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Results from an individual-tree thinning experiment in a 20-year-old Douglas Fir plantation

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P.G. Adlard* and J.P. Smith†

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DEPARTMENT OF FORESTRY
COMMONWEALTH FORESTRY INSTITUTE
UNIVERSITY OF OXFORD

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Commonwealth Forestry Institute
Oxford University

* Research Officer
† Research Assistant
Department of Forestry
Commonwealth Forestry Institute
Oxford University, England.

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SUMMARY

A thinning experiment using individual trees with five treatments and five replications in a 20-year-old Douglas Fir (Pseudotsuga menziesii (Mirb.) Franco) plantation provided data for evaluating the relation between diameter increment for 3 years following thinning at three stem levels and various measures of local stand density (LSD). LSD was defined either as point stand density or the mean stand density within an area dependent on the crown projection area of a tree. LSD was evaluated using four indices: growing space polygons, an overlap-zone index, point density and mean stand basal area within the crown projection area x 3.

The possible application of a measure based on the net basal area of varying numbers of near neighbours is discussed.

Multiple linear regressions were used to relate diameter increment to LSD and measures of absolute and relative tree size. Change of growing space resulting from the thinning, and the height of a subject tree relative to the mean height of the surrounding stand accounted for 73% of the growth variation at 1.3 m in the 25 trees studied, 64% of the growth just below the crown, but less than 35% of the growth within the crown. An overlap-zone index accounted for 38% of the growth variation within the crown.

Branch and foliage weights were assessed on 15 trees in one replication three years after thinning. Using close relations obtained between the sectional area of branches in a whorl, and branch and foliage weights, estimates of total crown weight, total foliage weight, foliage in the 'light' crown and weight of first-year foliage were obtained.

The best relation between diameter growth at 1.3 m was with the weight of foliage in the light crown using a simple power function, but only 63% of the variation was explained.

A tentative index of tree efficiency based on tree basal-area increment in relation to foliage weight and growing space is proposed and discussed.

CONTENTS

FIGURES:

1. INTRODUCTION

In order to predict the growth of an individual tree in a stand as distinct from the growth of the mean tree, the effect of near neighbours has to be determined. We call this the local stand density (LSD) in contrast to mean stand density (MSD). MSD is commonly quantified by number of stems, basal area or total volume per unit area or by some measure of crown closure. Such measures are widely used in forestry but are unsatisfactory as absolute standards of density. When comparing stands of differing age and site quality a measure of density is required that is related to some optimum , maximum or yield table value to quantity density in relation to the density at which inter-tree competition leads to the suppression and death of weaker individuals in the population.

A well known example of a measure of density in relation to maximum possible density is 'relative basal area' (Assmann, 1961). Reineke's stand density index (Reineke, 1933) relates density to incipient crown closure, using the mean crown projection area of open-grown trees. Many other measures, independent of site and age, have been applied to silvicultural research and management, e.g. the crown competition factor (Krajicek et al.,1961; Vezina, 1963), bole area index (Lexen, 1943), leaf area index (Ovington and Madgwick, 1959), Hart-Becking spacing percent (see Assmann, 1968) and tree area ratios (Chisman and Schumacher, 1940; Curtis, 1971). For the validation of individual tree growth models and for evaluating the competitive status of individual trees LSD may be evaluated using a variety of approximate methods. The different approaches to the quantification of LSD may be classified under five types:-

1 - growing space polygons (Jack, 1967; Mead, 1967; Prodan, 1968; Apostolov, 1973; Moore et al., 1973; Jensen, 1976; Pelz, 1978)

2 - influence zone overlap (Bella, 1969, 1971; Arney, 1973; Keister, 1971; Ker, 1975).

3 - relative tree size, e.g. Gerrard's competition quotient (1969)

4 - various uses of nearest-neighbour distance measures (Greig-Smith, 1964; Pielou, 1969; Hausburg, 1968; Batcheler, 1973).

5 - point-sampling applications (Stöhr, 1968).

In an attempt to discover which approach was most suitable for explaining the observed growth response to thinning an individual-tree thinning experiment was established in 1976 in a 20-year-old stand of Douglas Fir in the Forest of Dean in south-west England.

