

AN ABSTRACT OF THE THESIS OF

Brooks McCandlish for the degree of Master of Science
in Forest Science presented on July 29, 1980

Title: Leaf Area Index and Productivity in Eastern Washington
Forests

Abstract approved: _____

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The relationship between Leaf Area Index (LAI) and current stemwood production was examined in selected stands in eastern Washington. Stands were sampled with an angle gauge (prism). LAI was estimated from sapwood area; current stemwood production from DBH, height, and radial increment.

Maximum LAI attainable on a given site has been related to qualities of the environment. Where stocking varies on a given site, LAI is related to the degree of utilization of the available resources.

The average leaf area per tree, relative to average tree size, is a measure of stand vigor. To compare the relative sapwood area of trees of different sizes, allometric regressions of sapwood area from DBH were derived, for five species, from fully stocked stands.

In fully stocked stands with dominant Douglas-fir, current productivity was more closely related to average LAI than to either Site Index alone or predictions by Cochran (1979) based on Site Index, basal area, and age. Within stands displaying a range of stocking on a given site, wood production per unit of leaf area decreased as LAI

increased; nonetheless, productivity per hectare generally increased up to the highest LAI observed in each stand. Both the pattern and the scale of the relationship between LAI and productivity differed among sites.

Leaf Area Index And Productivity
in
Eastern Washington Forests

by

Brooks McCandlish

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed July 29, 1980

June 1981

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LEAF AREA INDEX AND PRODUCTIVITY IN EASTERN WASHINGTON FORESTS

INTRODUCTION

Although there is much interest in determining the productive potential of forest lands, it is not always clear how to do so. The rate of production of wood in a given stand depends not only on qualities inherent to the site, but on characteristics of the stand as well. This paper describes a study of the relationship between Leaf Area Index (the projected area of foliage per unit of ground area) and the rate of production of wood, both within and between a variety of sites in eastern Washington. Our objective was to determine if the potential productivity of sites supporting stands in various conditions could be projected from their current productivity and Leaf Area Index.

Many traditional methods of estimating forest productivity rely on Site Index systems to gauge site quality¹. However, Site Index is often an inadequate measure of site productivity for several reasons. Height growth, and thus Site Index, may be strongly influenced by characteristics of the stand as well as by the quality of the environment. Furthermore, potential basal area and volume growth rates may vary widely among sites with the same Site Index. Both these problems are particularly apparent in mountainous terrain with sharp and varied environmental gradients characteristic of western forests.

¹Site Index, in American forestry, is the height of dominant trees at a standard age, estimated from current age and height.

Ideally, from the current productivity and condition of an existing stand, we should be able to infer the potential productivity of that site. The influence of varying stand conditions must be recognized, and the interaction of varying conditions with different environments.

The genetic composition of a stand can affect its productivity to a large degree, though it may be quite difficult to distinguish hereditary from environmental influences. However, where extensive forestry is practiced using local seed or sprouts to provide regeneration, it may be appropriate to consider site quality in terms of the potential performance of the existing forest type. Some of the characteristics of the stand influencing productivity, in addition to site and genetic composition, are: age, stand density, and vigor.

It is generally recognized that productivity declines at some point in older stands. However, this may not be so much a function of chronology as of average tree size, stage of development, or physiological age (Assmann 1971).

The measurement of stand density, as well as its relationship to productivity, has long been subject to debate. Stand density may be defined as the intensity of utilization by a stand of the resources of an area of land, in particular, light, water and nutrients. Related to this concept is the average degree of competition experienced by the trees of the stand.

Since large trees command far more resources than small, simple tree density (number of stems per unit area) does not adequately express stand density. Many traditional measures of stand density [such as Reineke's (1933) Stand Density Index, Crown Competition Factor of Krajicek et al. (1961), and the Relative Density Index of Drew and Flewelling (1979)] consist of some function of stem size together with stem density. Such measures may be interpreted as expressing the resource area commanded by a tree as a function of its stem size (Curtis 1970).

A better measure of stand density, more closely related to the degree of utilization of site resources, might be foliage density, expressed as LAI. LAI is closely related to the degree of interception of light and to potential photosynthesis. While there is a general relationship between the stem size and leaf area of trees, and thus between LAI and traditional measures of stand density based on stem dimensions, there can also be considerable variation, particularly in less than fully stocked stands. Stands with different histories may support very different amounts of foliage on a similar number and size of stems, and vice versa (Assmann 1971).

Foliage density is certainly far more difficult to measure or estimate than stem diameters. However, several studies indicate that there is a high correlation, by species, between leaf area and the cross sectional area at breast height of sapwood, the active water conducting tissue. This relationship between sapwood area and leaf

area appears to be tighter than that for total DBH or basal area (Grier and Waring 1974, Whitehead 1978).

In well stocked stands, foliage density tends towards an equilibrium level largely determined by qualities of the environment (Grier and Running 1977, Waring et al. 1978, Aber 1979). On a given site there is an upper limit to gross photosynthetic production, no matter how many leaves are extended. Respiratory costs, however, continue to increase with each additional leaf. Thus, theoretically, on a given site, there will be an optimum foliage density for the greatest productivity. The question arises whether LAI in real stands commonly reaches or exceeds this optimum.

While a number of factors influence the rate of photosynthesis, including temperature, radiant energy, and water status, respiration is affected primarily by temperature. Thus the form as well as the scale of the relationship between LAI and productivity would be expected to differ among different types of environments.

Foliage density alone is not sufficient to predict productivity on a given site, for the effectiveness of that foliage is also dependent on the overall efficiency or vigor of the trees which support it. Thinning studies demonstrate that wood production after thinning depends substantially on the quality of the residual trees, their potential to aggressively utilize new growing space as it becomes available (Berg 1978).

One aspect useful in assessing tree vigor is the amount of foliage a tree supports relative to its size. Trees with reduced

crowns tend to compete less effectively with their neighbors, to be less vigorous in responding to changes in their competitive environment, and to be less able to resist or recover from damage by insects or pathogens (Miller and Keen 1960, Smith 1962, p. 54).

Thus, a measure of average leaf area per tree, relative to tree size, may provide useful information, in addition to foliage density, when predicting productivity.

METHODS

a. FIELD WORK

Selected stands in Washington, east of the Cascade crest, were sampled that covered a sufficiently large area (greater than one hectare) without obvious changes in slope, aspect, topographic position, vegetation or soil type. Within stands, sample units were defined with a metric 7 factor prism (each tree within a sample point representing 7 m² basal area per hectare). Stands with a wide range of stocking were visually stratified into density classes; within strata, one or more points, depending on the area available, were randomly located, avoiding edges and abrupt transitions in density, as well as obviously different microsites such as rock outcrops, stream beds and wet spots. By centering sample points in regions within the stand of reasonably homogenous density, we hope that the growth rates of the trees in each sample unit reflect the density measured from the center point.

At each point, species, DBH, five year radial increment, and sapwood thickness were recorded for each tree. DBH was measured with a circumference tape; sapwood thickness and radial increments were determined from increment cores taken at breast height on the side of the tree facing the sampling point.

Total height and age at breast height were recorded for a subsample of trees from each stand. The subsample was selected either

to represent the range of diameters in the stand, or from dominant trees suitable for Site Index determination.

Four to six sample points were taken per stand, as part of an extensive survey of Eastern Washington forests and their vegetation conducted in the summer of 1979 (see Schroeder 1980). In each of two ponderosa pine stands with particularly variable stocking, fifteen sample points were established. Table 1 lists some characteristics of the stands and sites studied.

b. CALCULATIONS

LAI, volume, and five year volume increment per hectare were calculated for stands composed only of any combination of the following five tree species:

Douglas-fir	-- <u>Pseudotsuga menziesii</u> Franco
ponderosa pine	-- <u>Pinus ponderosa</u> Laws.
grand fir	-- <u>Abies grandis</u> Lindl.
western larch	-- <u>Larix occidentalis</u> Nutt.
lodgepole pine	-- <u>Pinus contorta</u> Dougl.

