sapwood thickness. To be consistent only those cores which were used to measure sapwood thickness were used to determine ten year basal area increment for regression model 3.

TABLE 1 (CONT.)

TREE NO.	CROWN INDEX RATIO	TEN YEAR BASAL AREA INCREMENT (cm^2)	GROSS STEM VOLUME (m^3)	CROWN SURFACE AREA (m^2)	TEN YEAR BASAL AREA INCREMENT (cm^2)	SAPWOOD BASAL AREA (cm^2)	AGE
21	2.70	106.17	0.1580	41.258	106.17	210.59	26
22	2.97	120.56	0.1376	40.276	120.56	220.51	28
23	3.33	312.24	0.4603	70.424	312.24	375.98	32
24	3.14	137.12	0.2362	44.820	137.12	363.72	27
25	2.64	122.72	0.1258	27.738	122.72	227.61	35
26	2.21	223.24	0.3182	33.629	223.24	360.49	29
27	1.43	105.28	0.0491	40.526	105.28	110.49	48
28	2.25	197.51	0.0747	50.396	175.64	169.35	24
29	2.23	314.82	0.1527	81.158	314.82	283.90	25
30	2.97	81.37	0.0223	39.014	81.37	80.77	17
31	2.83	121.96	0.1290	46.991	121.96	157.19	24
32	2.22	337.95	0.1503	52.301	395.80	372.02	21
33	1.69	113.97	0.0597	54.624	113.97	110.91	16
34	2.52	115.00	0.0413	55.306	115.00	108.78	17
35	2.75	247.71	0.1057	76.290	247.71	205.81	17
36	2.40	101.61	0.0503	72.130	101.61	87.80	16
37	2.49	207.09	0.1926	59.560	207.09	258.77	24
38	2.95	82.75	0.0491	28.411	82.75	97.06	23
39	2.61	102.33	0.0705	37.309	102.33	95.69	20
40	2.03	424.20	0.3835	161.316	424.20	471.49	41

TABLE 1 (CONT.)

TREE NO.	CROWN INDEX RATIO	TEN YEAR BASAL AREA INCREMENT (cm^2)	GROSS STEM VOLUME (m^3)	CROWN SURFACE AREA (m^2)	TEN YEAR BASAL AREA INCREMENT (cm^2)	SAPWOOD BASAL AREA (cm^2)	AGE
41	2.14	158.13	0.1098	46.064	137.61	144.83	18
42	3.31	101.84	0.0769	63.231	101.84	103.69	18
43	3.73	223.30	0.1430	92.057	218.81	208.33	17
44	2.92	159.59	0.1306	38.382	159.59	175.83	18
45	2.83	174.56	0.1244	41.609	174.56	164.30	16
46	2.74	104.83	0.0481	30.025	104.83	85.57	16
47	2.45	199.86	0.1234	71.933	199.86	170.55	16
48	3.04	222.43	0.2004	58.734	222.43	250.42	19
49	4.26	266.00	0.1485	118.288	266.00	275.85	21
50	2.72	136.08	0.0564	51.276	136.08	136.93	16
51	2.98	96.71	0.0439	26.019	96.71	95.00	17
52	2.29	57.71	0.0359	15.090	57.71	55.96	17
53	2.85	69.08	0.0567	28.785	69.08	94.43	24
54	2.13	190.96	0.1456	46.147	190.96	241.53	28
55	2.28	405.98	0.3699	95.331	405.98	520.10	24
56	2.04	341.14	0.1655	92.393	341.14	326.06	21
57	2.43	158.62	0.1414	27.807	158.62	197.95	26
58	3.10	330.97	0.2432	104.965	330.97	362.42	20
59	2.96	170.47	0.1051	58.184	170.47	147.38	18
60	2.64	374.71	0.2126	128.532	374.71	398.93	23

TABLE 1 (CONT.)

TREE NO.	CROWN INDEX RATIO	TEN YEAR BASAL AREA INCREMENT (cm^2)	GROSS STEM VOLUME (m^3)	CROWN SURFACE AREA (m^2)	TEN YEAR BASAL AREA INCREMENT (cm^2)	SAPWOOD BASAL AREA (cm^2)	AGE
61	3.76	353.74	0.3738	81.098	353.74	425.51	25
62	3.41	152.83	0.2918	96.893	152.83	238.01	27
63	3.92	120.67	0.1829	61.307	120.67	228.71	29
64	2.53	202.01	0.2130	41.408	202.01	317.87	28
65	2.93	296.87	0.2443	56.449	296.87	380.21	26
66	2.99	241.97	0.1560	53.296	227.51	343.66	26
67	2.88	375.53	0.4180	81.030	375.53	486.97	27
68	3.30	144.13	0.1254	76.589	115.89	130.38	19
69	3.38	218.58	0.1535	63.755	218.58	186.25	21
70	3.53	288.05	0.1941	57.836	288.05	311.04	25
71	3.19	84.14	0.0991	22.888	84.14	121.78	30
72	2.97	174.34	0.1121	39.465	174.34	153.93	21
73	4.47	139.02	0.2222	84.647	146.94	200.39	28
74	4.78	349.31	0.4466	137.214	349.31	484.80	31
75	3.00	112.82	0.0995	29.513	112.82	146.19	19
76	3.66	100.16	0.0977	26.044	100.16	98.05	18
77	5.06	262.16	0.3663	100.313	262.16	335.45	22
78	5.24	150.96	0.2437	69.149	150.96	309.78	26
79	4.19	142.70	0.1743	72.026	142.70	182.20	23
80	6.00	352.48	0.6545	140.547	300.76	376.84	27

of the crowns to synthesize photosynthates. Four distinct morphological crown forms of western hemlock were observed on all three tree farms, however, the efficiency within and between the four forms was not determined. The crown forms are made distinct by the branching characteristics.

The four forms and their description are:

1) comb form: second order branches hang down in a comb-like curtain (Appendix I),

2) flat-branched form: second and third order branches develop in the same horizontal plane (Appendix II),

3) steeple form: the majority of the first order branches in the upper half of the tree crown droop straight down (average width approx. 1 m.), while the lower half of the crown have long branches more or less at right angles to the stem (Appendix III),

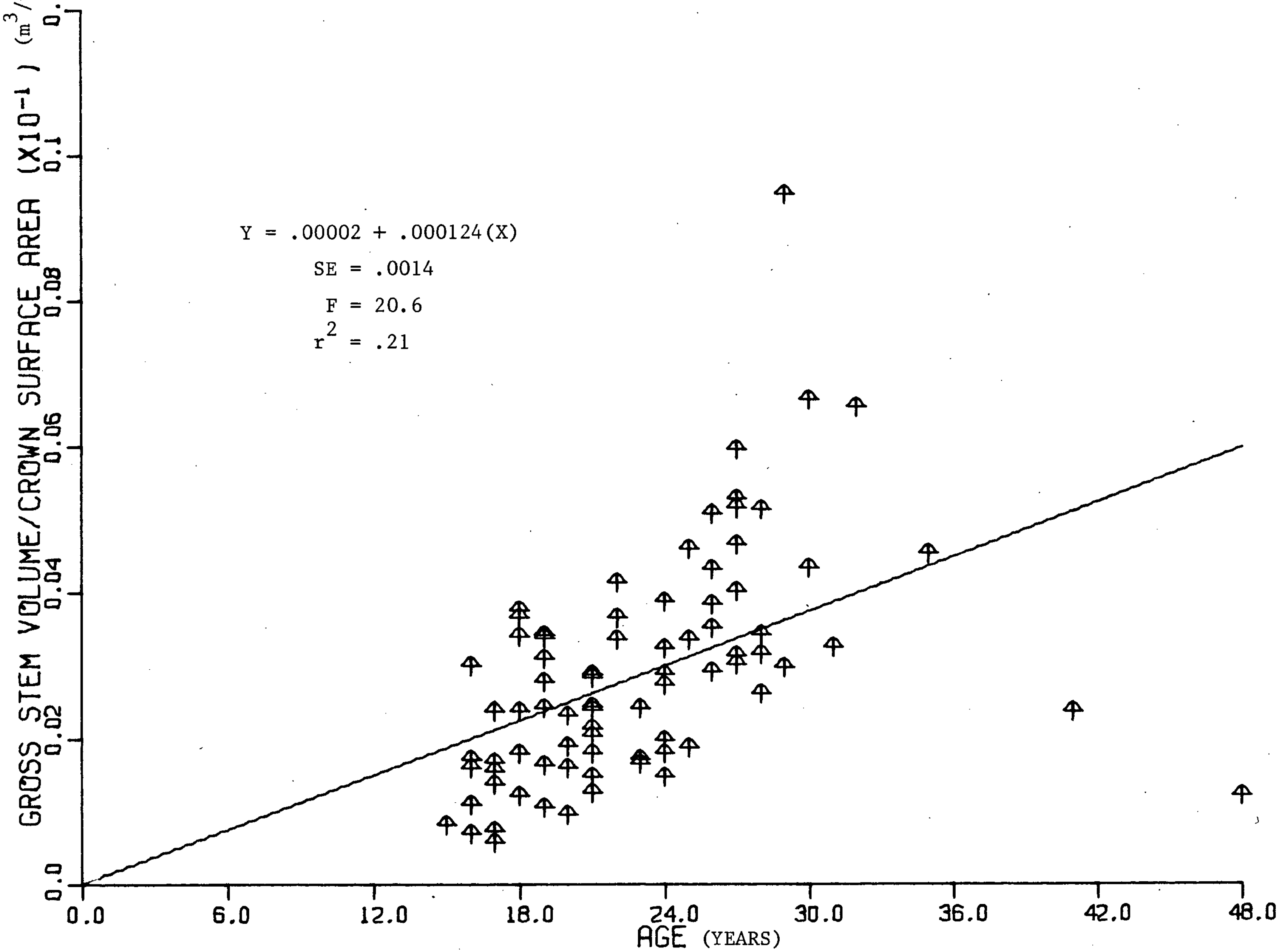
4) cedar form: fullness of the crown resembles a cedar crown with drooping branches (Appendix IV).

Differences in crown surface area are partly due to environment and partly due to heredity. The magnitude of these components are not defined for western hemlock, but crown width which will influence crown surface area is usually influenced more by stocking.

a) Model One: Growth Efficiency-Relating Gross Stem Volume/Crown Surface Area to Age

The range of variation in growth efficiency by relating gross stem volume (m^3)/crown surface area (m^2) to age for the 80 individual observations is shown in Figure 6. Observations above the regression line indicate efficient

FIGURE 6 MODEL 1: VARIATION IN GROWTH EFFICIENCY



wood producers in relation to their crown surface area and age, while observations below the regression line are less efficient for wood production in relation to their crown surface area and age. Of the 80 observations, 35 occurred above the regression line, while 45 occurred below the regression line. Figure 7 shows a plot of the standardized residuals with a variable range of 4.189 for tree #26 to -3.422 for tree #27.

The regression equation,

$$y = .00002 + .000124(x)$$

where y = gross stem volume/crown surface area, and

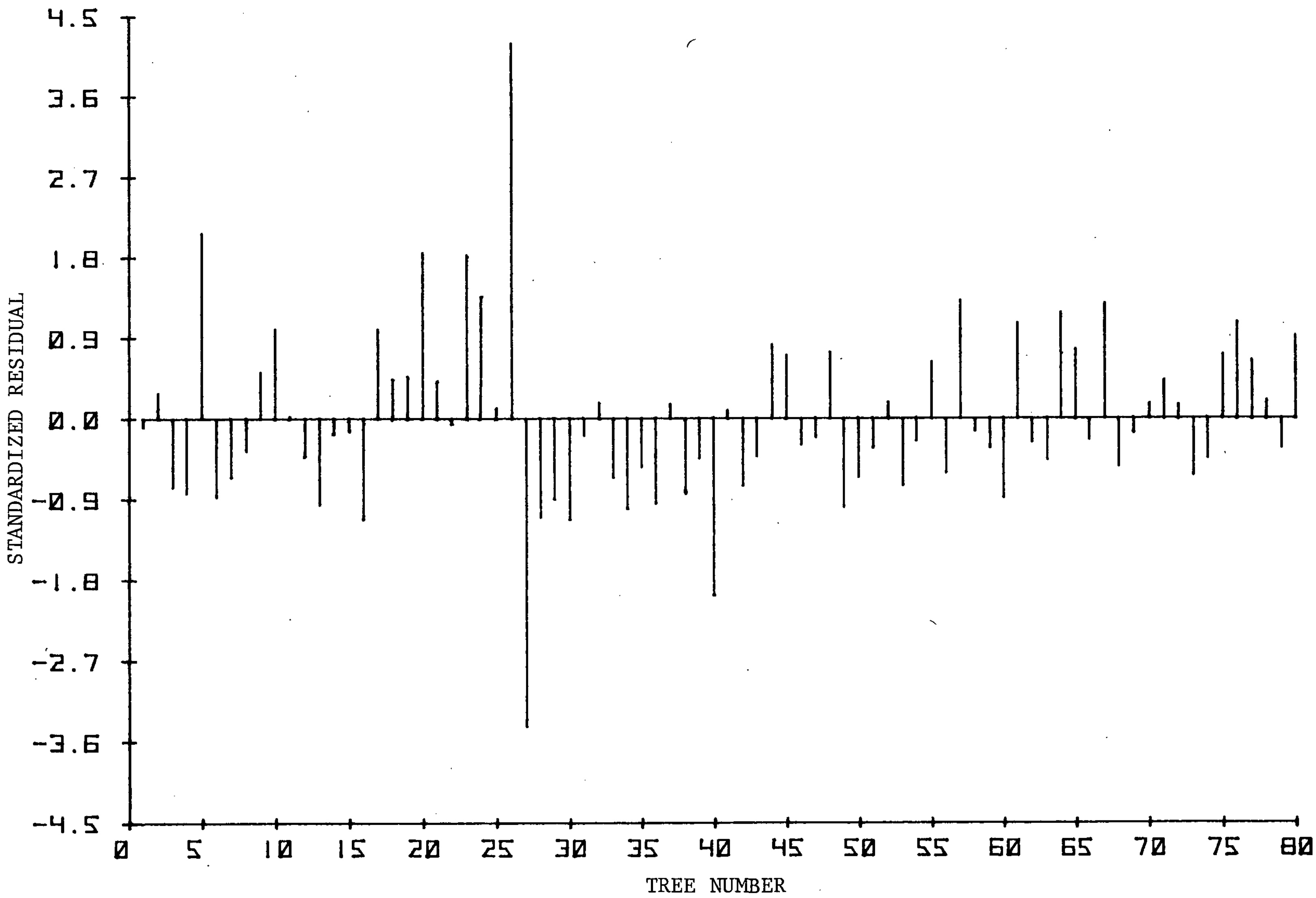
x = age,

takes into account the competitive influence to which a tree has been subjected, and according to Ledig (1974) is theoretically a sound approach. If the crown surface area can be considered a good indication of the competition a tree has undergone, then selection of gross stem volume at a given age should be based on individuals which produced the largest gross stem volume in relation to their crown surface area.