2. LOCAL STAND DENSITY

The methods used to quantify LSD in this study are:

Growing space	(GS)
Influence-zone overlap	(CI)
Mean stand density within crown-projection area	(G(n))
Net basal area stress of nearest neighbours	(Net G)

In addition crown weights (branches and foliage) were assessed on a small sample of trees to qualify the growing space estimates based merely on potential crown-projection areas.

2.1 Growing space (GS)

This is the ground surface area 'occupied' by a tree. Crown projection is often taken as the parameter best expressing the physiological space. Without also considering crown length and structure it can only be a crude measure of the amount of actively photosynthesising foliage. It can however be quantified precisely from data of tree positions and size using certain assumptions about the relation of crown spread and bole diameter. Growing space is defined here as the area included by the vertices of a Thiessen* polygon whose coordinates are dependent on the distance to, and size of, all near neighbours. The method of polygon construction is a modification of that of Schulz (1968) and an earlier version has already been described (Adlard, 1974). Far more elegant and efficient methods of constructing such polygons have been developed recently (Fraser, 1977; Green and Sibson, 1977). The method used here has imperfections and fails in a few cases of very irregular distribution but it partitions growing space adequately for our purposes.

Where no neighbour restricts growth, as estimated by its distance and size relative to the subject tree, the position of a polygon vertex is determined by the diameter of the crown of a free-growing tree of the same diameter at breast height (dbh). The 'weighting' given to trees of differing size may be varied so that different growing space values are obtained dependent on whether competition for space between two trees is proportional to the relative diameters, basal areas or volumes of the two trees. See Appendix 1.

2.2 Influence-zone overlap (CI)

This is calculated as the sum of the areas of neighbour tree influence zones overlapping the influence zone of the subject tree. A free-growing tree has an overlap area, or competitive influence (CI), of zero. CI of suppressed trees may be 5 or more. Formulae used to calculate the CI are given by Arney (1973). As with growing space, used as a two-dimensional static measure, it is still inadequate to describe the competitive potential of a tree in relation to its neighbours. As applied here it does not discriminate between positive and negative competitive stress, so that a high value can mean a subject tree is overlapping, or shading, the influence zones of a large number of smaller neighbours, or that a small subject tree is overlapped or overshadowed by large competing neighbours. Another disadvantage is its dependence on the method of estimation of influence zone. It is not correct to assume that it is the same as the crown projection area of a free-growing tree of the same bole diameter. The plasticity of crown structure when subjected to crowding shows this assumption to be unrealistic. Under competition from neighbouring crowns a crown may alter its form and pattern of foliage distribution, presumably to maximise the space available, either by an increase in surface by development of a greater intensity of foliage within the same crown space, or by a physiological modification allowing for photosynthesis to be maintained under reduced light conditions - see Discussion. Nevertheless the radius of the influence zone was assumed to be a function of dbh in this study. A number of regressions (Table 3) were tested and the one which estimated influence

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* "polygon containing one sample point and the part of the whole area nearer to that sample point than to any other." See Webster (1977) p.227.

zones to explain observed growth most closely was taken as the best estimate of radius of influence of a tree. Thus the experiment provided data to evaluate the influence zones of the subject trees.

2.3 Mean stand density within crown-projection area (G(n))

The basal area of a stand is the sum of the basal areas of all trees on a unit area, usually expressed as the mean basal area of a large sample of fixed-area or point samples located throughout the stand. The variation between plots is dependent on the plot area, or in the case of point sampling, on the basal area 'factor' used. Point samples were simulated at systematic intervals of 1.2m throughout the experimental stand, using the coordinates of tree positions and their diameters stored on a computer file. A basal area factor of 7 was found to give counts of 1 to 9 trees at each point. LSD was then determined as the average of all point samples falling within circular areas round each tree. The areas chosen were multiples of the crown area calculated from crown radius/dbh regressions.

This measure has the advantage of being easily related to stand basal area. A plot of the point densities on the 1.2 metre grid gives a density contour diagram (Figure 1). Insofar as tree height is correlated with dbh this gives a measure of the average stand density in the immediate environment of a tree. The contribution of the subject tree itself is not included in the calculation.