Formulae of Faurot (1977) were used to estimate total cubic tree volumes from diameter and height for Douglas-fir, ponderosa pine, western larch, and lodgepole pine. For grand fir, the Douglas-fir equation was used.

Unknown tree heights were estimated as follows: using data from stands in which heights were measured over the range of diameters, a

regression was fitted by least squares of the form,

$$\ln (H/H^*) = b \ln(D/D^*)$$

where H = height, D = DBH, H* - height of dominant trees, and D* = DBH of dominant trees. The coefficient b was estimated to be .63 with an R² for the relationship of .987. Five year radial increments were estimated from current height, DBH, radial increment, species, and Daubenmire Habitat Type, using models of Stage (1975).

We calculated sapwood area (SA) from sapwood thickness and DBH, assuming the sapwood to be concentric. Since sapwood area has been shown to be a better predictor of foliage area than DBH, and since we specifically desired to recognize the potential variation in leaf area relative to tree size in stands with different management histories, we wanted to estimate leaf areas from our values for sapwood area rather than those for DBH. Unfortunately, the preliminary work needed to relate sapwood area directly to leaf area has not been done for most east-side species; however, Brown (1978) has developed equations to estimate foliage biomass as a function of DBH for coniferous species in the intermountain region.

Regressions were fitted by least squares to the model:

$$\ln(\text{DBH}) = B_0 + B_1 \ln(\text{SA}) + E \quad (2)$$

for each species. These regressions, transformed and corrected for bias as suggested by Baskerville (1972), were substituted for DBH in Brown's equations. Foliage biomass was converted to projected leaf

area using the factors in Table 2, resulting in the Sapwood Area - Leaf Area equations given in Table 3 and Figure 1.

In effect, the SA-DBH regressions provide a consistent means of scaling our measurements of sapwood area so that they are compatible with Brown's equations. Two trees with the same DBH may have different sapwood areas and correspondingly different leaf areas; if we had used our measurement of DBH directly in Brown's equations, the same foliage biomass would have been predicted for both trees. However, instead of measured DBH, values determined by our sapwood area measurements, using the SA-DBH regressions, were entered into Brown's equations.

With the substitution of values from our regression lines into Brown's equations we have assumed that our SA-DBH regressions would have applied equally to the trees in Brown's study; even if this were so, by substituting estimated values for independent variables of a least-squares regression, bias may be introduced. These potential sources of error make it impossible to place exact confidence limits on our estimates of leaf area; however, we feel the equations of Table 3 should permit assessment of relative differences in foliage density. For comparison, sapwood area-leaf area relationships for two species from previous studies are shown in Figure 1 together with the equations arrived at by our methods.

To develop a standard for comparison of sapwood area relative to stem size (and, by extension, leaf area relative to stem size), only those stands or portions of stands which appeared to be fully stocked

were considered. Stands were judged fully stocked if they had evidence of mortality through suppression, but no recent stumps or serious insect, disease, or storm damage. From these stands regressions were fitted for each species of the form:

$$\ln(\overline{SA}_g) = b_0 + b_1 \ln(\overline{DBH}_g) \quad (3)$$

where \overline{SA}_g is the geometric mean sapwood area and \overline{DBH}_g is the geometric mean DBH of the trees of a species at a sample point. We used as an expression of relative sapwood area (RSA) the ratio of actual SA divided by sapwood area predicted from DBH using the regression equation above. Thus, on the average, fully stocked stands should have an RSA of 1.0; less than fully stocked stands, consisting of trees with more leaf area relative to tree size would have an RSA greater than one, while over stocked stands with reduced crowns would have an RSA of less than one.

The relationships of mean current production to: mean LAI; Site Index; and productivity predicted from Site Index, age, and basal area (Cochran 1979) were compared for fully stocked stands using least-squares regression. Apparent curvilinearity in the relationships of LAI and Site Index to productivity were accounted for by power transforms of the independent variables derived with "Matchacurve" techniques (Jensen and Homeyer 1971).

RESULTS AND DISCUSSION

Statistics for the regressions of mean sapwood area from mean diameter in fully stocked stands (Equation 3) are given in Table 4.

Under our methods, sampling variation proved too great for only four to six points per stand to allow more than preliminary inferences about the relationship between LAI and productivity on specific sites. In general, on a given site, foliage efficiency did decrease with increasing leaf area. Fifteen out of twenty stands of the extensive survey had a negative linear correlation coefficient between LAI and production per unit leaf area. Only seven of these were significant at the 90% confidence level (see Figure 2), but none of the positive correlations were significant. The stands with significant correlation between LAI and production per unit leaf area all had a wide range of LAI due to partial thinning or harvesting. Variation in LAI in undisturbed stands may be the result of microsite or genetic influences which tend to depress foliage efficiency as well as foliage density.

Figure 3 compares production per hectare (derived by multiplying production per unit leaf area by LAI) for the seven stands of Figure 2. In no stands in the study was there a dramatic decrease in production per hectare at higher LAI. In fifteen out of twenty stands, the sample points with the highest LAI also had the greatest growth increment; data from only five stands indicated possible peaking of productivity before reaching the highest LAI. Although Donald (1963)

has suggested that, in agronomic crops, excessive foliage density can develop leading to reduced productivity, our data indicates that in many stands LAI is maintained at levels below those which would cause reduction in growth rate.

Some stands are able to maintain greater rates of production at any given leaf area than other stands. This may be due to a more favorable environment and/or to genetic attributes of the trees. However, corresponding differences may not necessarily be apparent in the vegetation present. For example, on stand #64 only two thirds the productivity of #74 was recorded, although the dominant age and height, and the composition of tree species as well as the subordinate vegetation were very similar in the two stands (Figure 3). Both were on level ground, with less than 15 meters difference in elevation and less than 15 kilometers between them. The only obvious difference between the two sites was in their topographic positions; #74 lay in a valley while #64 was on a hilltop. Deeper valley soils may affect the productivity of the trees more than the relatively shallow rooted understory species.

In fully stocked stands with dominant Douglas-fir, mean stemwood volume production over the past five years was more closely related to LAI than to either Site Index alone, or gross volume production predicted from Site Index, basal area and age using curves developed by Cochran (1979) (Figures 4-6). Linear regression of current production from LAI to the 1.5 power gave an R^2 value of .95; current

production from Site Index gave an R^2 of .73; current production from production predicted using Cochran's (1979) methods gave an R^2 of .91 (Figures 4-6).

In our data, neither age, basal area, mean DBH, nor our measure of relative sapwood area significantly improved the precision of a model predicting current productivity from LAI to the 1.5 power (Table 5). However, in stands with a marked stagnant appearance, ie. #39 and the unthinned parts of Goman Peak, production was lower than would be expected from their LAI.

The two intensively sampled stands revealed different patterns in the relationship between LAI and productivity. At Goman peak, current wood production peaked at less than the maximum LAI observed (Figure 7). Twelve years after thinning, the treated area supported about one half the leaf area on one third as many trees per hectare as the unthinned control. However, gross cubic volume production over the last five years was equal to or better than that in the control.

The Kaiser Butte stand was clearly growing on a better site and/or consists of a more productive ecotype. The maximum observed LAI, 20, and productivity, over $13 \text{ m}^3/\text{ha}/\text{yr}$, at Kaiser Butte were more than double the corresponding values at Goman Peak of 9.5 LAI and $5.5 \text{ m}^3/\text{ha}/\text{yr}$ stemwood production (Figure 8).

In both stands thinning increased both the relative leaf area per tree and the production per unit leaf area. However, at Kaiser Butte, unlike at Goman Peak, the production per hectare was markedly

lower in the thinned parts of the stand. While at Goman Peak foliage efficiency decreased regularly with increasing LAI, there was little change in productivity per unit leaf area at Kaiser Butte evident at LAI from 5 to 15 (Figure 9).