Based on the above observations, a correlation coefficient of .46 was calculated between the independent variable, age, and the dependent variable, gross stem volume/crown surface area. The regression is significant at the .01 level of significance. Referring again to Figures 6 and 7, it is apparent that there is a wide range of variation in growth efficiency when gross stem volume/crown surface area is related to age. A coefficient of variation of 48.6% was computed by this regression model.

It is not unreasonable to suspect that at least part of this variation

FIGURE 7 MODEL 1: VARIATION IN GROWTH IN GROWTH EFFICIENCY REPRESENTED BY STANDARDIZED RESIDUALS



is due to heritable factors. Therefore, selection for gross stem volume in relation to crown surface area and age could be worthwhile.

b) Model Two: Growth Efficiency-Relating Ten Year Basal Area Increment to Crown Surface Area

The range of variation in growth efficiency by relating ten year basal area increment (cm^2) to crown surface area (m^2) for the 80 individual observations is shown in Figure 8. A scatter diagram of ten year basal area increment on crown surface area showed a V-shaped distribution with the variances increasing linearly with crown surface area. Therefore, a weighted least square regression technique was used in the analysis.

For this regression model crown surface area accounted for 52 percent of the variance of ten year basal area increment. The regression is significant at the .01 level of significance. Observations above the regression line in Figure 8 indicate trees efficient in radial growth in relation to their crown surface area, while observations below the regression line indicate trees which are less efficient in radial growth in relation to their crown surface area.

Of the 80 observations, 36 occurred above the regression line, while 44 occurred below. Figure 9 shows a plot of the standardized residuals with a variable range of 2.541 for tree #17 to -1.659 for tree #36.

Again, the regression equation,

$$y = 51.55 + 2.495(x),$$

where y = ten year basal area increment, and

x = crown surface area,

FIGURE 8 MODEL 2: VARIATION IN GROWTH EFFICIENCY

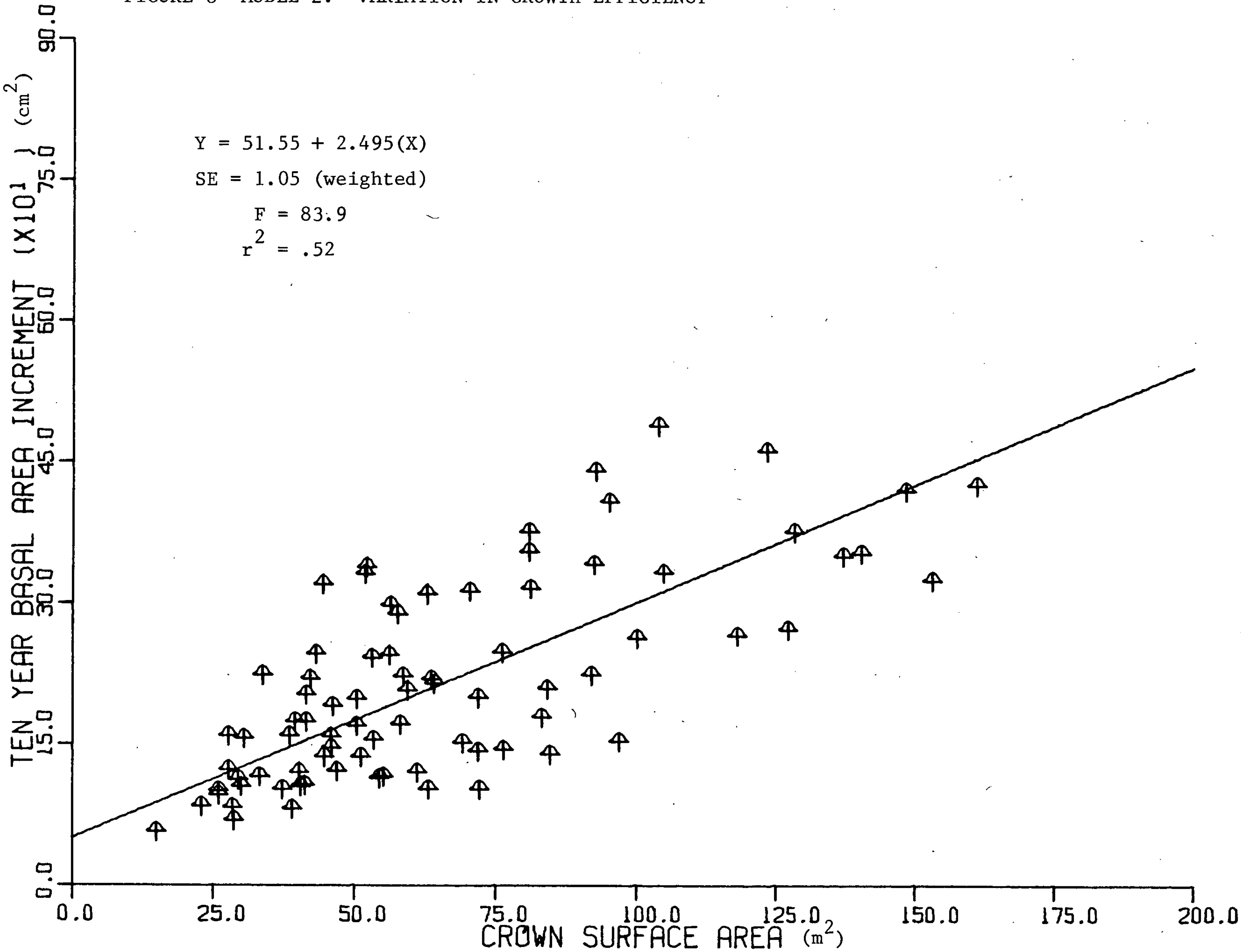
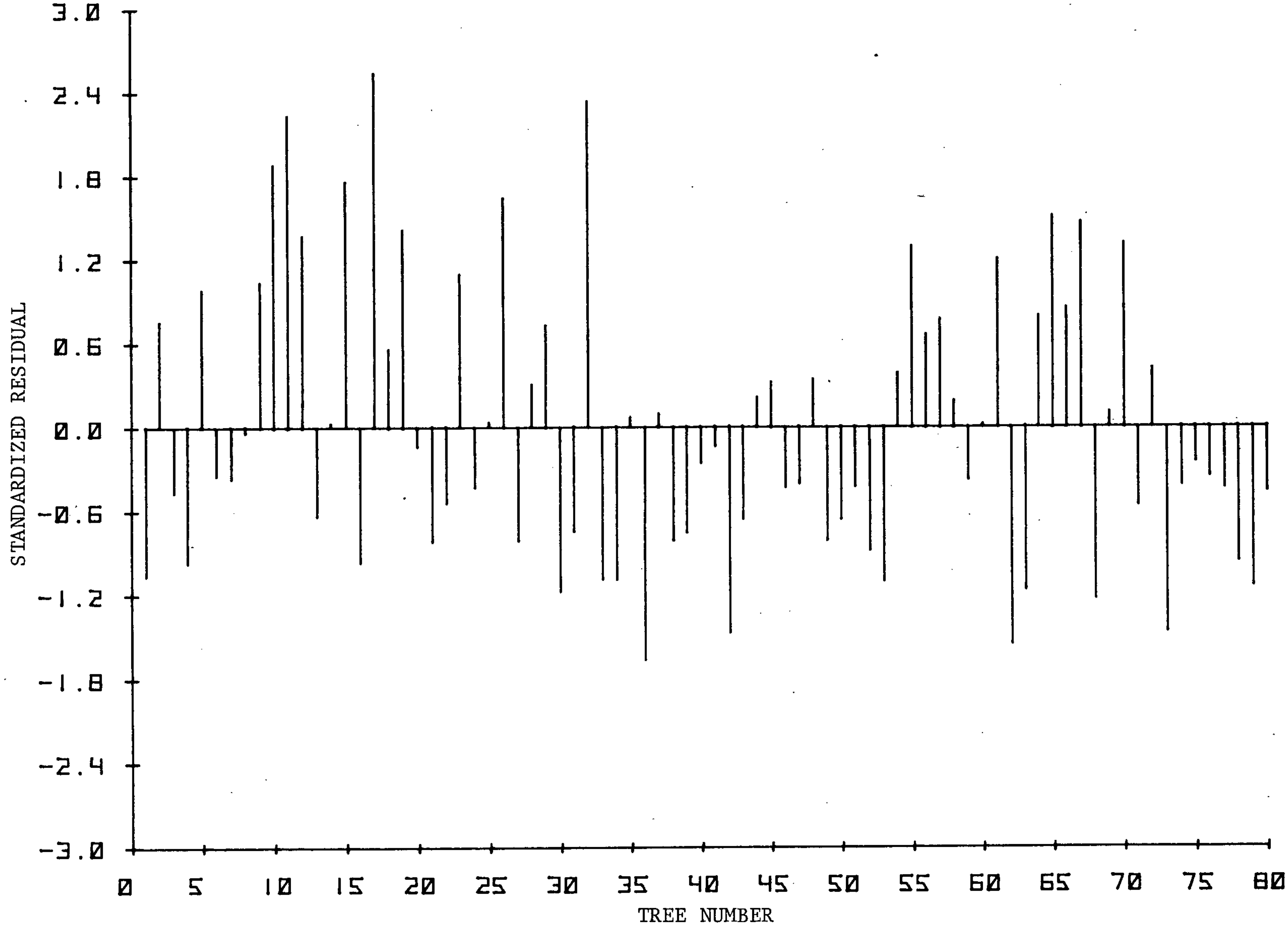


FIGURE 9 MODEL 2: VARIATION IN GROWTH EFFICIENCY REPRESENTED BY STANDARDIZED RESIDUALS



takes into account the competitive influence to which a tree has been subjected.

The use of ten year basal area increment as the dependent variable instead of gross stem volume has several advantages over the later. First, crown surface area is an estimate of past growth potential for a short span of time. Therefore, present crown surface area may not be a good representation of gross stem volume which is an accumulation of past growth. Assuming that the current crown is not much different from the crown at the start of the ten year period, and that the duration of the period has not seen major changes in the status of the crown; then the preceeding ten year period of growth is advantageous over gross stem volume. A second advantage is the relative ease to measure ten year basal area increment rather than gross stem volume.

Referring again to Figures 8 and 9, it is apparent that there is a wide range of variation of ten year basal area increment in relation to crown surface area. For the observations measured a coëfficient of variation of 16.3% was computed.

Again, it is not unreasonable to suspect that at least part of this variation is due to heritable factors. Therefore, selection of growth efficiency by relating ten year basal area increment to crown surface area may be worthwhile.

c) Model Three: Growth Efficiency-Relating Ten Year Basal Area Increment to Sapwood Basal Area

As mentioned in the literature review, sapwood basal area is a direct measurement of a tree's leaf area or crown surface area. Previous regressions using sapwood basal area to predict projected foliage area (Whitehead, 1978) and foliage mass (Grier and Waring, 1974) were found to be highly correlated.

The regression of crown surface area on sapwood basal area for the 80 observations is shown in Figure 10. This relationship has a correlation coefficient of .63 and is significant at the .01 level of significance.