2.4 Net basal area stress

This is a measure of the influence of a neighbour on a subject tree based on its relative size and proximity. In terms of an angle-gauge sample, the basal area factor, K_{01}, that would just include any given neighbour when observed from the subject tree is calculated. The reverse factor, K_{10}, where the subject tree is 'observed' from the position of its neighbour is also calculated. The net basal area of this single neighbour is $K_{10}-K_{01}$. Thus a negative value is obtained when a neighbour is smaller than the subject tree and competition pressure on the subject tree can be considered negative. The sum of the differences for n nearest neighbours is then calculated. See Appendix 2.

A plot of successive values of net G in terms of m^2 ha^{-1} for 3 to 10 and 15 nearest neighbours illustrates the effect of size and position of neighbours. This has greater relevance for evaluating the competitive status of a tree in unevenaged stands. In evenaged stands no more than 3 to 6 immediate neighbours normally determine the LSD around a tree and this is best evaluated as growing space.

3. EXPERIMENTAL DESIGN

A single-tree thinning experiment was superimposed on a species trial established in 1956 by the U.K. Forestry Commission in Flaxley Wood, Forest of Dean. The original design was a randomised block with 5 replications of six treatments comparing the natural regrowth of native Oak scrub woodland with pure or mixed plantations of different species. In one treatment Douglas Fir (*Pseudotsuga menziesii* (Mirb.) Franco) was planted at 6 x 6 ft (1.83 x 1.83 m) spacing after clearing the existing woodland. Plots were square and of approximately 0.2 ha. The five replications of the Douglas Fir plots provided the experimental material for the thinning experiment laid down in the autumn of 1975 when the stands were 20 years old from planting. No thinning had been applied during this time though some natural mortality had occurred. Dbh size class distributions showed a left-handed skewness resulting from the dominance of a few large trees and the survival of large numbers of small trees growing under evident competitive stress. It was considered that the stands provided suitable material for testing the growth response to release from competition.

Five trees in each block (replication) were selected as subject trees. These were subjectively chosen from dominants and codominants of good form, roughly equally spaced at the centre and four corners of each plot. Thinning treatments were applied randomly within each block. These are defined in Table 1. Stand data and dbh of the subject trees are given in Table 2A and B.

4. ASSESSMENTS

4.1 Standing trees

The coordinates of all trees in the assessment plots were mapped by taking bearings and measuring distances and slope from a fixed point or points within each plot. Dbh of all trees and total height of 15% of all trees were recorded. Diameter at three heights, breast height or 1.3 m (dbh), below the live crown base (u1) and at approximately one-third of crown length above the crown base (u2) was measured at intervals of 4-6 weeks, except during the winter, using permanently fixed vernier girth bands. Crown class and an index of vigour, dependent on density and colour of needles, were assessed on all trees.

Crown radius was measured on four radii (more if the crown was assymetric) on a sample of all trees two years after thinning had been applied. These measurements were used for the derivation of one of the crown radius/dbh regressions used in the local density calculations describing 'minimum' crown spread for a tree of given size.

4.2 Felled trees for bole volume measurement

140 trees were felled in the winter of 1975-76 during the application of the thinning treatments. These were measured for total height, dbh, and diameter both over and under bark at 3 m intervals along the bole to a minimum diameter of 2 cm over bark. A further 15 trees were similarly measured in block 2 at the end of the experiment. These included five subject trees together with 10 randomly selected trees from the remainder of the stand. Trees measured for volume were representative of all size classes in the stand. Volume regressions were derived using the weighted regression program (VOLTAB) written by H.L.Wright (C.F.I.,Oxford).

4.3 Felled trees for crown weight assessment

The following variables, in addition to bole volume were recorded for the 5 subject trees felled in block 2 at the end of the experiment:-