As is clear from Figure 10, the parts of the Kaiser Butte stand with a LAI between 3 and 6 produce no more than the Goman Peak stand at similar LAI; thus, from these sample points at low LAI alone, it is not evident that the Kaiser Butte site has a considerably greater productive capacity.

There are several interpretations possible to explain the different patterns of productivity versus LAI in the two stands. The differences may indeed reflect real aspects of the interaction of foliage density and environment on productivity; if the two sites differ primarily in water availability, there may not be sufficient water to efficiently support high levels of LAI at Goman Peak; at a lower LAI, water may be less limiting at Goman Peak and available in surplus at Kaiser Butte.

Another factor which may be involved in the different patterns of productivity in the two stands is the selection criteria used in thinning. While the Goman Peak study was designed as an experimental precommercial thinning, at Kaiser Butte irregular stocking and the variable condition of the trees suggested that thinning costs and the value of the logs removed may have been considerations in addition to the condition of the residual stand. It is possible that current gross productivity at Kaiser Butte might be somewhat higher at lower

LAI if the most vigorous and thrifty trees only had been selected to be left after thinning.

Higher values of our measure of sapwood area relative to tree size (RSA) appear to be associated with the better site, with lower LAI, and with the more productive points at a given LAI (Figures 9 and 10). It may be possible to reduce the scatter in these relationships by using more accurate methods of estimating sapwood area.

The relationship between leaf area and net wood production (gross wood production minus the volume of mortality) may be less direct than that between LAI and gross production. Assuming that the LAI of fully stocked stands approximates a maximum equilibrium level determined by the environment, our study suggests that maximum gross stemwood production can occur at this level. For a fully stocked stand to keep up a high level of productivity as its trees grow larger, a sufficiently high average leaf area per tree, relative to tree size, must be maintained through a regular process of crown stratification and self-thinning.

Our study suggests that the Leaf Area Index of fully stocked stands does have merit as an index of gross stemwood productivity. However, as stocking varies, the relationship between LAI and productivity differs among different sites. More work needs to be done to elucidate the interactions of environment, stocking, and stand vigor on productivity.

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Table 1.

Stand Designation	Sample points	Elevation	Slope	Aspect	Topo. Position	Parent Material	County	Tree Species
Goman Peak	15	2175 ft.	25%	WNW	lower 1/3	granitic	Chelan	Pp, Df
Kaiser Butte	15	2950	0	---	tableland	basalt	Klickitat	Pp, Df
27	5	4600	40	W	upper 1/3	granitic	Okanogan	Wl, Df, Lp
28	5	4425	35	SE	upper 1/3	"	"	Df, Pp
30	6	4500	45	NW	upper 1/3	"	"	Wl, Df, Lp
33	5	5275	45	SSE	mid 1/3	"	"	Df
34	5	3500	50	NNE	lower 1/3	"	"	Df, Pp
35	5	3500	45	W	lower 1/3	"	"	Pp, Df
37	6	4125	5	SSE	mid 1/3	"	"	Lp, Wl
39	5	1525	50	NW	mid 1/3	basalt	"	Df
40	5	3000	5	SE	mid 1/3	granitic	"	Pp
42	5	2325	60	N	lower 1/3	sandstone	Chelan	Df
45	5	2625	60	NW	mid 1/3	"	"	Df, Pp
50	4	2475	50	E	mid 1/3	basalt	Yakima	Gf, Df
51	5	2625	0	--	valley	"	"	Gf, Df, Wl
59	5	3250	0	--	tableland	"	"	Df, Pp
60	5	3550	5	W	lower 1/3	"	"	Pp
61	5	4550	0	--	tableland	"	Klickitat	Pp
64	5	2950	0	--	hilltop	"	Skamania	Gf, Df, Wl
74	6	2925	0	--	valley	"	Klickitat	Gf, Df, Pp, Wl
83	4	2775	5	NNW	mid 1/3	granitic	Stevens	Df, Wl, Lp
99	5	3325	25	SE	upper 1/3	basalt	Kittitas	Df, Pp

Table 2.

Factors used to convert foliage bioamass to projected leaf area.

Species	m ² per kg
Douglas-fir (east-side)	5.
Ponderosa pine	4.
Grand fir	6.
Western larch	8.
Lodgepole pine	3.

Sources:

- Anderson, H. E. et al. 1978.
- Gholz, H. et al. 1976.
- Smith, R. S. 1980.
- Waring, R. H., personal communication.

Table 3.

Equations¹ used to estimate the projected leaf area (m²) of a tree from sapwood basal area (cm²)

Douglas-fir	-- LA = .59325 SA ÷ 3.738
Ponderosa pine	-- LA = exp(1.91694 ÷ 1.1002 ln(SA) - 2.927 SA ^{.530462})
Grand fir	-- LA = 1.7499 SA ^{.9562} / (1.5916 + 5.4811 SA ^{.5948})
Western larch	-- LA = exp(-.08400 + .10225 ln (SA) - 6.7014 SA ^{.6092})
Lodgepole pine	-- LA = .26253 SA - .716

¹Sapwood basal area substituted for DBH in equations of Brown (1978).

Table 4. Allometric regression equations of geometric mean Sapwood Area from geometric mean DBH for trees of a given species at sample points in fully stocked stands.

$$\ln(\overline{SA}_g) = b_0 + b_1 \ln(\overline{DBH}_g)$$

Species	b_0	SE(b_0)	b_1	SE(b_1)	n	MSE	R ²
Douglas-fir	-10.0145	.2491	1.80112	.07352	60	.07260	.912
Ponderosa pine	-9.0268	.2241	1.73458	.06340	31	.02622	.954
Grand fir	-9.4189	.4862	1.71292	.14375	17	.06435	.904
Western larch	-8.8099	.6139	1.35071	.18550	17	.07312	.747
Lodgepole pine	-9.6877	.2407	1.84255	.08302	15	.01664	.974

Table 5. Correlations with the residuals of the regression:

$$\hat{P} = .449 + .186 \text{ LAI}^{1.5}$$

where \hat{P} is the estimate of current annual stemwood production for fully stocked stands with dominant Douglas-fir.

Variable	r
Relative sapwood area ¹	+0.35
Basal area/ha.	-0.34
$\overline{\text{DBH}}_g$	+0.28
Standing volume/ha.	+0.19
Age (breast height, of dominants)	+0.19
% intolerant species (Pipo, Pico, Laoc)	-0.11
% <u>Abies grandis</u>	+0.10

¹See methods, p. 9.

Figure 1. Equations used to estimate leaf area from sapwood area. Solid lines represent equations, used in this study, derived by substituting sapwood area for DBH in equations of Brown (1978). Dashed lines represent relationships from Grier and Waring (1974), for comparison.