The correlation coefficient of .63 is lower than those observed by Whitehead (1978) for Scots pine (r=.98, n=11), and Grier and Waring (1974) for Douglas-fir (r=.98, n=33), noble fir (r=.99, n=10), and ponderosa pine (r=.98, n=9). This may be due to a higher relationship between sapwood basal area and foliage area or mass, than sapwood basal area and crown surface area. The difference may also be due to differences in shade tolerance. Western hemlock is considered a shade tolerant species, whereas Douglas-fir, ponderosa pine, Scots pine, and noble fir are considered shade intolerant (Fowells, 1965). However this does not negate the use of substituting sapwood basal area for crown surface area to predict ten year basal area increment.

The use of sapwood basal area at 1.3 meters above ground rather than crown surface area to predict ten year basal area increment has an obvious advantage in measurement. Since three increment cores have already been extracted to measure ten year basal area increment the staining and measuring of these same three cores to determine sapwood basal area presents more ease and less time than measuring the live crown length and twelve crown radii to determine crown surface area.

The range of variation in growth efficiency by relating ten year basal area increment (cm^2) to sapwood basal area (cm^2) for the 80 observations is shown in Figure 11. A scatter diagram of ten year basal area increment on sapwood basal area showed a V-shaped distribution with the variances increasing linearly with sapwood basal area. Again, a weighted least square regression technique was used in the analysis.

For this regression model, sapwood basal area accounted for 82 percent of the variance of ten year basal area increment. This regression model is

FIGURE 10 REGRESSION OF CROWN SURFACE AREA ON SAPWOOD BASAL AREA

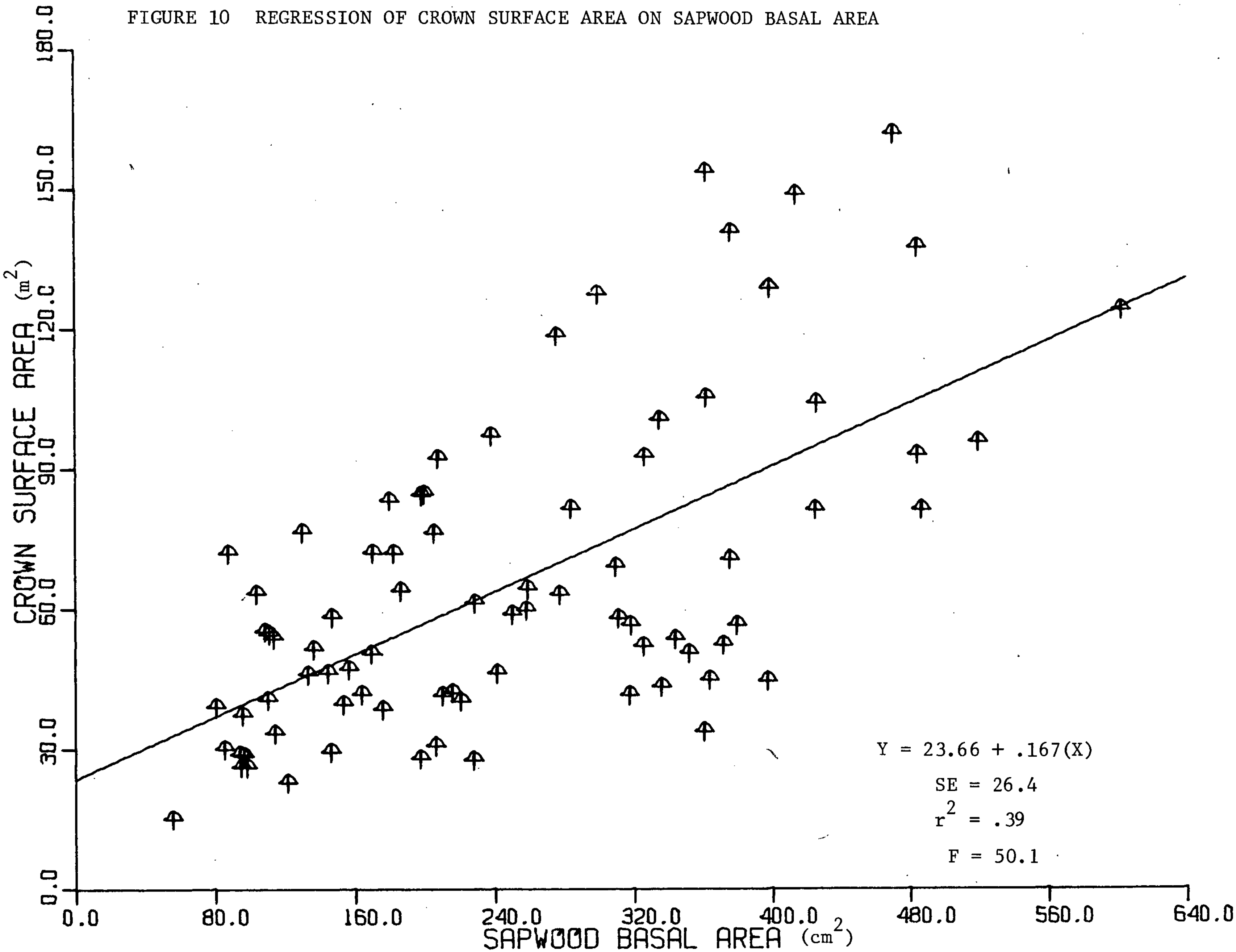
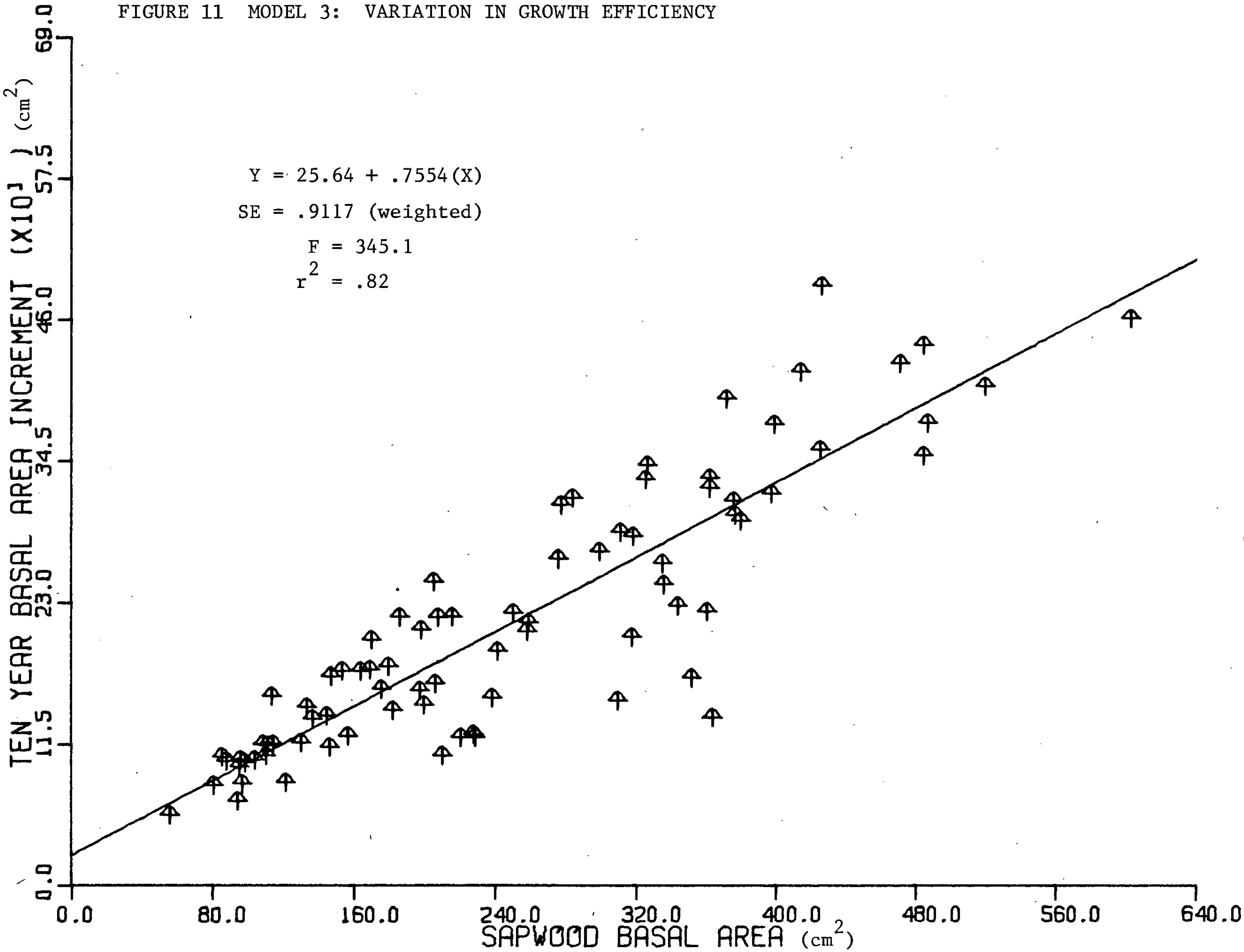


FIGURE 11 MODEL 3: VARIATION IN GROWTH EFFICIENCY



also significant at the .01 level of significance. Again, observations above the regression line indicate trees efficient in radial growth in relation to their sapwood basal area, while observations below the regression line indicate trees which are less efficient in radial growth in relation to their sapwood basal area.

Of the 80 observations, 42 occurred above the regression line, while 38 occurred below the regression line. Figure 12 shows a plot of the standardized residuals with a variable range of 2.361 for tree #10 to -2.979 for tree #24.

Since sapwood basal area is related to crown surface area the regression equation,

$$y = 25.64 + .7554(x)$$

where y = ten year basal area increment, and

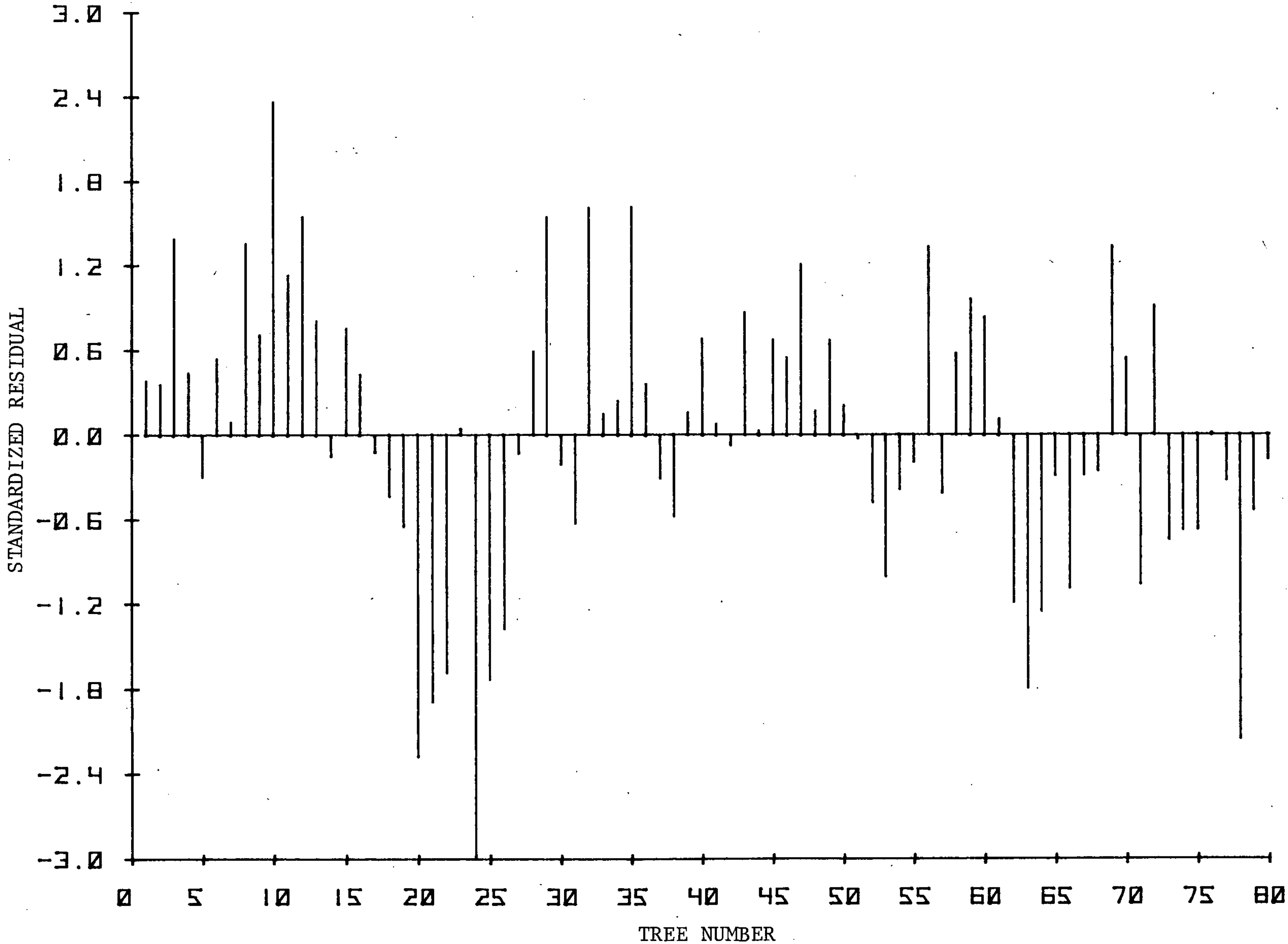
x = sapwood basal area,

takes into account the competitive influence to which a tree has been subjected.