Table 1. Thinning treatments

1. No thinning

2. All surviving trees removed from positions adjacent to subject tree

3. Trees in adjacent positions left, all trees two rows distant from subject tree removed

4. Trees in two adjacent rows to subject tree removed

5. As for 4 but any other trees in crown contact with the subject tree to be removed during the course of the experiment

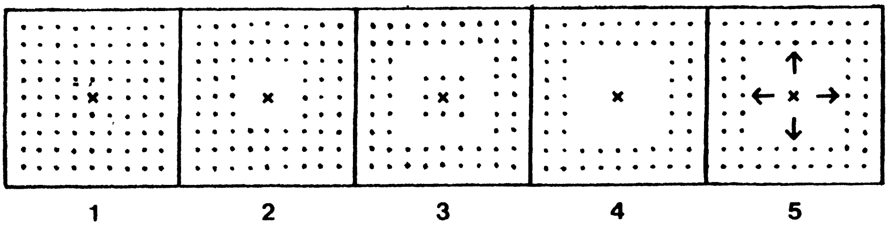

Table 2. Flaxley experiment. Douglas Fir

A: Stand data before (b) and after (a) thinning 1976

Block	$N\ ha^{-1}$		Mean dbh cm		Mean basal area $m^2\ ha^{-1}$		Height m
	b	a	b	a	b	a	a
1	2127	1761	12.0	12.1	24.0	20.2	10.4
2	2231	1836	12.8	12.8	28.7	23.6	12.4
3	2052	1679	12.2	12.4	24.0	20.3	11.1
4	2343	1910	12.9	13.1	30.6	25.7	12.7
5	2343	1948	13.7	13.9	34.5	29.5	14.2

Height given is the mean height of a random sample of ≃ 40 trees per block weighted by tree basal area.

B: Subject tree data 1976

Tree No:	1		2		3		4		5	
Block	Ht m	dbh cm	Ht m	dbh cm	Ht m	dbh cm	Ht m	dbh cm	Ht m	dbh cm
1	13.2	18.3	10.8	13.7	10.9	16.8	11.2	18.0	9.6	16.7
2	15.0	25.0	10.1	15.9	11.1	11.1	12.7	16.5	12.6	18.3
3	9.6	14.8	12.0	16.9	12.2	17.5	10.1	11.6	12.3	17.4
4	13.6	21.1	11.2	15.5	11.8	14.6	12.5	22.4	13.8	23.2
5	14.8	20.0	13.2	20.0	14.8	22.7	14.0	21.2	16.8	31.6

Height to each whorl of live branches
Diameter of bole, over bark, just below whorl height
Branch diameter 1 cm from point of insertion
Branch length
Branch orientation

and, on two randomly selected branches per whorl:-

Green weight of branch sections bearing 1st year foliage
" " " " " " older foliage
" " " " " without foliage

Dry weight of 1st year foliage
" " " branchwood bearing 1st year foliage
" " " older foliage
" " " branchwood bearing older foliage
" " " branchwood without foliage

The same measurements were also taken on the other ten trees felled for volume measurements, except that sample branches were selected from every fourth whorl and not from each whorl as for the subject trees. The first measured whorl was selected at random from whorl numbers 1 to 4 from the crown base.

Separate sets of regressions were derived for each subject tree relating branch and foliage weight to branch sectional area 1 cm from the point of insertion, or further from the main stem when the branch base was noticeably swollen. Only one set of regressions was obtained from the less intensive sample of the other ten trees. Branch and foliage weight parameters were related to the sum of the branch sectional areas in a whorl. Internodal shoot sectional areas were added to the branch area of the whorl below if ≥ 0.5 cm diameter. All smaller internodal shoots were weighed. Whorl weights were derived from the two sets of branch and foliage weights at each whorl in proportion to the ratio

$$\frac{\text{sectional area of sample branches}}{\text{sectional area of all branches in whorl}}$$

Position, sectional area and length of all branches on the sampled trees were recorded. Total tree weights of the 10 other trees were obtained using the regression estimates, plus internode shoot weights.

5. RESULTS

5.1 Crown area or influence zone?

The relation between crown radius and dbh that best fitted our data was:

$$CR = a + b.\ln(dbh) \qquad \text{.... (CR 1)}$$

where CR is crown radius in dm
dbh is diameter breast height in cm
$a = -19.38$
$b = 15.87$
$r^2 = 0.562$

This provides a function describing the crown spread of trees mainly growing in competition in a stand in which density dependent mortality had been occurring. All the crowns observed were subject to lateral interference except for the released subject trees and their neighbours. Measurements were taken in the second year after thinning. A second regression was derived, arbitrarily, by assuming that the actual influence zone of a tree is larger than the observed crown spread and that the increase is constant throughout the range of diameter size classes. Assuming that maximum crown spread had been attained on released trees (treatments 4 and 5) by the end of the third growing season, increasing the value of the constant in equation CR1 to -10 was found to give realistic predictions of potential crown spread, and perhaps of the tree influence zone insofar as it is related to crown projection of free-growing trees. This is equation CR2.