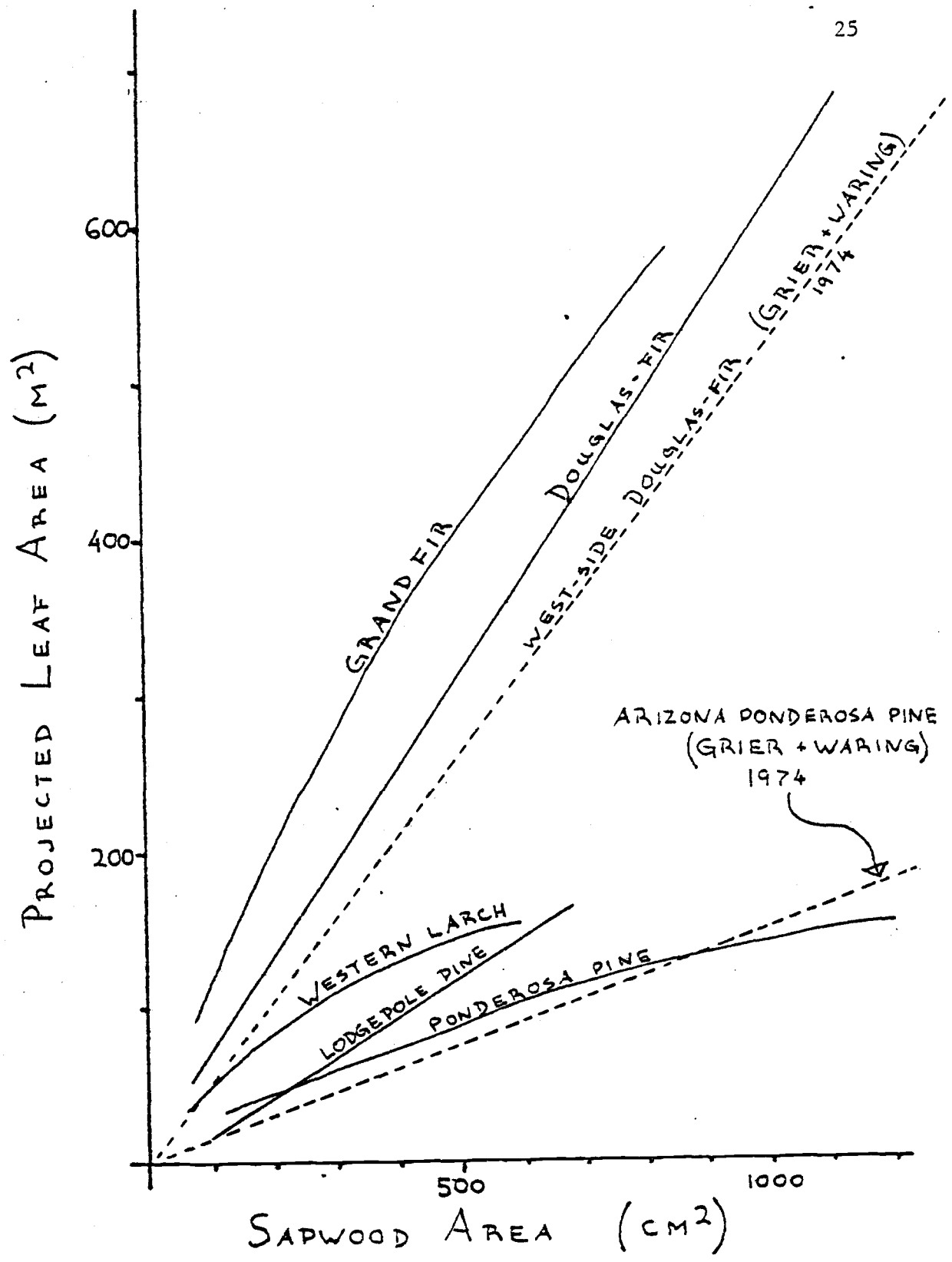


FIGURE 1. EQUATIONS USED TO ESTIMATE LEAF AREA FROM SAPWOOD AREA.

Figure 2. Foliage efficiency versus LAI, within stands. Data for seven stands with negative linear correlations between production per unit leaf area and LAI are displayed. Lines represent least-squares fits for each stand for either production per unit leaf area from LAI, or the natural logarithm of both variables, depending on which gave the higher R^2 .

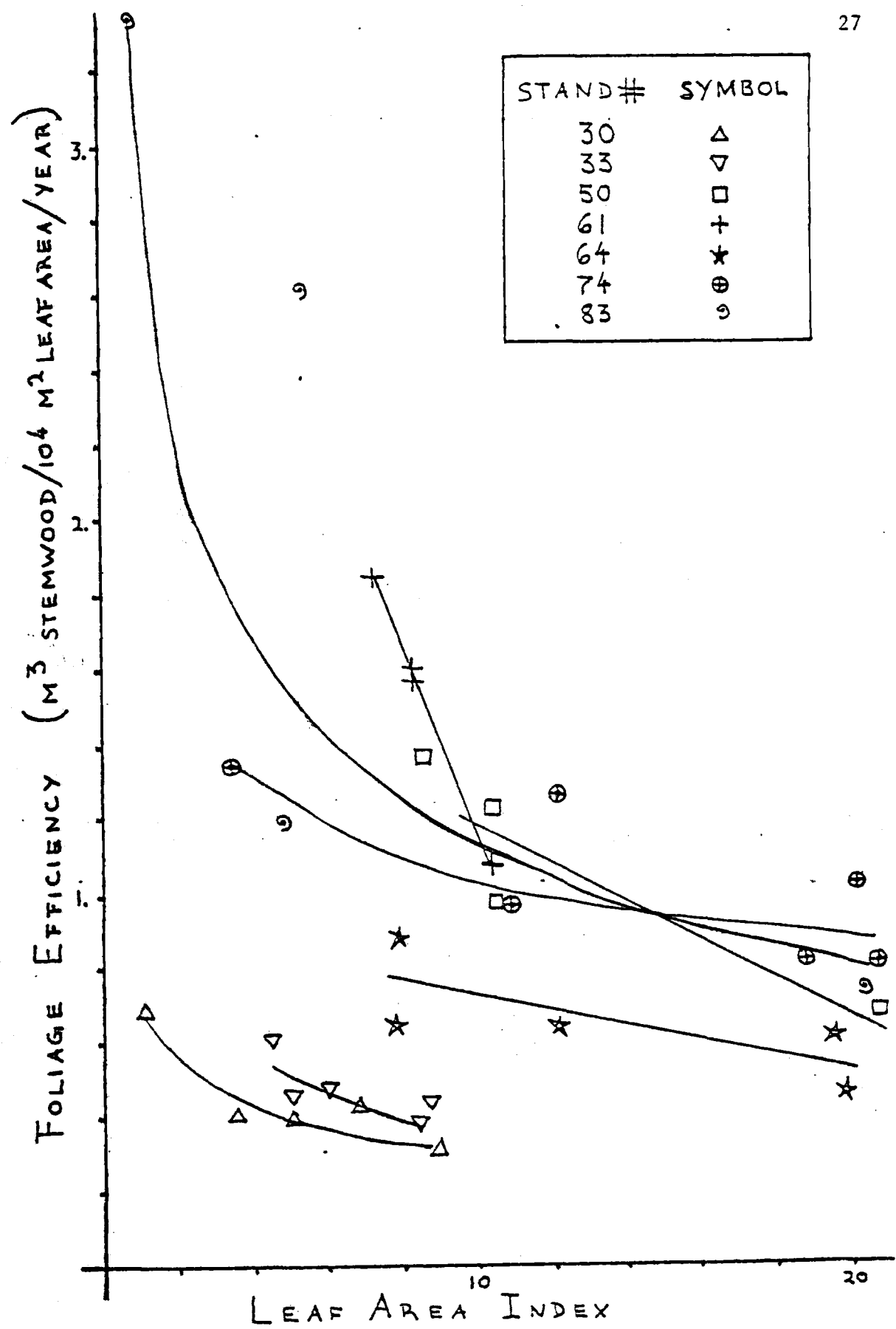


FIGURE 2. FOLIAGE EFFICIENCY VS. LAI, WITHIN STANDS.

Figure 3. Current production versus Leaf Area Index, within stands.

In this figure, the lines represent transformations of the least-squares fits for the seven stands displayed in Figure 2.