Again, it appears in Figures 11 and 12 that there is a wide range of variation of ten year basal area increment in relation to sapwood basal area. A coefficient of variation of 3.1% was computed by this regression model.

Therefore, as in the other two regression models, it is not unreasonable to suspect that at least part of this variation is due to heritable factors. Therefore, selection for ten year basal area increment in relation to sapwood basal area could be worthwhile.

FIGURE 12 MODEL 3: VARIATION IN GROWTH EFFICIENCY REPRESENTED BY STANDARDIZED RESIDUALS



2. Utilization of Variation in Growth Efficiency

Knowing that a sufficient range of variation in growth efficiency exists for all three regression models, we should consider how to utilize this variation. In order to locate superior phenotypes to be tested for genetic superiority a statistical relationship between the observations and the mean of the population is necessary to predict the degree of improvement that can be expected.

There are different methods to utilize this information, but one approach is the use of base-line selection. As mentioned in the literature review, base-line selection provides standards with which to compare the growth efficiency of individual trees.

The regression of the dependent variable on the independent variable can be considered the base-line. The base-line, which is the regression line, serves as an environmental reference and the residual variation is equated with genetic variance. Therefore, selection for growth efficiency of the measured trees is based on individuals with residuals above a desired standard such as two standard errors of the estimate.

In order to use standard errors of the estimate to select for efficiently growing trees, the frequency distribution of the residuals should be normal. The residuals from all three regression models approximate a normal distribution. Figures 13, 14, and 15 show the plotting of the cumulative normal and observed distribution for the three regression models. Table 2 shows the cumulative percent under the normal and observed distributions at various standard errors of the estimate. Although the observed distributions for each model are skewed to some degree, a t-test for skewness showed that the distributions were not significantly different from normal at the .05 level of significance.

FIGURE 13 CUMULATIVE NORMAL AND OBSERVED DISTRIBUTIONS FOR MODEL 1

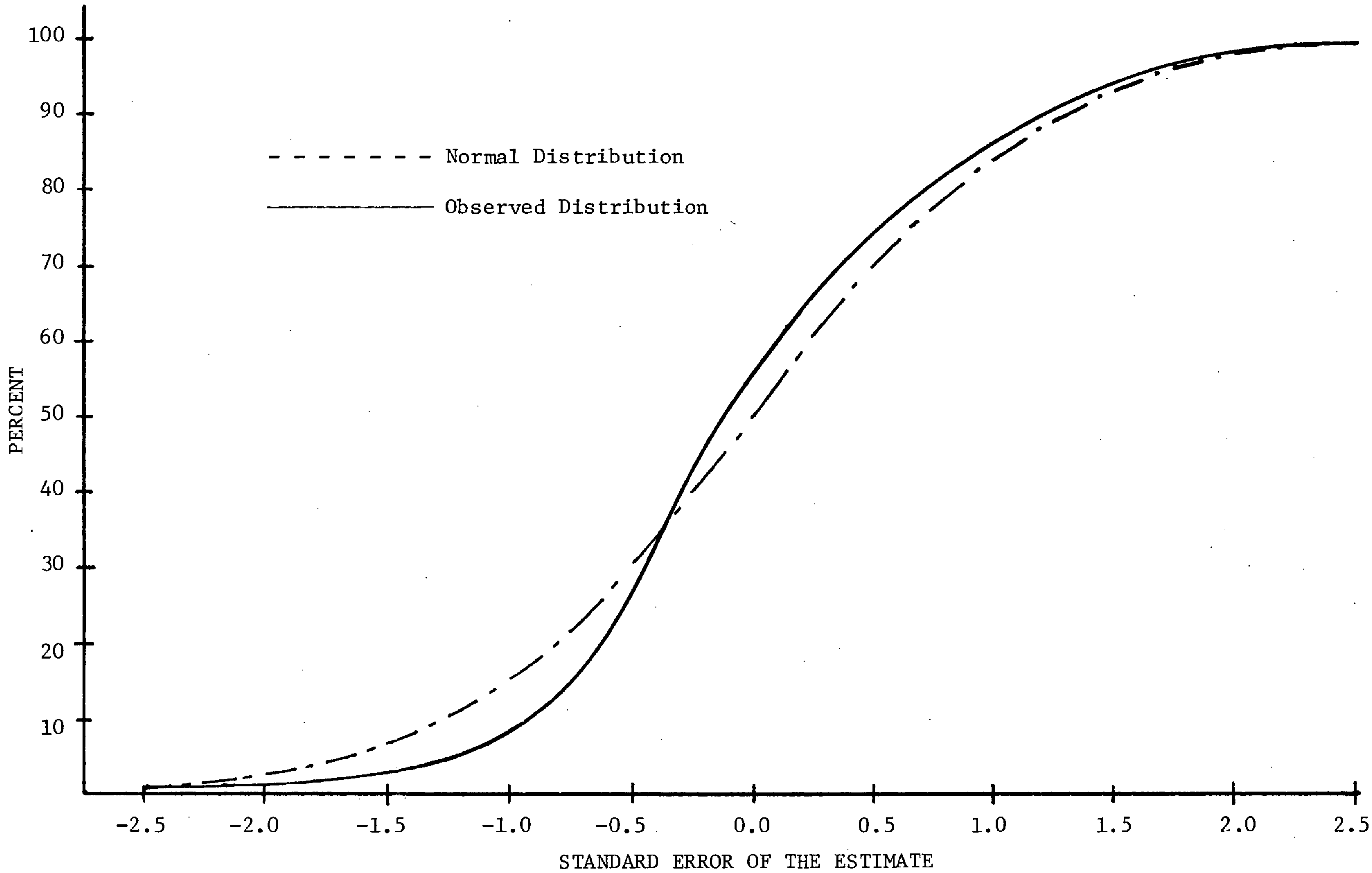


FIGURE 14 CUMULATIVE NORMAL AND OBSERVED DISTRIBUTIONS FOR MODEL 2

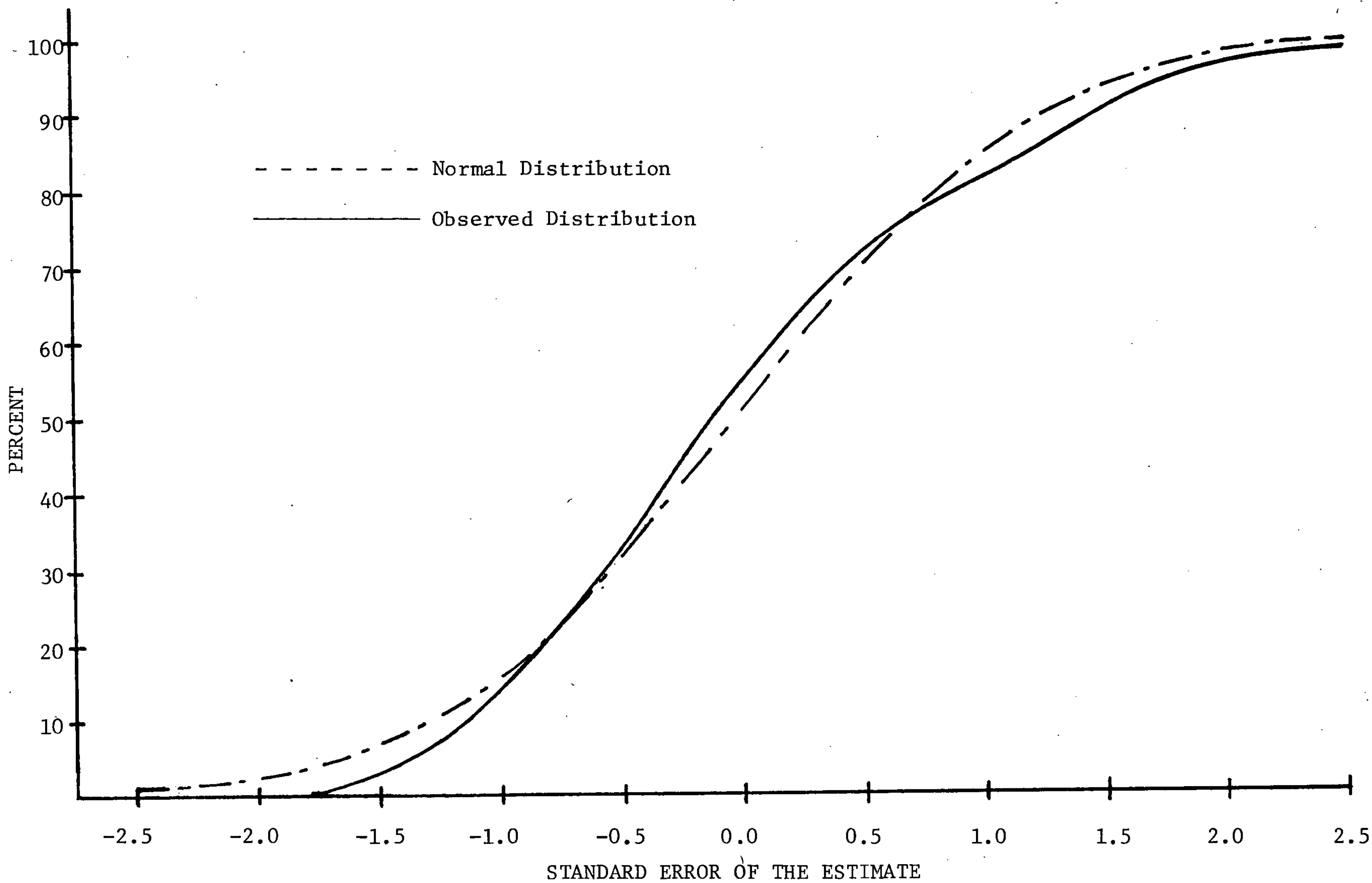


FIGURE 15 CUMULATIVE NORMAL AND OBSERVED DISTRIBUTIONS FOR MODEL 3

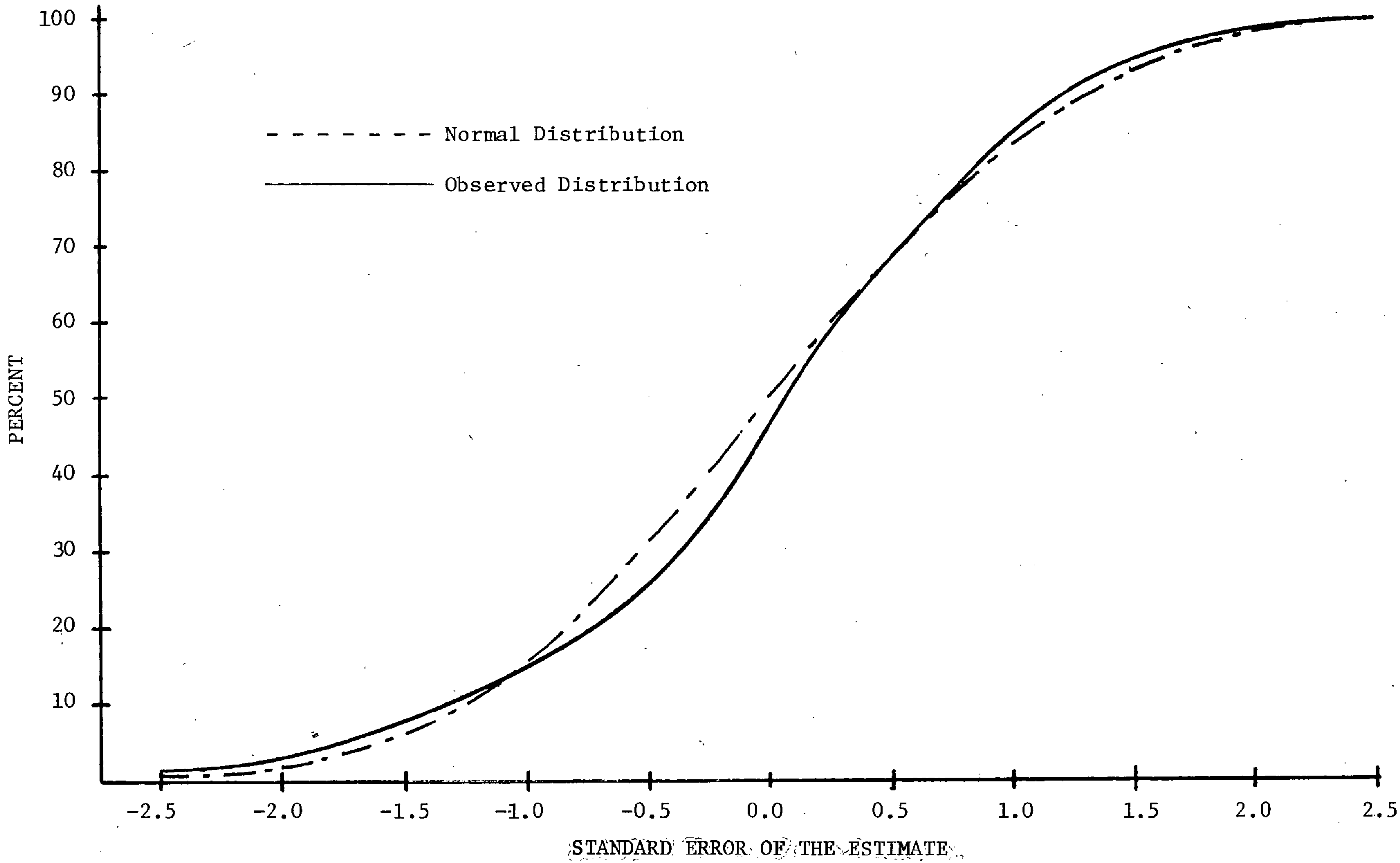


TABLE 2: CUMULATIVE PERCENT UNDER THE NORMAL AND OBSERVED DISTRIBUTIONS

STANDARD ERROR OF THE ESTIMATE	% NORMAL DISTRIBUTION	% OBSERVED DISTRIBUTION MODEL 1	MODEL 2	MODEL 3
-2.5	0.62	1.25	0.0	1.25
-2.0	2.28	1.25	0.0	3.75
-1.5	6.68	2.50	2.50	8.75
-1.0	15.87	6.25	15.00	15.00
-0.5	30.85	30.00	33.85	25.00
0.0	50.00	56.25	55.00	47.50
0.5	69.15	73.75	71.25	67.50
1.0	84.13	86.25	81.25	86.25
1.5	93.32	93.75	91.25	93.75
2.0	97.72	97.50	96.25	98.75
2.5	99.38	98.75	98.75	100.00

According to the needs of a particular tree improvement program any level of standard errors of estimate can be employed as a selection guideline. In all three regression models, +2.054 and +2.33 standard errors of the estimate, which is equivalent to selection intensities of one in fifty and one in a hundred respectively, are used as selection guidelines for growth efficiency. Therefore, only those trees whose standardized residual exceeds 2.054 or 2.33 will be selected for growth efficiency.