A third regression was derived from the relation between diameter and stem numbers given in the U.K. Forestry Commission Management Tables (1971) for Douglas Fir, General Yield Class 14. This gives unrealistic values of crown radius for small diameters, explained by the current thinning practice in Britain. A single crown radius/dbh regression based on stand mean values cannot be applied to a stand grown under such different conditions at different stages. Two other arbitrary regressions were used in the estimation of influence-zone overlap, for determining the limit of crown spread in growing space calculations (Table 3 and Figure 2). Testing the goodness-of-fit of these indices of local stand density with observed growth showed which function described the radius of influence of trees in the stand under investigation - see section 5.5.

Table 3. Coefficients of crown radius regressions

$CR = a + b.\ln(dbh)$; CR in dm; dbh in cm

Regression No.	a	b	
CR1	-19.38	15.87	Crown radii measured
CR2	-10.00	15.87	Fits observed extension of released crowns
CR3	-27.36	19.73	Intermediate between CR1 and CR2
CR4	-10.56	11.80	(Arbitrary)
CR5	-34.29	19.12	For. Management Tables GYC14

5.2 Tree bole volume

The best fit for estimation of volume was given by the linear regression:

$$\ln(V) = a + b.\ln(h) + c.\ln(dbh) \qquad \text{.... (V1)}$$

where V is total volume to 7 cm diameter over bark in m^3
h is tree height in m
dbh is diameter breast height in cm
$a = -8.5100$
$b = 0.1745$
$c = 2.1226$
$r^2 = 0.92$; Furnival's index = 0.0178

The simpler regression:

$$\ln(V) = a + b.\ln(dbh) \quad .... \text{(V2)}$$

where $a = -8.365$
$b = 2.225$

gave almost as good a fit with $r^2 = 0.92$ and Furnival's index = 0.0179

Bole underbark volume (Vu) was given by:

$$\ln(Vu) = -8.578 + 2.253.\ln(dbh) \quad .... \text{(V3)}$$

5.3 Diameter growth

The course of diameter growth at three stem levels on the 25 subject trees is shown in Figures 3 to 7. Data at all levels are only available for the complete growing seasons of 1977 and 1978 and most of the discussion is limited to this period. However, analysis of variance of diameter growth at the end of the 1976 growing season showed significant differences in response to thinning at both breast height and below the live crown (dbh and ul). The main growth period started at the end of February at all levels though some growth was recorded on most released trees between September and March. Rapid diameter growth terminated in late June, though significant growth occurred later in 1978 - a wet summer, but little in 1977 when it was dry from July to October.

Diameter measurements were taken too infrequently to relate growth to climatic factors in detail. Perhaps also for this reason we could not detect the sequence of flushing and shootgrowth that Cantiani (1971) found to result in waves of increment along the stem in Douglas Fir in Italy. He recorded that growth in the early part of the season started in mid-crown, spread to the base of the tree and finally to the top of the crown.

Diameter growth at the three stem heights has been correlated with local stand density. A series of determinations of growing space and of the influence-zone overlap index (CI) were carried out using various weighting factors and crown radius regressions. A weighting factor of 2 and crown radius regression CR2 were found to give growing space estimates best correlated with observed growth at the two lower points of measurement. Diameter growth within the crown was not closely correlated with growing space or any of the indices of LSD tested.

In addition to the measurements on 25 subject trees the diameters at the beginning and at the end of the experiment of the 1200 other trees in the assessment plots were recorded. The first measurement was delayed in some blocks but all diameters were adjusted to a common datum before the 1976 growing season.

5.3.1 Diameter growth at 1.3 m (i_{dbh})

Response to thinning was rapid. Analysis of variance of i_{dbh} at the end of the first growing season showed significant differences in response. Diameter growth at 1.3 m on the 25 subject trees for three growing seasons is given in Table 4 together with selected measures of LSD. A preliminary analysis gave a simple linear correlation with $r^2 = 0.71$ between increment and growing space at the beginning of the period after thinning. Observed and estimated growth based on the regression are shown in Table 5.