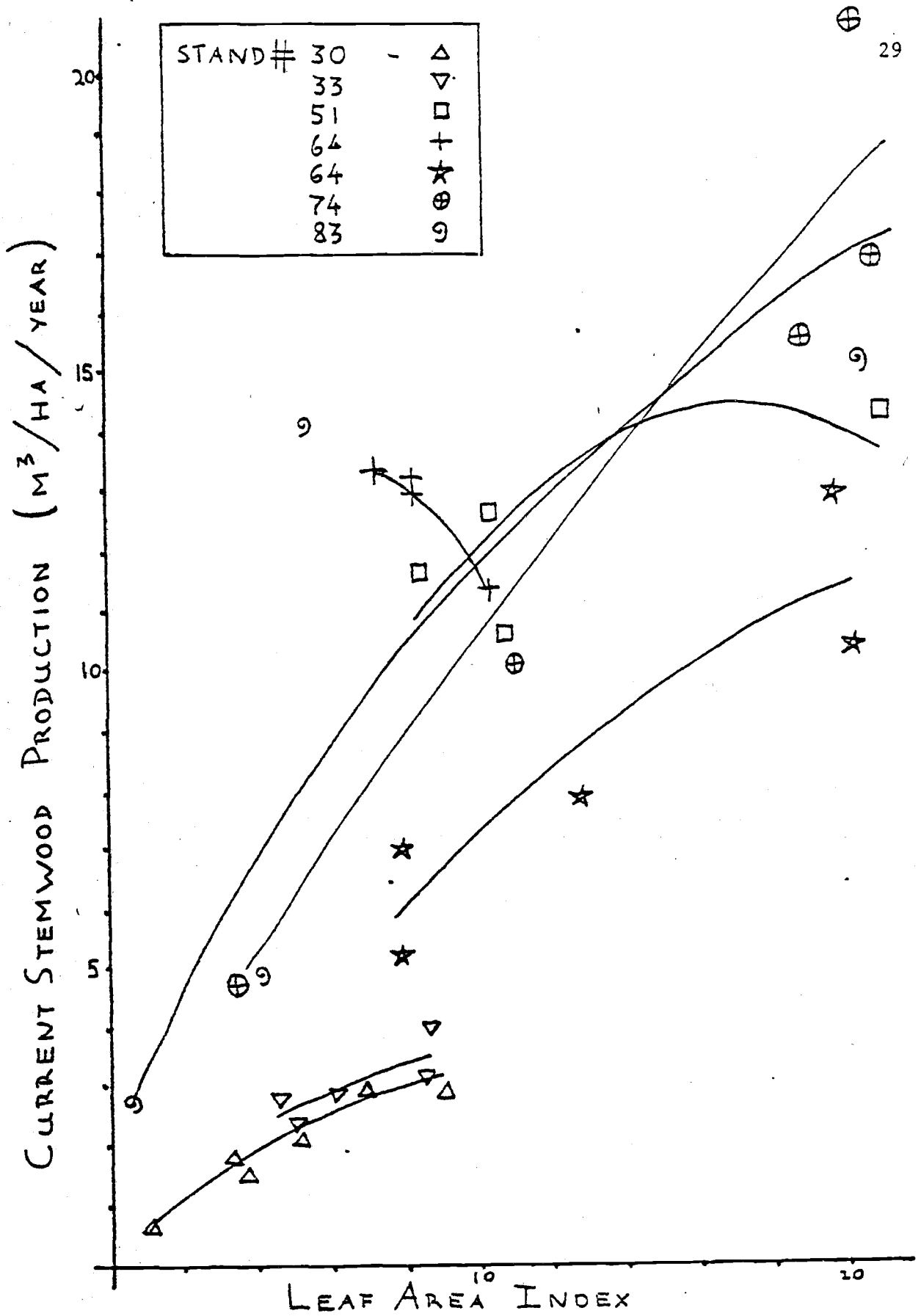


FIGURE 3. CURRENT PRODUCTION VS. LAI, WITHIN STANDS.

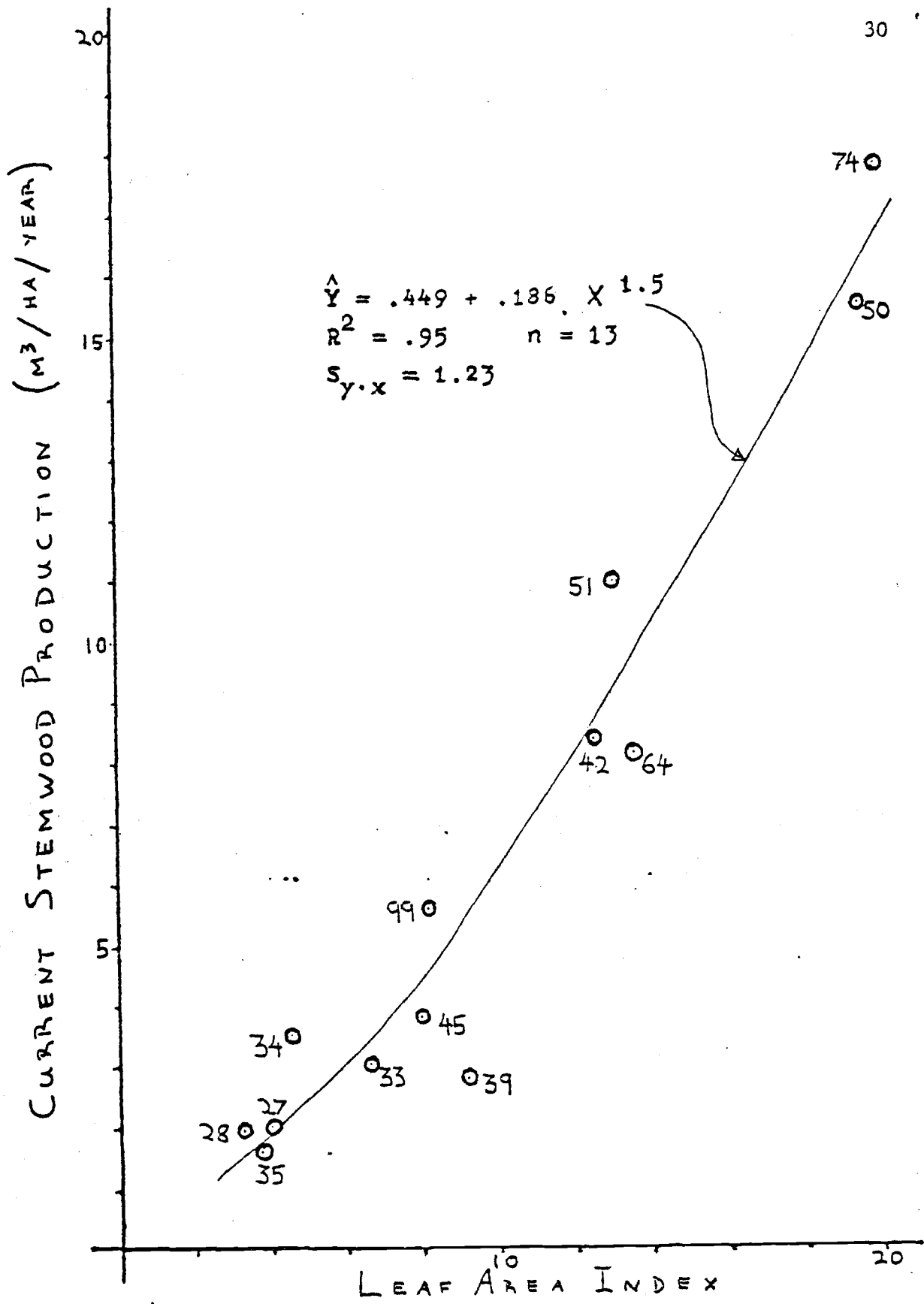


FIGURE 4. MEAN LAI VERSUS CURRENT PRODUCTION IN FULLY STOCKED STANDS WITH DOMINANT DOUGLAS-FIR.