Figure 16 shows the selection of efficient individuals for the first regression model of gross stem volume/crown surface area on age. A selection intensity of one in fifty will select trees #5 and #26 which have standardized residuals of 2.075 and 4.189 respectively, while only tree #26 will be selected at an intensity of selection of one in a hundred.

For the second regression model, Figure 17, of ten year basal area increment on crown surface area, only three trees will be selected with a selection intensity of one in fifty, namely trees #11, 17 and 32. For this regression model, two trees had standardized residuals greater than 2.33. Hence, trees #17 and #32 are selected at the selection intensity of one in a hundred.

The selection of efficient individuals by the last regression model of ten year basal area increment on sapwood basal area is shown in Figure 18. Only one tree is selected, tree #10, whose standardized residual exceeds both levels of intensity.

Table 3 shows the standardized residual and ranking of the 80 individual observations for all three regression models. All three regression models of evaluating growth efficiency are plausible and will locate superior phenotypes to be tested for genetic superiority, but there appears to be a wide range of variation between the ranking of the observations by the three regression models.

FIGURE 16 MODEL 1: SELECTION OF EFFICIENTLY GROWING INDIVIDUALS

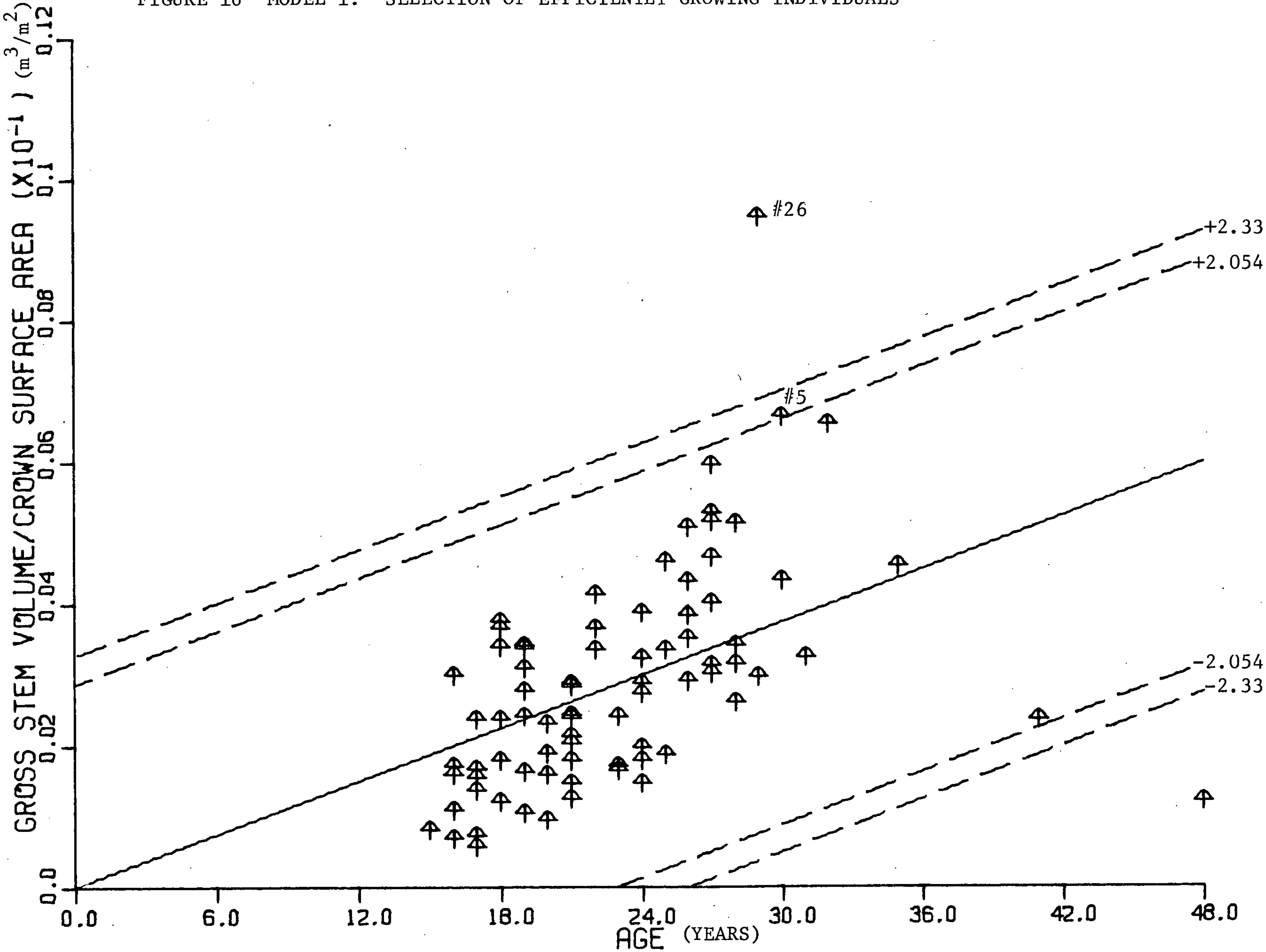


FIGURE 17 MODEL 2: SELECTION OF EFFICIENTLY GROWING INDIVIDUALS

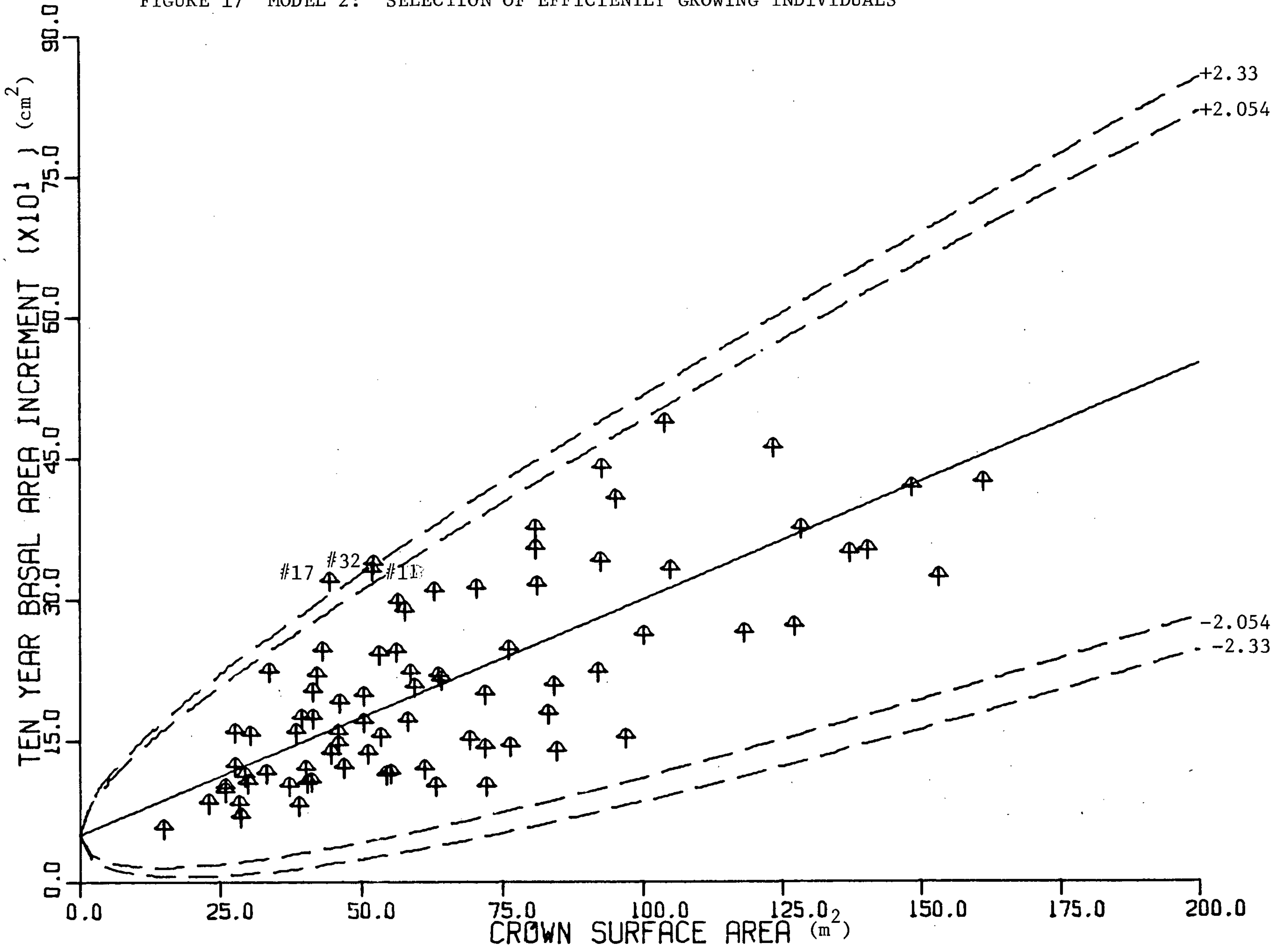


FIGURE 18 MODEL 3: SELECTION OF EFFICIENTLY GROWING INDIVIDUALS

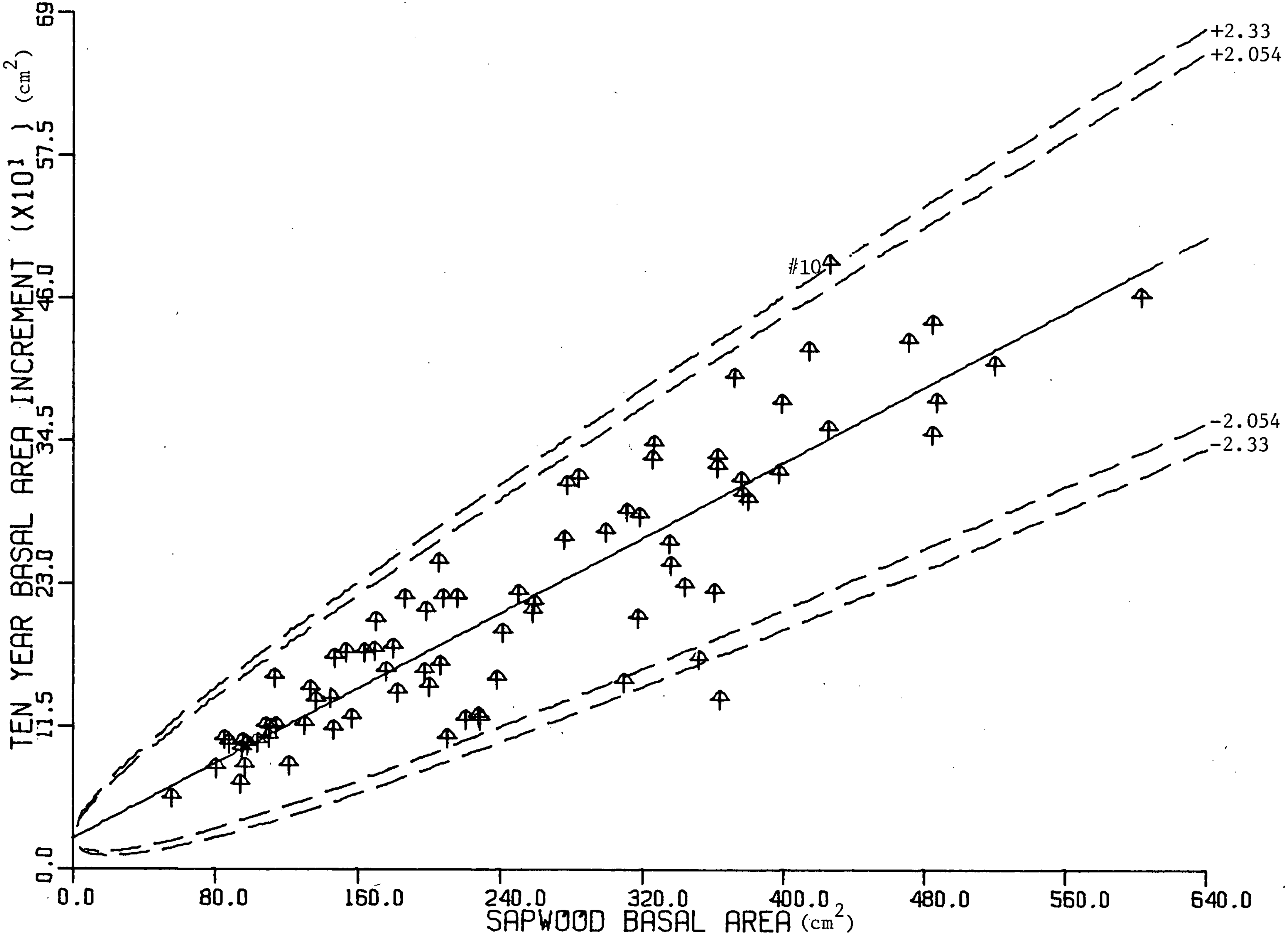


TABLE 3: STANDARDIZED RESIDUALS AND RANKING OF THE 80 OBSERVATIONS

TREE NO.	MODEL 1 STD. RESIDUAL	RANK	MODEL 2 STD. RESIDUAL	RANK	MODEL 3 STD. RESIDUAL	RANK
1	-0.093	37	-1.060	69	0.385	29
2	0.288	26	0.758	20	0.357	31
3	-0.759	66	-0.462	53	1.392	7
4	-0.827	68	-0.966	68	0.439	27
5	2.075 *	2	0.985	16	-0.294	54
6	-0.865	69	-0.341	42	0.540	26
7	-0.649	61	-0.362	44	0.089	38
8	-0.353	51	-0.039	37	1.357	6
9	0.522	21	1.041	15	0.711	18
10	1.001	11	1.882	4	2.361 **	1
11	0.033	35	2.239 *	3	1.131	11
12	-0.416	53	1.374	10	1.547	4
13	-0.947	73	-0.635	56	0.808	16
14	-0.171	41	0.035	35	-0.147	47
15	-0.138	39	1.762	5	0.755	17
16	-1.112	77	-0.964	67	0.427	28
17	0.989	12	2.541 **	1	-0.122	45
18	0.442	23	0.560	23	-0.430	59
19	0.468	22	1.415	9	-0.642	64
20	1.848	3	-0.133	38	-2.274	78

* exceeds selection intensity of 1/50
** exceeds selection intensity of 1/100

TABLE 3 (CONT.)

TREE NO.	MODEL 1 STD. RESIDUAL	RANK	MODEL 2 STD. RESIDUAL	RANK	MODEL 3 STD. RESIDUAL	RANK
21	0.416	25	-0.816	64	-1.883	77
22	-0.059	36	-0.538	54	-1.679	74
23	1.822	4	1.098	14	0.047	40
24	1.361	5	-0.425	49	-2.979	80
25	0.120	33	0.040	34	-1.726	75
26	4.189**	1	1.641	6	-1.369	73
27	-3.422	80	-0.807	62	-0.126	46
28	-1.089	76	0.309	28	0.590	22
29	-0.891	71	0.731	21	1.543	5
30	-1.117	78	-1.172	75	-0.204	50
31	-0.183	42	-0.741	59	-0.622	63
32	0.177	29	2.338**	2	1.608	3
33	-0.654	63	-1.084	70	0.150	36
34	-0.993	75	-1.087	77	0.240	32
35	-0.534	58	0.072	33	1.615	2
36	-0.939	72	-1.659	80	0.358	30
37	0.167	30	0.097	32	-0.303	55
38	-0.823	67	-0.808	63	-0.572	62
39	-0.439	54	-0.751	60	0.157	35
40	-1.963	79	-0.255	41	0.679	19

TABLE 3 (CONT.)

TREE NO.	MODEL 1 STD. RESIDUAL	RANK	MODEL 2 STD. RESIDUAL	RANK	MODEL 3 STD. RESIDUAL	RANK
41	0.093	34	-0.134	39	0.074	39
42	-0.745	65	-1.466	78	-0.073	44
43	-0.414	52	-0.655	57	0.863	14
44	0.823	14	0.215	29	0.030	41
45	0.706	18	0.322	27	0.673	20
46	-0.289	47	-0.428	50	0.547	24
47	-0.208	43	-0.400	46	1.209	10
48	0.741	16	0.344	26	0.168	34
49	-0.984	74	-0.805	61	0.670	21
50	-0.650	62	-0.658	58	0.208	33
51	-0.318	48	-0.420	48	-0.025	43
52	0.182	28	-0.879	65	-0.474	60
53	-0.739	64	-1.097	72	-0.998	68
54	-0.246	45	0.387	25	-0.383	57
55	0.630	20	1.294	12	-0.191	49
56	-0.600	59	0.666	22	1.333	8
57	1.316	6	0.775	19	-0.409	58
58	-0.134	38	0.185	30	0.577	23
59	-0.321	49	-0.373	45	0.960	12
60	-0.877	70	0.023	36	0.831	15

TABLE 3 (CONT.)

TREE NO.	MODEL 1 STD. RESIDUAL	RANK	MODEL 2 STD. RESIDUAL	RANK	MODEL 3 STD. RESIDUAL	RANK
61	1.064	10	1.202	13	0.113	37
62	-0.260	46	-1.548	79	-1.186	71
63	-0.458	56	-1.161	74	-1.788	76
64	1.180	8	0.794	18	-1.244	72
65	0.774	15	1.508	7	-0.285	53
66	-0.231	44	0.853	17	-1.083	70
67	1.280	7	1.467	8	-0.283	52
68	-0.532	57	-1.221	76	-0.251	51
69	-0.158	40	0.108	31	1.332	9
70	0.166	31	1.314	11	0.542	25
71	0.418	24	-0.556	55	-1.056	69
72	0.154	32	0.420	24	0.909	13
73	-0.626	60	-1.459	77	-0.739	67
74	-0.442	55	-0.413	47	-0.672	66
75	0.712	17	-0.247	40	-0.669	65
76	1.075	9	-0.348	43	0.016	42