Table 4. Diameter growth at 1.3 m and changes in measures of local stand density 1976-78. Flaxley Douglas Fir Single Tree Thinning Experiment

Block	Tree	Dbh growth 1976-78	Dbh 1976	Dbh 1978	Before thinning 1976 GS	Before thinning 1976 Net G	Before thinning 1976 CI	Before thinning 1976 G(3)	After thinning 1976 GS	After thinning 1976 Net G	After thinning 1976 CI	After thinning 1976 G(3)	1978 GS	1978 Net G	1978 CI	1978 G(3)
1	1	1.9	18.9	20.8	13.55	-3.9	4.23	34.1	13.55	-3.9	4.20	35.5	13.78	-4.8	4.55	40.0
	2	2.3	13.7	16.0	9.11	-13.3	4.14	32.3	15.99	0.2	1.66	19.9	18.85	0.1	2.10	26.7
	3	1.9	16.8	18.7	7.94	-5.6	4.81	35.1	8.12	-5.6	2.80	24.1	8.19	-7.1	3.10	29.9
	4	3.3	18.0	21.3	14.71	-4.5	4.48	38.9	29.43	-0.7	1.19	17.2	33.15	-1.1	1.42	21.5
	5	3.6	16.7	20.3	8.20	-8.4	3.98	29.2	37.78	-0.5	0.11	7.9	41.77	-0.8	0.41	13.4
2	1	1.9	25.0	26.9	12.83	-8.3	4.64	40.2	12.83	-8.3	4.63	40.4	12.58	-9.7	4.93	45.3
	2	1.5	15.9	17.4	6.46	-3.2	5.48	39.3	15.80	-0.8	2.86	25.7	15.40	-0.9	3.26	32.3
	3	1.3	11.1	12.4	3.04	-0.1	6.01	47.6	3.96	-0.1	3.99	30.9	3.94	-0.4	4.23	35.9
	4	3.2	16.5	19.7	8.59	-11.5	4.85	38.3	35.51	-0.4	0.29	10.6	41.43	-0.7	0.56	16.2
	5	3.2	18.3	21.5	7.31	-5.7	4.91	42.7	32.01	-0.6	0.42	9.6	37.21	-0.9	0.74	11.4
3	1	0.7	14.8	15.5	8.20	1.9	4.32	31.7	8.20	1.9	4.32	31.7	8.73	3.0	4.42	35.3
	2	2.5	16.9	19.4	9.77	-5.3	4.38	33.4	24.58	-1.6	2.40	24.2	27.37	-2.2	2.74	27.8
	3	1.5	17.5	19.0	7.15	-3.9	4.27	33.3	7.13	-3.9	2.97	24.7	6.97	-4.5	3.22	29.6
	4	1.3	11.6	12.9	5.23	-0.5	3.92	33.1	14.23	0.4	0.26	11.4	12.53	0.6	0.41	14.9
	5	3.7	17.4	21.1	9.53	-6.7	4.12	32.7	33.51	-0.2	0.40	11.7	38.64	-0.4	0.64	15.7
4	1	0.8	21.1	21.9	18.17	-4.9	4.14	36.7	18.17	-4.9	4.14	36.3	17.73	-5.3	4.39	42.0
	2	2.5	15.5	18.0	5.91	-0.2	5.25	42.5	19.56	-0.6	2.28	27.2	21.46	-0.9	2.90	37.2
	3	1.7	14.6	16.3	7.60	-2.0	5.33	43.1	8.94	-2.0	3.28	29.8	9.05	-2.5	3.54	34.9
	4	1.9	22.4	24.3	10.39	-8.9	5.51	45.2	36.46	-1.0	0.72	11.2	37.35	-1.2	1.01	14.3
	5	2.9	23.2	26.1	10.70	-9.9	5.49	40.9	43.38	-1.0	0.70	20.1	45.99	-1.3	0.91	25.4
5	1	1.6	20.0	21.6	12.29	-8.3	5.73	35.7	12.29	-8.3	5.73	35.7	16.84	-5.3	5.66	39.8
	2	2.4	20.8	23.2	9.88	-4.3	5.63	50.0	28.33	-0.1	2.83	36.0	21.62	-0.1	3.27	42.8
	3	1.8	22.7	24.5	10.73	-5.6	6.10	54.5	10.83	-5.6	3.88	37.7	10.76	-6.2	4.24	45.0
	4	3.1	21.3	24.4	14.66	-7.9	5.12	43.6	40.07	-0.7	0.52	17.7	44.70	-1.0	0.72	22.6
	5	4.9	31.6	36.5	22.09	-13.9	5.23	38.7	53.79	-2.7	1.95	23.2	58.29	-3.7	2.27	29.3