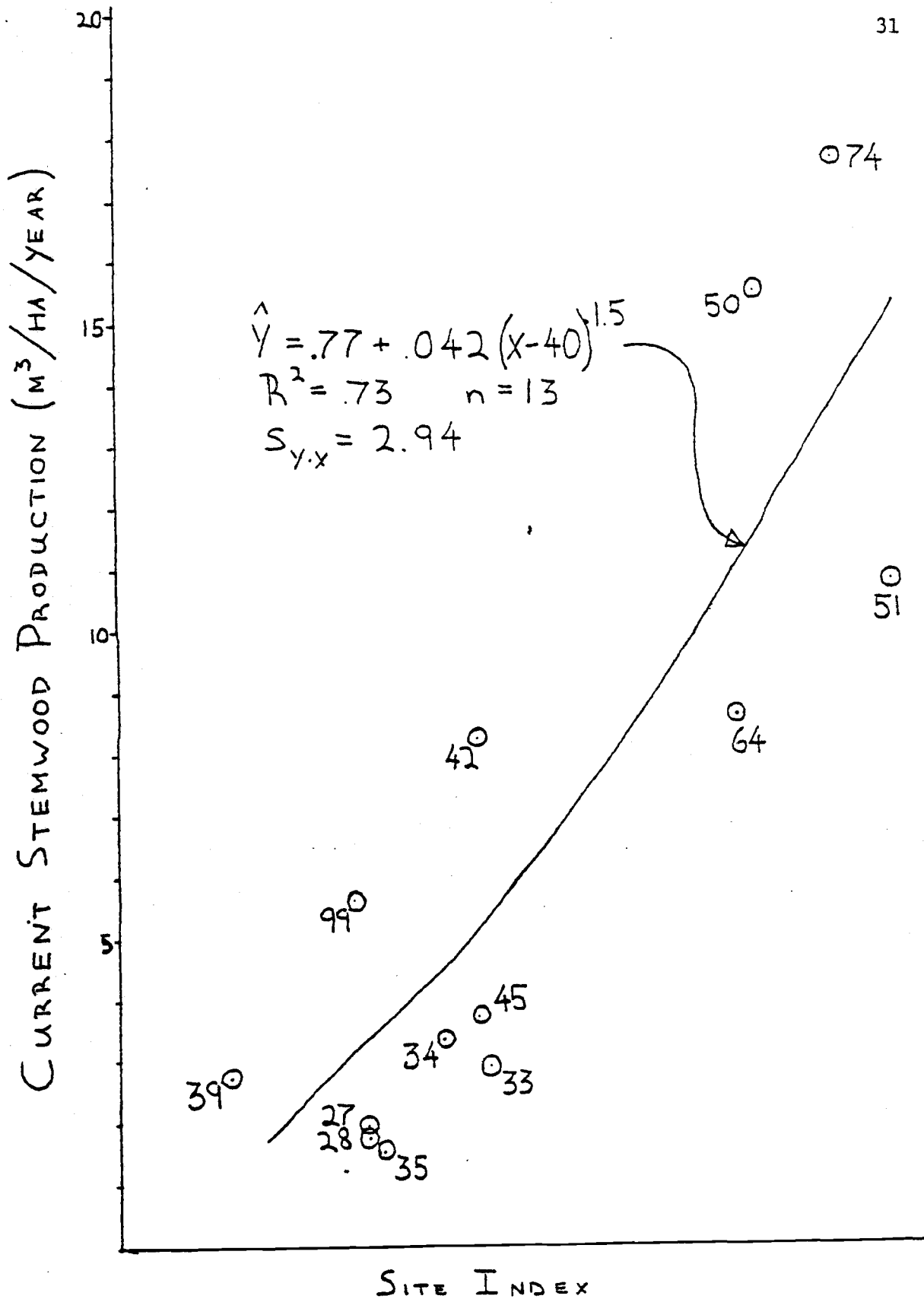


FIGURE 5. SITE INDEX (COCHRAN 1979) vs. CURRENT PRODUCTION IN FULLY STOCKED STANDS.

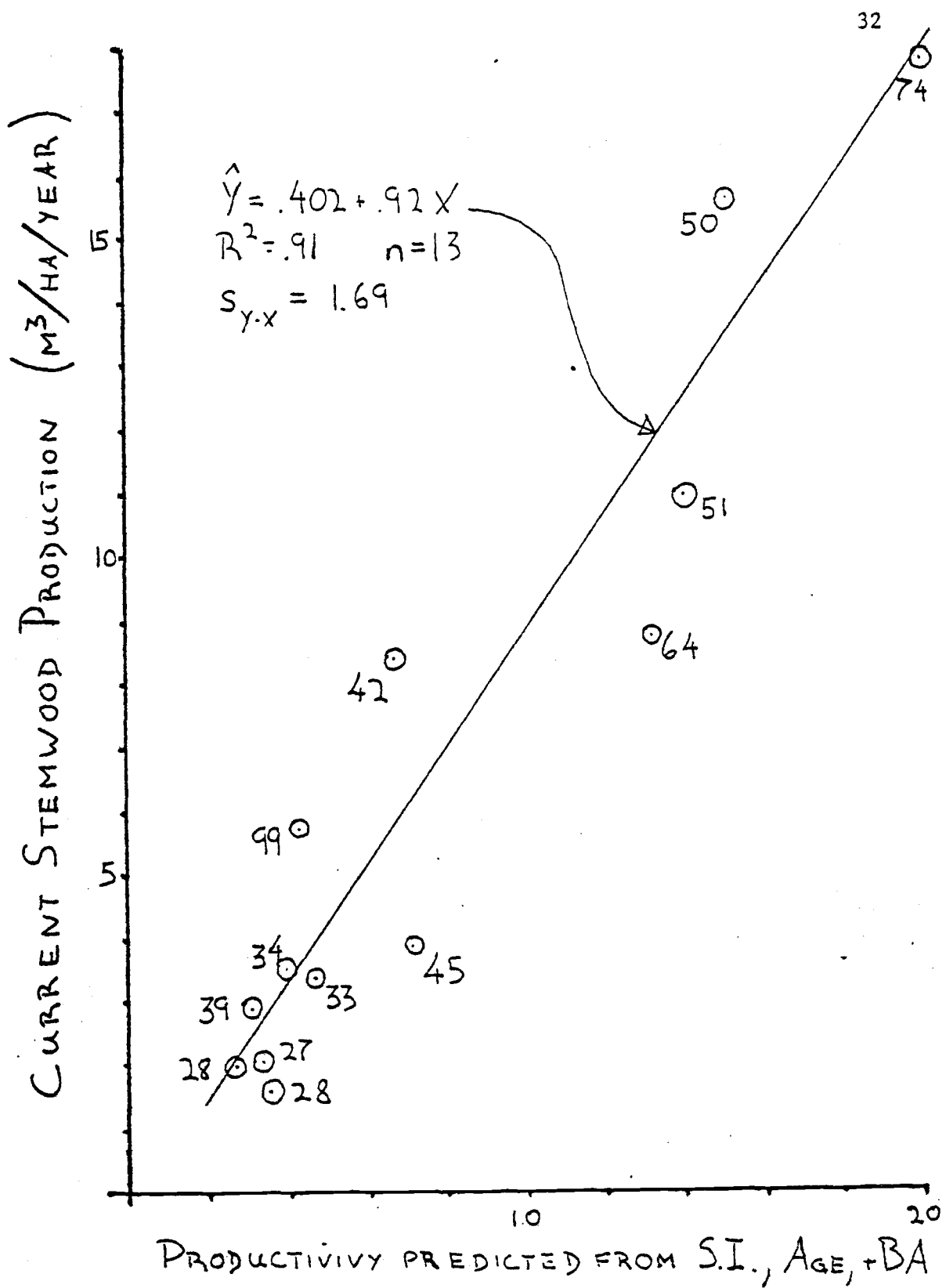


FIGURE 6. PRODUCTIVITY PREDICTED FROM SITE INDEX, AGE, AND BASAL AREA (COCHRAN 1979) VERSUS CURRENT PRODUCTION IN FULLY STOCKED STANDS.