77	0.645	19	-0.430	51	-0.320	56
78	0.197	27	-0.954	66	-2.149	79
79	-0.327	50	-1.132	73	-0.530	61
80	0.920	13	-0.455	52	-0.171	48

To determine which variables and regression model is best to evaluate the growth efficiency of individual trees will rest on the outcome of inheritance studies. However, the last regression model that is relating ten year basal area increment to sapwood basal area, is the desired model to evaluate growth efficiency. This is based on the ease of measurement of the two variables and the high correlation between them.

The significance of the variation in growth efficiency becomes apparent in Table 4 which shows predicted ten year basal area increment/hectare (m^2) for various sapwood basal areas. Ten year basal area increment/hectare was estimated from the product of ten year basal area/tree (Model 3) and the number of trees/hectare for the corresponding sapwood basal area. By relating the variable base crown width to sapwood basal area, the number of trees/hectare can be estimated for a given sapwood basal area. The regression is significant at the .01 level of significance and has a correlation coefficient of .56.

For each given sapwood basal area, the ten year basal area increment/hectare was calculated for five classes of growth efficiency based on Model 3. The classes are defined as--

<u>low growth efficiency</u>: trees which are -2.33 standard errors of the estimate from the regression line

<u>medium low growth efficiency</u>: trees which are -2.054 standard errors of the estimate from the regression line

<u>average growth efficiency</u>: trees on the regression line

<u>medium high growth efficiency</u>: trees which are +2.054 standard errors of the estimate from the regression line

<u>high growth efficiency</u>: trees which are +2.33 standard errors of the estimate from the regression line

TABLE 4: PREDICTED TEN YEAR BASAL AREA INCREMENT/HECTARE AT VARIOUS SAPWOOD BASAL AREAS AND CLASSES OF EFFICIENCY

SAPWOOD BASAL AREA (cm^2)	CLASSES OF EFFICIENCY				
	LOW (m^2)	MED.LOW (m^2)	AVE. (m^2)	MED.HIGH (m^2)	HIGH (m^2)
60	2.7	3.6	10.2	16.8	17.7
70	3.1	4.1	10.9	17.8	18.7
80	3.5	4.5	11.6	18.7	19.6
90	3.9	4.9	12.2	19.5	20.4
100	4.3	5.3	12.7	20.1	21.1
110	4.7	5.7	13.2	20.8	21.8
120	5.1	6.1	13.7	21.3	22.3
130	5.4	6.5	14.1	21.8	22.9
140	5.8	6.8	14.5	22.3	23.3
150	6.1	7.2	14.9	22.7	23.7
160	6.4	7.5	15.3	23.0	24.1
170	6.7	7.8	15.6	23.4	24.4
180	7.0	8.1	15.9	23.6	24.7
190	7.3	8.4	16.1	23.9	24.9
200	7.6	8.6	16.4	24.1	25.2
210	7.9	8.9	16.6	24.3	25.4
220	8.1	9.1	16.8	24.5	25.5
230	8.4	9.4	17.0	24.7	25.7
240	8.6	9.6	17.2	24.8	25.8
250	8.8	9.8	17.4	24.9	25.9

TABLE 4 (CONT.)

SAPWOOD BASAL AREA (cm^2)	CLASSES OF EFFICIENCY				
	LOW (m^2)	MED.LOW (m^2)	AVE. (m^2)	MED.HIGH (m^2)	HIGH (m^2)
260	9.0	10.0	17.5	25.0	26.0
270	9.2	10.2	17.6	25.1	26.1
280	9.4	10.4	17.8	25.2	26.2
290	9.5	10.5	17.9	25.2	26.2
300	9.7	10.7	18.0	25.2	26.2
310	9.9	10.8	18.1	25.3	26.3
320	10.0	11.0	18.1	25.3	26.3
330	10.1	11.1	18.2	25.3	26.3
340	10.3	11.2	18.3	25.3	26.3
350	10.4	11.3	18.3	25.3	26.2
360	10.5	11.4	18.4	25.3	26.2
370	10.6	11.6	18.4	25.2	26.2
380	10.7	11.7	18.4	25.2	26.2
390	10.8	11.8	18.5	25.2	26.1
400	10.9	11.8	18.5	25.1	26.0
410	11.0	11.9	18.5	25.1	26.0
420	11.1	12.0	18.5	25.1	25.9
430	11.2	12.0	18.5	25.0	25.8
440	11.2	12.1	18.5	24.9	25.8
450	11.3	12.2	18.5	24.9	25.7

TABLE 4 (CONT.)

SAPWOOD BASAL AREA (cm^2)	CLASSES OF EFFICIENCY				
	LOW (m^2)	MED.LOW (m^2)	AVE. (m^2)	MED.HIGH (m^2)	HIGH (m^2)
460	11.4	12.2	18.5	24.8	25.6
470	11.4	12.3	18.5	24.7	25.6
480	11.5	12.3	18.5	24.6	25.5
490	11.6	12.4	18.5	24.6	25.4
500	11.6	12.4	18.5	24.5	25.3
510	11.7	12.5	18.4	24.4	25.2
520	11.7	12.5	18.4	24.3	25.1
530	11.7	12.5	18.4	24.3	25.1
540	11.8	12.5	18.3	24.1	24.9
550	11.8	12.6	18.3	24.1	24.8
560	11.8	12.6	18.3	24.0	24.8
570	11.9	12.6	18.2	23.9	24.6
580	11.9	12.6	18.2	23.8	24.6
590	11.9	12.7	18.2	23.7	24.5
600	11.9	12.7	18.1	23.6	24.4
610	11.9	12.7	18.1	23.5	24.2
620	11.9	12.7	18.0	23.4	24.1
630	12.0	12.7	18.0	23.3	24.0
640	12.0	12.7	18.0	23.2	24.0

The significance of the variation in growth efficiency is realized when percent differences are considered between medium high or high growth efficiency classes and the average growth efficiency. By selecting trees for growth efficiency which are +2.054 or +2.33 standard errors of the estimate from the regresssion line for a given sapwood basal area, the ten year basal area increment/hectare may increase by approximately 39 to 45% respectively. These values are based on the assumption that a hectare is fully stocked with uniform spacing. These results can be seen more clearly in Figure 19.