Note: Growing space calculated using a weighting coefficient of a = 2. (see Appendix 1)
Max. crown, or zone of influence, radius was derived from regression C2, Table 3; G(3) is mean stand density within 3 times this zone. Net G is based on the 3 nearest neighbours

Table 5: Diameter growth at 1.3m for 3 years 1976-78 in relation to initial growing space

Block	Tree no.	GS m^2	i_{dbh} estimated† cm	i_{dbh} observed cm	Difference obs.-est. cm
1	1	13.55	1.73	1.9	+0.2
	2	15.99	1.89	2.3	+0.3
	3	8.12	1.40	1.9	+0.5
	4	29.43	2.72	3.3	+0.4
	5	37.78	3.24	3.6	+0.4
2	1	12.83	1.68	1.9	+0.2
	2	15.80	1.87	1.5	-0.4
	3	3.96	1.14	1.3	+0.2
	4	35.51	3.10	3.2	+0.1
	5	32.01	2.88	3.2	+0.3
3	1	8.20	1.40	0.7	-0.7
	2	24.58	2.42	2.5	+0.1
	3	7.13	1.33	1.5	+0.2
	4	14.23	1.78	1.3	-0.5
	5	33.51	3.00	3.7	+0.7
4	1	18.17	2.02	0.8	-1.2
	2	19.56	2.10	2.5	+0.4
	3	8.94	1.45	1.7	+0.3
	4	36.46	3.15	1.9	-1.1
	5	43.38	3.59	2.9	-0.7
5	1	12.29	1.65	1.6	0
	2	28.33	2.65	2.4	-0.2
	3	10.83	1.56	1.8	+0.2
	4	40.07	3.38	3.1	-0.3
	5	53.79	4.24	4.9	+0.7

† $i_{dbh} = 0.890 + 0.06226(GS)$; $r^2 = 0.71$

Note: the evident bias may be partially explained by the omission of tree height in this simple regression: cf. Table 2B. This is accounted for below by the inclusion of relative height of subject tree to stand height in the regressions of section 5.3.2.

To illustrate how far this relation between i_{dbh} and GS reflects a thinning response, or merely describes the result of vigorous trees creating their own growing space through suppression of neighbours in a dense stand, change in growing space after thinning has been used as an independent variable in the main set of analyses. Also a preliminary analysis of the correlation of growth of a systematic sample of trees from the unthinned stand in one block (4) showed growing space to account for a similar proportion of the variation in i_{dbh} as with the 25 subject trees, though the range of growing space included was smaller:-

$$i_{dbh} = 0.477 + 0.1362(GS); \; r^2 = 0.70 \qquad \text{.... (E1)}$$

For comparison the relation between diameter growth and tree diameter for the same sample of trees in the unthinned stand was:-

$$i_{dbh} = 0.617 + 0.1276(dbh); \; r^2 = 0.54 \qquad \text{.... (E2)}$$

and for comparison with another variable that was expected to describe LSD well, net basal area stress:-