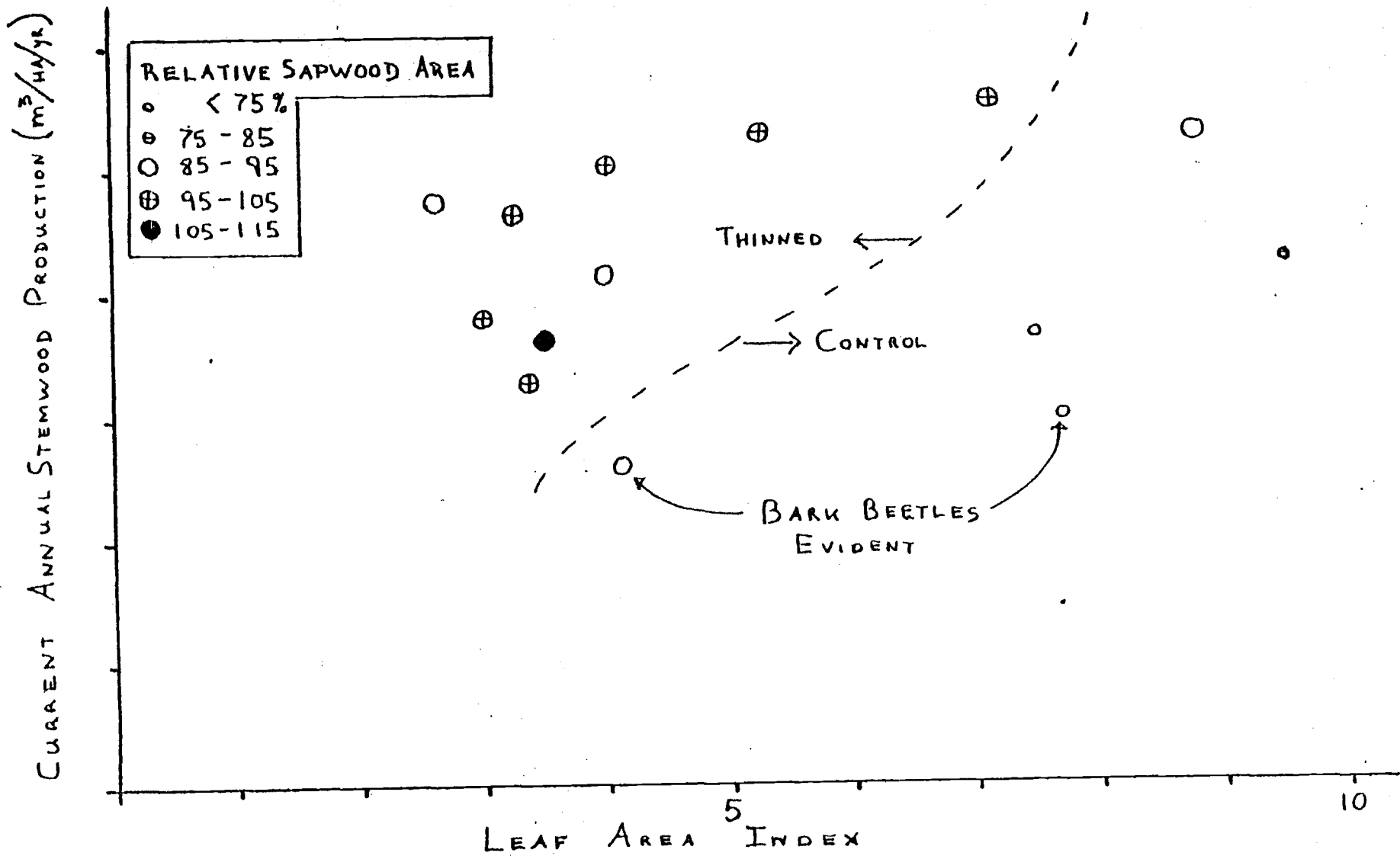


FIGURE 7. GOMAN PEAK SAMPLE POINTS: LAI VERSUS PRODUCTION PER HA.

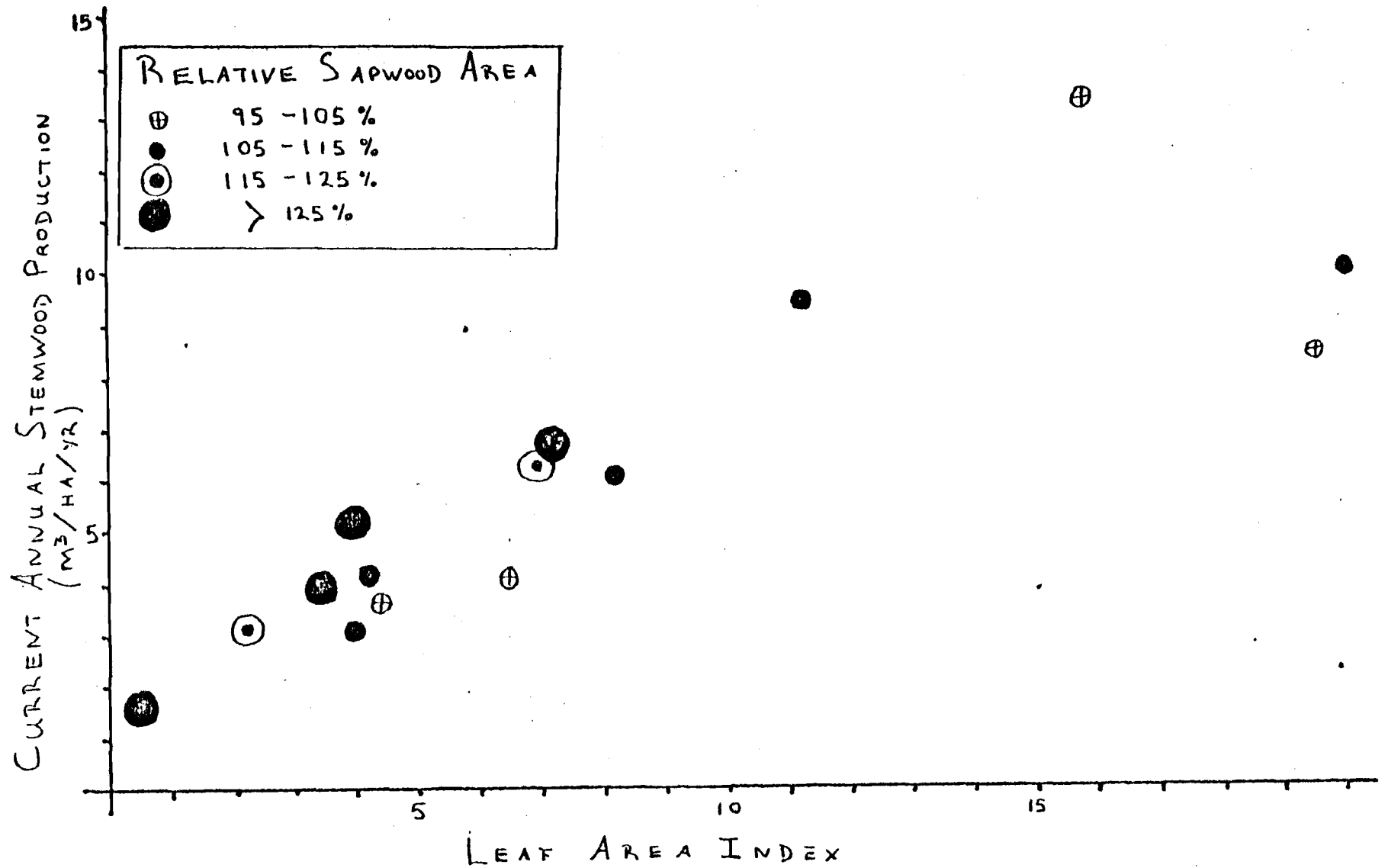


FIGURE 8. KAISER BUTTE SAMPLE POINTS: LAI VERSUS PRODUCTION PER HA.