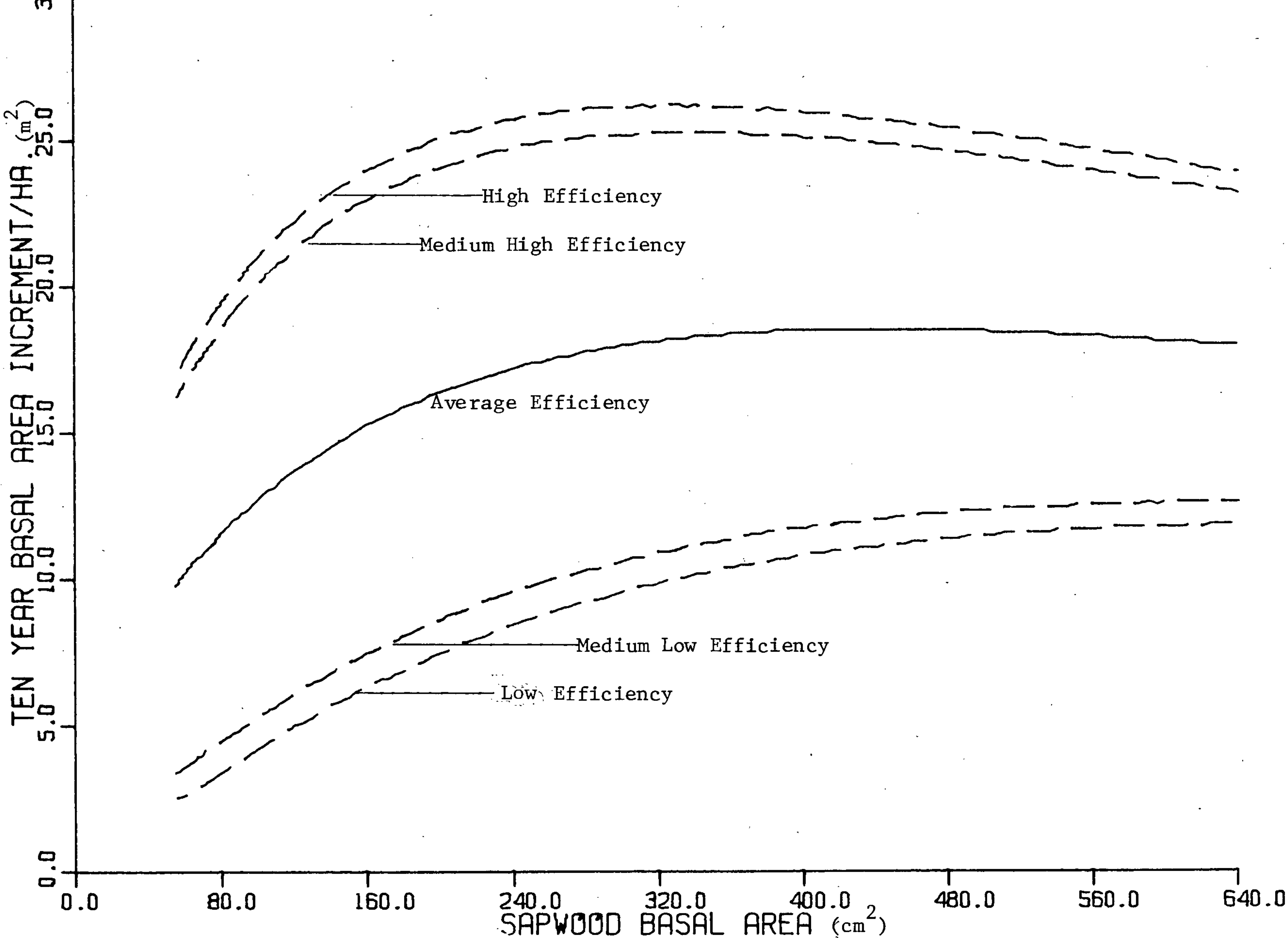
3. Efficiency of Narrow Crown Western Hemlock Trees

The third objective of this study was to determine the efficiency of narrow crown western hemlock trees as wood producers. If the same amount of wood can be added to the bole by a slimmer, more efficient crown rather than a wider crown, then more trees could be maintained on a unit area and hence the production of wood per unit area may increase.

The crown index ratio was used as a measurement of slenderness or broadness of a tree crown. The higher the ratio, the slimmer the crown. For the trees measured, an average crown index ratio of 2.94 was computed. Considering Walkup's (1978) average ratio of 2.5, a 17.6% increase is substantial when the difference in the number of trees per unit area is considered. For example, by increasing the ratio from 2.5 to 2.94 for trees at age 20, with a live crown length/total height ratio of 40% on a site index of 115 (base 50), 38% more trees could be maintained on a hectare.

To determine the efficiency of narrow crown western hemlock trees as wood producers, a simple linear regression of the standardized residuals from the three previous regressions were related to the crown index ratio. The plots of the three regressions are shown in Figures 20, 21, and 22.

FIGURE 19 TEN YEAR BASAL AREA INCREMENT/HECTARE FOR VARIOUS SAPWOOD BASAL AREAS AND CLASSES OF EFFICIENCY



Only the standardized residuals or efficiency from the first regression model (Figure 20) showed an increase as the crown index ratio increased. However, the coefficient of determination was only 2.0%, and the regression was not significant at the .05 level of significance. For the other two regression models (Figures 21 and 22), the efficiency decreased as the crown index ratio increased. Both regressions have very low r^2 values, 4.2% (Figure 21) and 8.2% (Figure 22). Figure 21 is also not significant at the .05 level of significance, whereas Figure 22 is significant.

In view of all three regressions, it appears that narrow crown western hemlock trees are less efficent for radial growth than wider crown trees. It is possible that the narrow crown trees measured in this study, trees with ratios greater than 4.0, may have been suppressed to some degree.

Although the growth efficiency (standardized residuals) increased as the crown index ratio increased in Figure 20, the increase is not substantial. Furthermore, the crown index ratio for all three regressions accounts for only a small part of the variance in growth efficiency.

Therefore, in the selection process of efficiently growing trees, selection for trees with efficient crowns should be based only on the ability of the crown to produce wood efficiently, and not on the degree of slenderness of the crown.