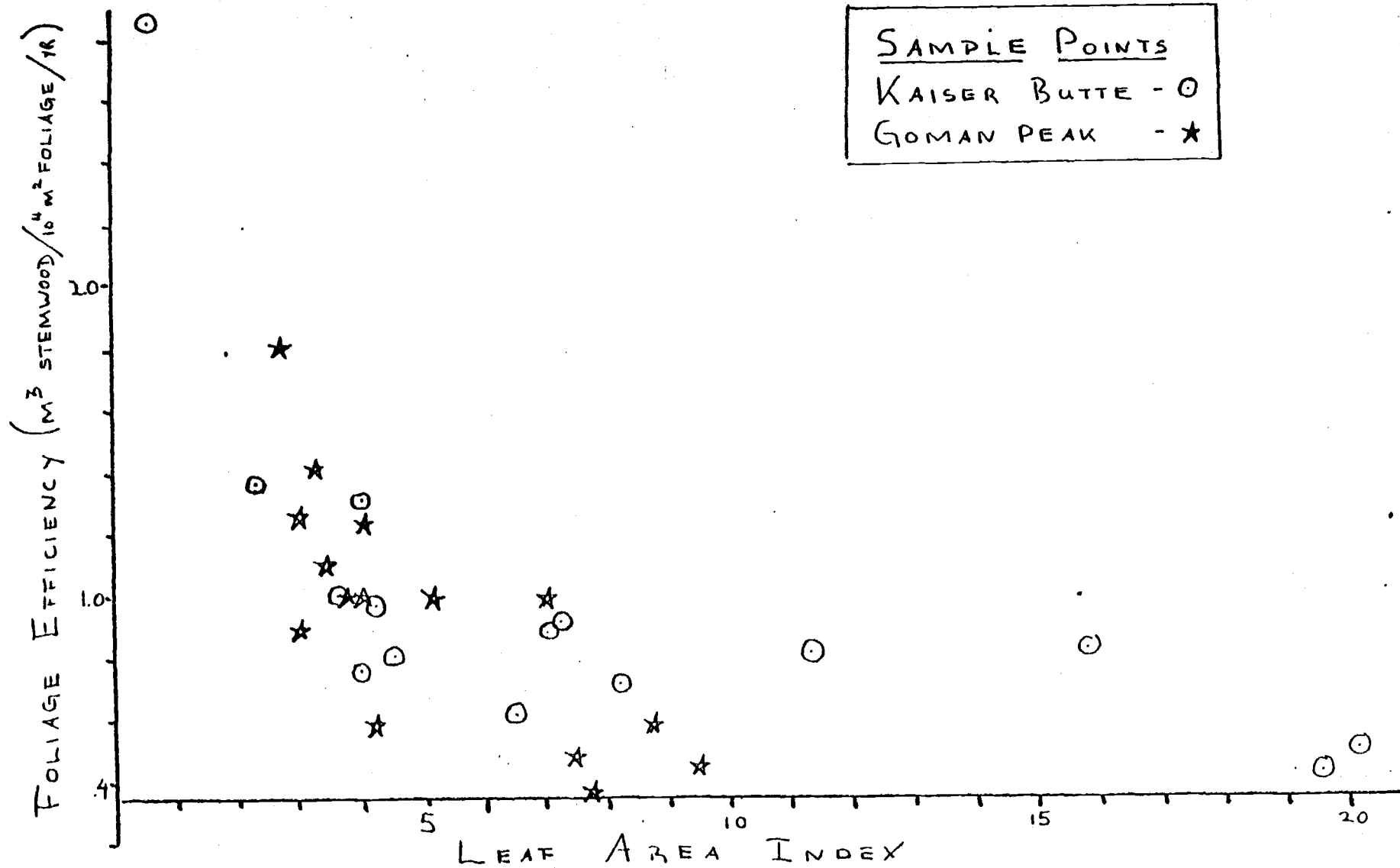


FIGURE 9. LAI VERSUS FOLIAGE EFFICIENCY AT KAISER BUTTE AND GOMAN PEAK. 5

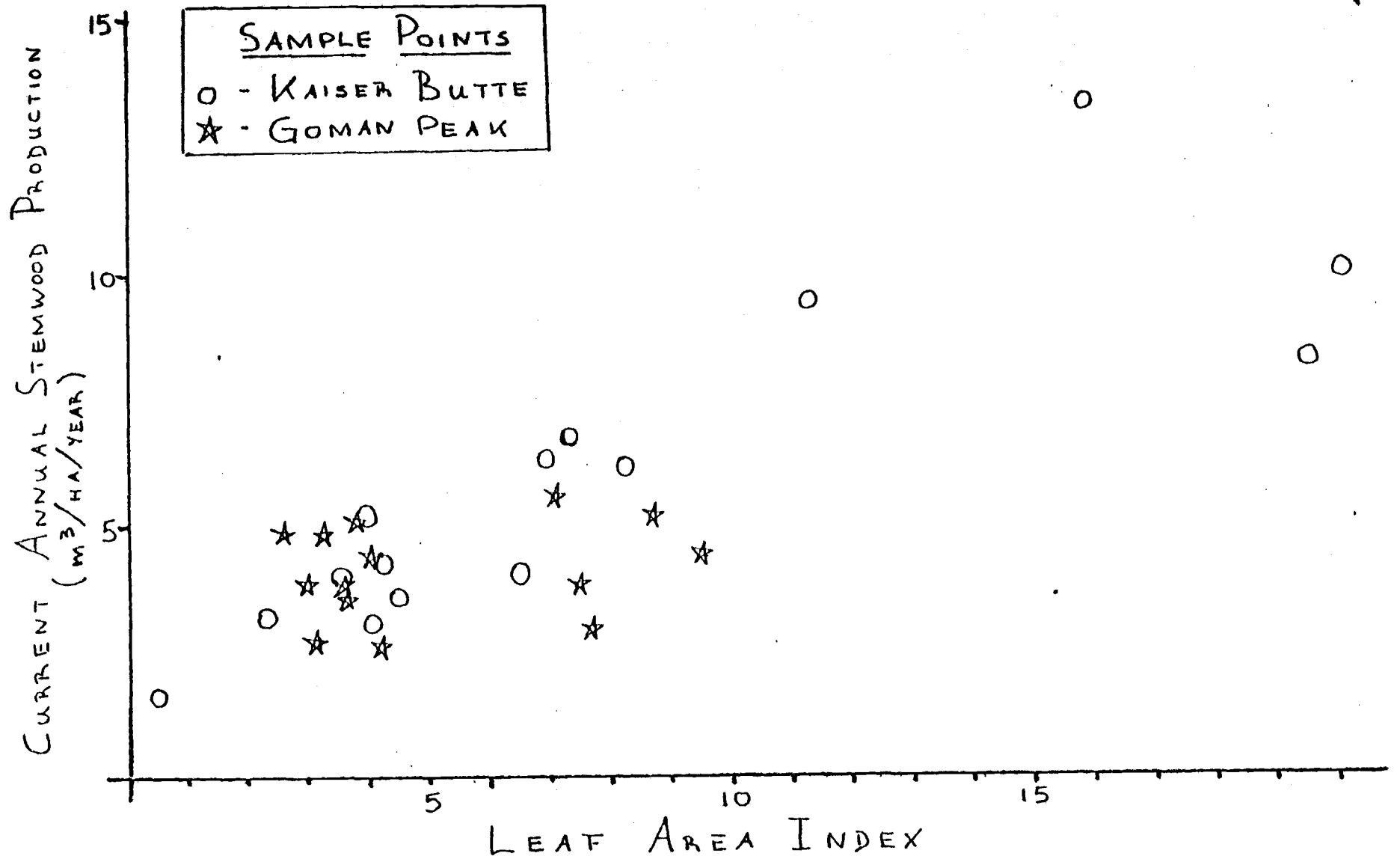


FIGURE 10. LAI vs. PRODUCTIVITY PER HA. AT KAISER BUTTE AND GOMAN PEAK.