FIGURE 20 REGRESSION OF STANDARDIZED RESIDUALS FROM MODEL 1 ON THE CROWN INDEX RATIO

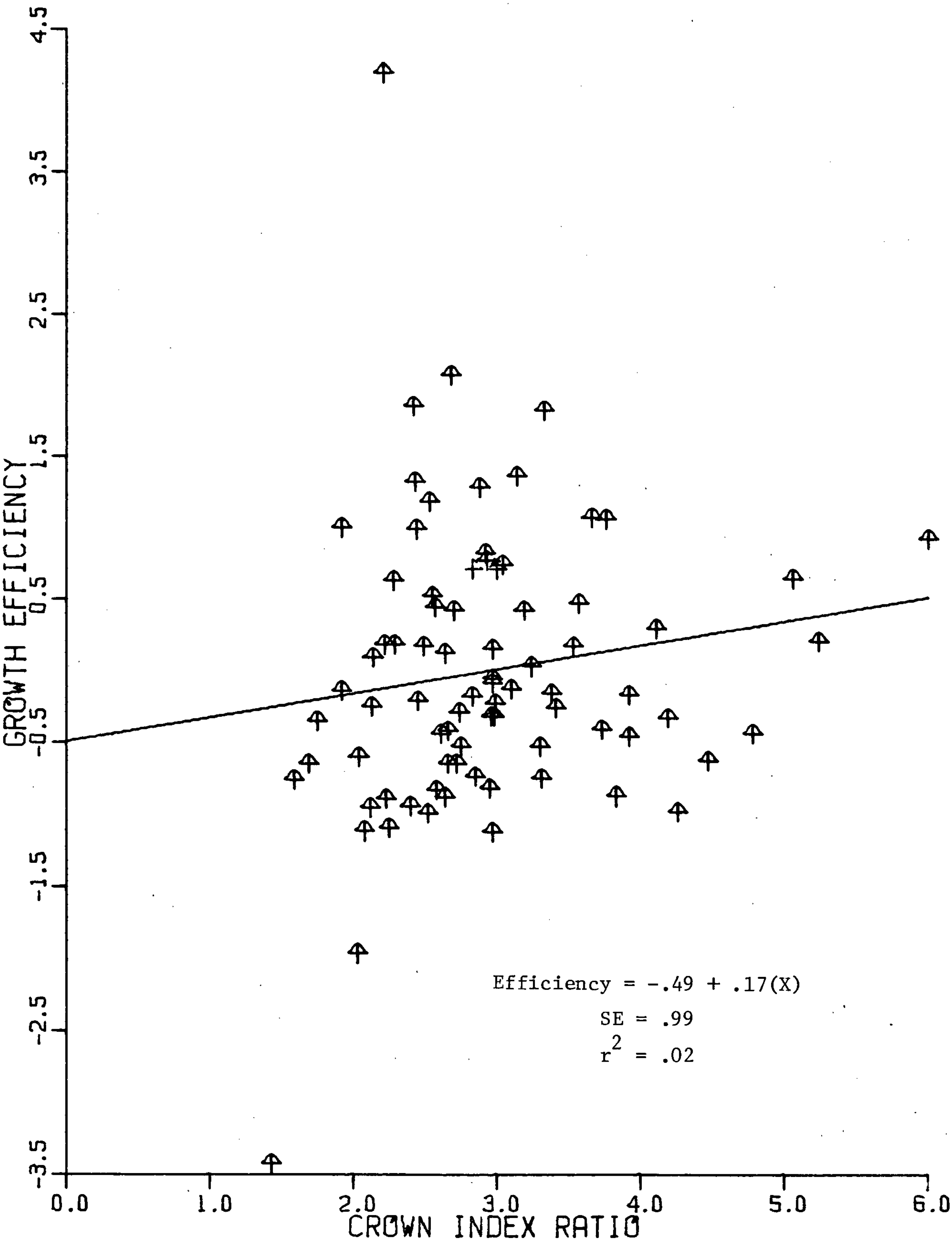


FIGURE 21 REGRESSION OF STANDARDIZED RESIDUALS FROM MODEL 2 ON THE CROWN INDEX RATIO

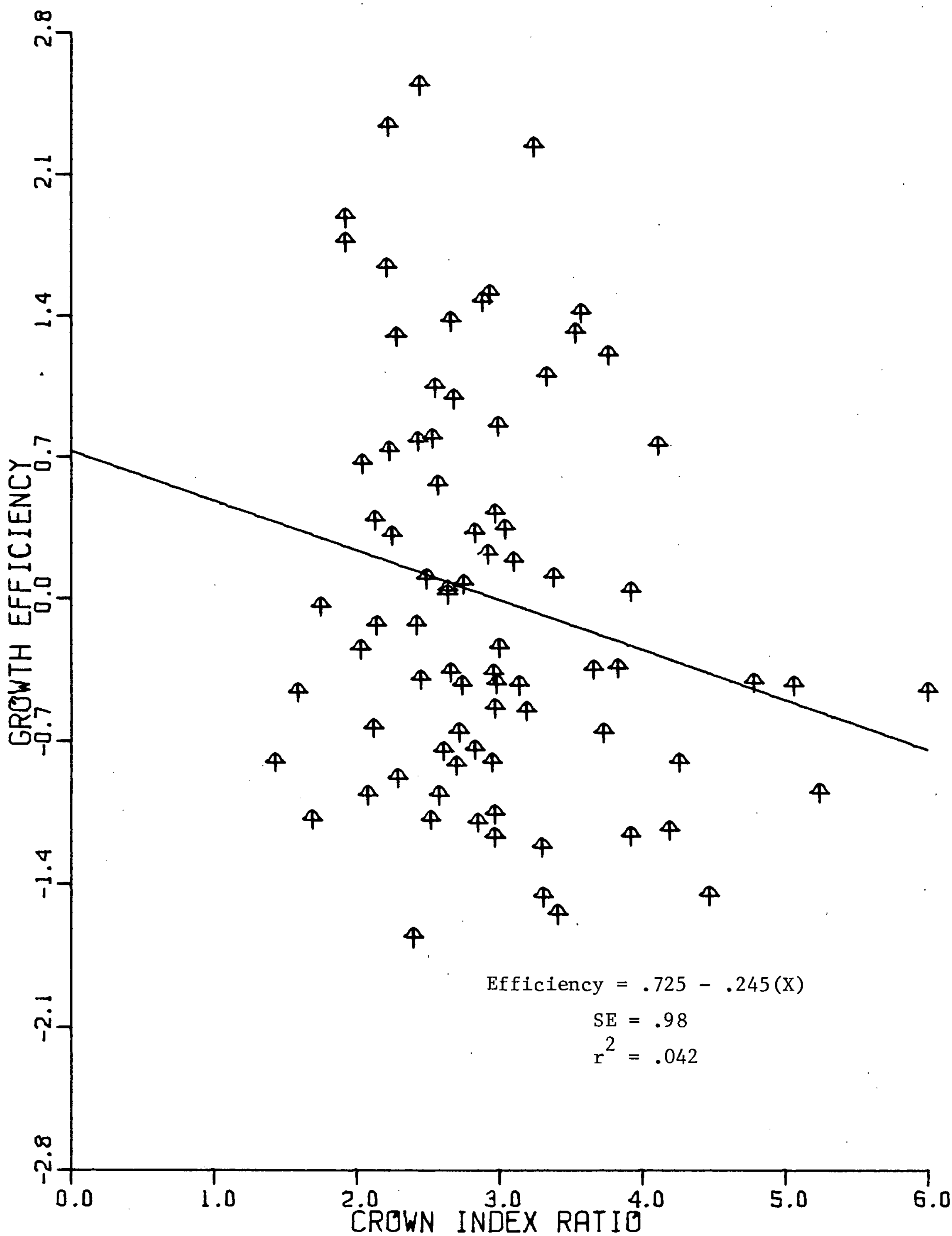
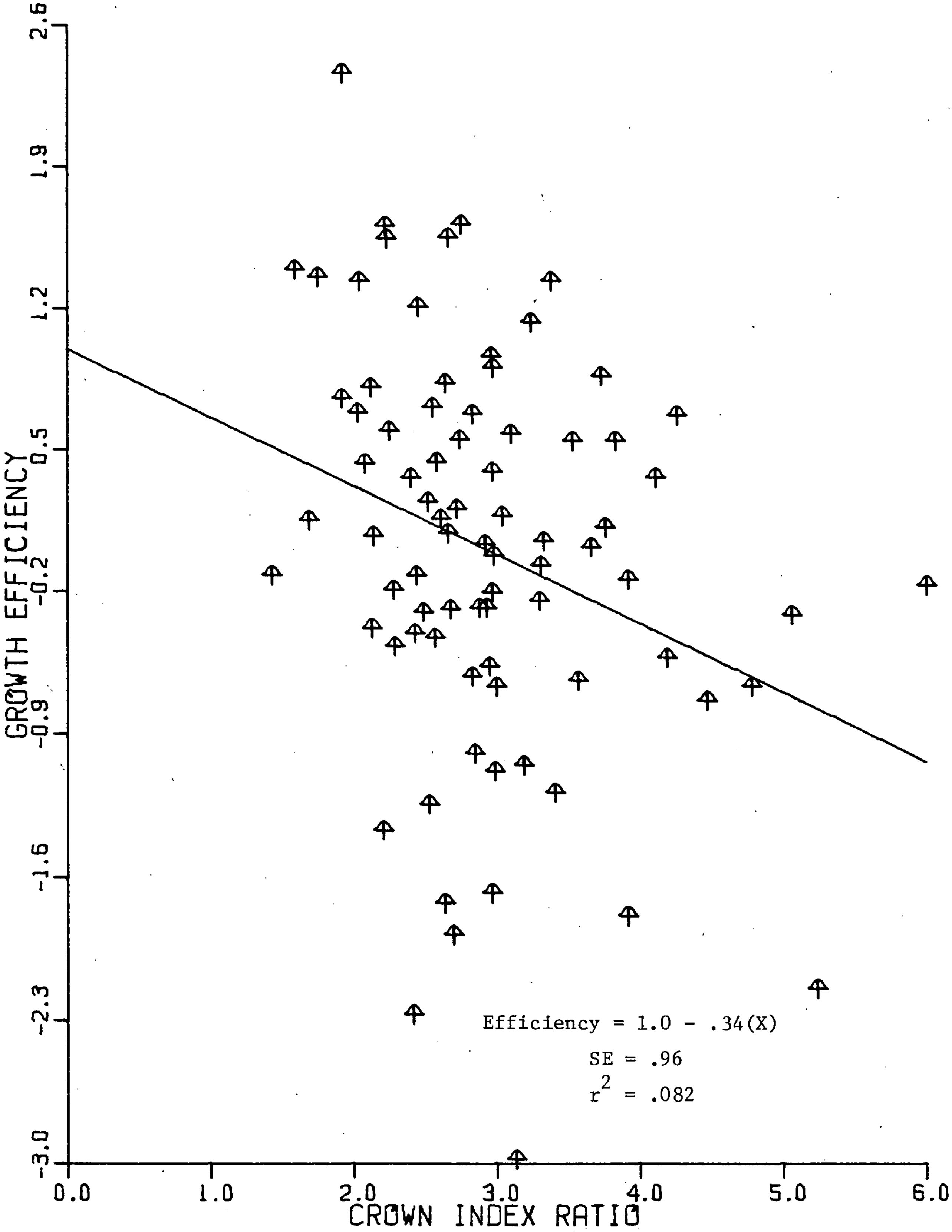


FIGURE 22 REGRESSION OF STANDARDIZED RESIDUALS FROM MODEL 3 ON THE CROWN INDEX RATIO



SUMMARY

The efficiences of the crown surface area for the individual trees should only be applied to the geographic region in which they were selected. Differences in efficiency of given leaf quantities may fluctuate in different climates, because the less favorable the climate, the larger the leaf quantities will be required to produce equal quantities of wood (Assman, 1970).

Three models,

1) gross stem volume/crown surface area = $a_1 + b_1$(age),
2) ten year basal area increment = $a_2 + b_2$(crown surface area), and
3) ten year basal area increment = $a_3 + b_3$(sapwood basal area),

were employed using least square regression techniques to determine the range of variation in growth efficiency of individual western hemlock trees. Growth efficiency is defined as the ability of the crown to produce the maximum amount of wood in relation to its crown surface area. The measure of growth efficiency was based on the size of the standardized residual.

It appears that for all three regression models, there is a sufficient range of variation in growth efficiency for western hemlock to make selection worthwhile. This is based on the range of sizes of the standardized residuals and the coefficients of variation of 48.6% for model 1, 16.3% for model 2, and 3.1% for model 3. Though the coefficient of variation for model 3 is small it should not be assumed that selection of trees with large ten year basal area increment is due to a correspondingly large sapwood basal area.

The crown surface area or sapwood basal area, which is related to crown surface area, is assumed to be a indication of the competition a tree has under-

gone. Therefore, all three regression models of evaluating growth efficiency are plausible since the size of the crown surface area is accounted for in the regression models.

The last regression model of relating ten year basal area increment to sapwood basal area is the desired model to evaluate growth efficiency. This is based on the ease of measurement of the two variables and the high correlation between them. Therefore, when selecting for plus trees it may be advisable to include the sapwood basal area measurement along with other traits of interest.

In all three regression models, +2.054 and +2.33 standard errors of the estimate which is equivalent to selection intensities of one in fifty and one in a hundred, respectively, were used as selection guidelines for growth efficiency. By selecting trees which are +2.054 or +2.33 standard errors of the estimate from the regression line instead of trees on the regression line in model 3, there may be an increase in ten year basal area increment/hectare of approximately 39 to 45 percent for the observations measured. The increase in ten year basal area increment/hectare demonstrates the importance of selecting for growth efficiency by evaluating the competition to which a tree has been subjected.

Though there is little relationship between growth efficiency and the degree of slenderness of the crown, it appears that narrow crown western hemlock trees are less efficient for radial growth than wider crown trees. Therefore, selection of trees with efficient crowns should be based only on the ability of the crown to produce wood efficiently and not on the degree of slenderness of the crown.

LITERATURE CITED

Alexandrov, A. 1971. The occurrence of forms of Norway spruce based on branching habit. Silvae Genetica 20: 204-208.

Assman, E. 1970. The principles of forest yield study. Pergamon Press; 506 pp, Oxford.

Barber, J.C. and M. Reines. 1956. Forest tree improvement in Georgia. Ga. For. Res. Counc. Rep. 1, 11p.

Barton, G.M. 1973. Chemical color tests for Canadian woods. Canadian Forest Industries, 93(2): 57-62.

Berlyn, G.P. 1962. Some size and shape relationships between tree stems and crowns. Iowa State J. Sci. 37(1): 7-15.

Brown, C.L. and R.E. Goddard. 1961. Silvical considerations in the selection of plus phenotypes. J. For. 59: 420-426.

Cable, D.R. 1958. Estimating surface area of ponderosa pine foliage in central Arizonia. For. Sci. 4(1): 45-49.

Campbell, R.K. 1961. Phenotypic variation and some estimates of repeatability in branching characteristics of Douglas-fir. Silvae Genetica 10: 109-118.

Campbell, R.K. and J.H. Rediske. 1966. Genetic variability of photosynthetic efficiency and dry-matter accumulation in seedling Douglas-fir. Silvae Genetica 15: 65-72.

Dimock, E.J. 1958. Don't sell western hemlock short. Pulp and Paper 32(13): 112-114.

Dorman, K.W. 1976. The genetics and breeding of southern pines. USDA For. Serv. Agri. Handbook No. 471, 407 pp.

Einsphar, D.W., J.R. Peckman, and M.C. Mathes. 1964. Base-lines for judging wood quality of loblolly pine. For. Sci. 10: 165-173.

Fowels, H.A. 1965. Silvics of forest trees of the United States. USDA For. Serv. Agri. Handbook No. 271, 762 p.

Grier, C.C. and R.H. Waring. 1974. Conifer foliage mass related to sapwood area. For. Sci. 20(3): 205-206.

Harlow, W.M. and E.S. Harrar. 1969. Textbook of dendrology. McGraw-Hill Inc. 512 pp, New York.

Hogue, C.J. 1929. Western Hemlock: its potentialities. Timberman 31 (1): 108-110.

Holsoe, T. 1948. Crown development and basal area growth of red oak and white ash. Harvard Forestry Paper, 1(3): 28-33.

Ledig, F.T. 1974. An analysis of methods for the selection of trees from wild stands. For. Sci. 20: 2-16.

Matthews, J.D. 1963. Some applications of genetics and physiology in thinning. Forestry 36: 172-180.

Meagher, M.D. 1976. Studies of variation in hemlock (Tsuga) populations and individuals from southern British Columbia. PH.D Thesis, University of British Columbia, 381 pp.

Minor, C.O. 1951. Stem-crown diameter relations in southern pine. J. For. 49: 490-493.

Moller, C.M. 1945. Untersuchugen uber Laubmenge, Stoffverlust und Stoffproduktion des Waldes. Forstl. Forsogsv. Denmark 17: 1-287.

Morgenstern, E.K., M.J. Holst, A.H. Teich, and C.W. Yeatman. 1975. Plus-tree selection: review and outlook. Can. For. Serv. Publ. No. 1347, 72 pp.

Piesch, R.F. 1974. Establishment of a western hemlock tree improvement program in coastal British Columbia. Can. For. Ser. Inf. Rpt. BC-X-89, 87 pp.

Piesch, R.F. 1976. Tree improvement in western hemlock. 155-165, In "Western Hemlock Management Proc." (W.A. Atkinson and R.J. Zasoski, ed.) University of Washington.

Rothacher, J.S., F.E. Blow, and S.M. Potts. 1954. Estimating the quantity of tree foliage in oak stands in the Tennessee Valley. J. For. 52: 169-173.

Rudolph, P.O. 1956. Guide for selecting superior forest trees and stands in the Lake States. U.S. For. Serv., Lake States For. Exp. Stn. Pap. 40, 32 pp.

Smith, J.H.G. and J.W. Ker. 1960. Growing Douglas-fir and western hemlock at desired rates. Univ. of B.C. Fac. of For. Res. Note No. 24, 5 pp.

Smith, J.H.G., J.W. Ker, and J. Csizmazia. 1961. Economics of reforestation of Douglas-fir, western hemlock, and western red cedar in the Vancouver Forest District. Univ. of B.C. Fac. of For. Bull. No. 3, 144 pp.

Stephenson, G.K. and E.B. Snyder. 1969. Genetic variation - key to superior trees. USDA For. Serv. South. For. Exp. Stn., 12 pp.

Thomas, C.A. and R.D. Stevens. 1977. The influence of competition from nearby trees on the selection of western hemlock plus trees. Final Report, Forestry Operations, MacMillan Bloedel Limited, 62 pp.

Toda, R. 1954. A method to indicate the degree of crown slenderness of individual trees. J. of the Japanese For. Soc. 36(5): 123-127.

Vézina, P.E. 1962. Crown width-d.b.h. relationships for open-grown balsam fir and white spruce in Quebec. For. Chron. 38(4): 463-473.

Walkup, R. 1978. Personal communication.

Walters, J., J. Soos, and P.G. Haddock. 1960. The selection of plus trees on the University of British Columbia Research Forest, Haney, B.C. Univ. of B.C. Fac. of Forest. Res. Pap. 33.

Weck, H. 1944. Crown dimensions and increment production. Forstarchiv, 20: 73-78.

Wellwood, R.W. 1960. Specific gravity and tracheid length variation in second-growth western hemlock. J. For. 58: 361-368.

Whitehead, D. 1978. The estimation of foliage area from sapwood basal area in Scots pine. Forestry 51: 137-149.

Wright, J.W. 1962. Genetics of forest tree improvement. FAO For. and For. Prod. Stud. 16, 399 pp, Rome.

Wright, J.W. 1976. Introduction to forest genetics. Academic Press, 463 pp, New York.

APPENDIX I. WESTERN HEMLOCK COMB FORM

First order branches of comb form, notice the second order branches hanging down in a comb-like fashion

APPENDIX II. WESTERN HEMLOCK FLAT-BRANCHED FORM

First order branches of flat-branched form, notice the second and third order branches develop in the same plane

APPENDIX III. WESTERN HEMLOCK STEEPLE FORM

Top section cut off from steeple form, notice the droopiness of the first order branches

APPENDIX IV. WESTERN HEMLOCK CEDAR FORM