$$i_{dbh} = 0.906 + 0.1158(net\ G); \; r^2 = 0.54 \qquad \text{.... (E3)}$$

Neither tree diameter nor net basal area stress explain diameter growth at 1.3 m on the subject trees and trees in the surrounding stand as well as growing space. This suggests it may be the size and position of <u>immediate</u> neighbours that affect i_{dbh} rather than the presence of large trees, not in direct contact with the tree measured, which may nevertheless have a strong influence on measures of LSD based on overlap zones or point sampling methods. However a large proportion of the variation in i_{dbh} remains unexplained by these simple regressions. The results of multiple regressions using various combinations of LSD indices calculated on a range of assumptions are presented in the next section. Net basal area stress (net G) has not been included in the multiple regressions as it is not a suitable measure for assessing LSD after thinning but does offer interesting possibilities for characterising the competitive status of individual trees. Though not fully analysed here one illustration of its function is given. The values of net G for the five subject trees and 20 other trees covering the range of diameter classes in block 4 for 3 to 10 and for 15 near neighbours are shown in Figure 8. Trees under positive stress appear at the top of the figure and those with negative values below the zero horizontal line. Strongly dominant trees have sharply descending slopes. Those dominating their immediate neighbours, but beyond them surrounded by relatively large trees, are shown by lines that descend at first then flatten out. Trees at the centre of a cluster surrounded by less dense stand will be shown by a line that changes slope where the number of neighbours included in the calculation of net G is greater than the number of trees in the cluster, as for subject tree 3. As presented here trees subjected to thinning cannot be compared directly with those in the unthinned parts of the stand. Thinning immediate neighbours automatically reduces the negative value of net G while increasing GS. Table 6 shows the changes in net G of 6 nearest neighbours for the five subject trees of block 4.

Table 6. Change in net G and growing space for subject trees in block 4

b = before, a = after thinning 1976

Tree No.	Net G m^2			GS m^2		
	b	a	Diff.	b	a	Diff.
1	-6.7	-6.7	0	18.17	18.17	0
2	-1.6	-1.0	0.6	5.91	19.56	13.65
3	-2.8	-2.8	0	7.60	8.94	1.34
4	-14.1	-2.1	12.0	10.39	36.46	26.07
5	-15.0	-1.7	13.3	10.70	43.38	32.67

None of the static measures of LSD can discriminate, without further qualification, between negative stress due to competitive success in the past with the predication of future success, from positive stress under pressure from neighbours with predication of reduced future growth and reduced probability of survival. Large dbh, large negative net G and large GS before thinning clearly describe the past success of an individual. Changes in net G in the absence of interference by thinning over time could be used as a dynamic index of competitive status particularly if combined with a measure of height. In the present study where thinning effects are being assessed this index cannot be combined with the other measures of LSD in multiple regression analysis without confusion. The value of net G, or of changes in net G over time are being investigated in uneven-aged stands but as the measure is closely dependent on tree diameter in even-aged stands it is not considered further in this study. In the next section tree size (dbh^2 x height) is used instead as an independent variable in predicting diameter growth at the three stem heights.

5.3.2 Diameter growth at three stem heights

The next stage of the analysis considered the diameter growth at 1.3 m, below the crown and within the crown for the two growing seasons 1977 and 1978 for which complete records were available. A large number of regressions were run in an attempt to determine which measure of LSD accounted for observed growth on all 25 subject trees most satisfactorily.

Linear relations between growth for two growing seasons and various combinations of the following independent variables were tested:-

Tree size (dbh^2 x h of subject tree)	VOL
Tree class (h of subject tree as ratio of mean height of neighbouring stand -	HR1
or of mean height of block) -	HR2
Growing space after thinning	GS
Growing space release, i.e. change of growing space due to thinning	ΔGS
Influence-zone overlap index	CI
Mean basal area density within crown projection area x 3	G3

Values of GS and ΔGS were calculated using weighting factors of 1, 2, 2.5 and 2.75. Values of GS, ΔGS and CI were calculated using all five crown radius regressions.

Inter-correlations between independent variables are shown below:

	VOL	HR1	HR2	GS	ΔGS	CI	G3
VOL	1	0.422	0.647	0.539	0.332	0.069	0.196
HR1	0.422	1	0.787	0.263	0.144	-0.031	-0.002
HR2	0.647	0.787	1	0.422	0.245	-0.120	-0.032
GS	0.539	0.263	0.422	1	0.953	-0.697	-0.577
ΔGS	0.332	0.144	0.245	0.953	1	-0.817	-0.715
CI	0.069	-0.031	-0.120	-0.697	-0.817	1	0.931
G3	0.196	-0.002	-0.032	-0.577	-0.715	0.931	1

Stepwise elimination of non-significant variables gave consistent results. The regressions, including only the significant variables, that best explained variation in diameter growth at three stem heights were:-

Dbh growth:-

$$i_{dbh} = -1.265 + 2.355(HR2) + 0.04811\,(\Delta GS) \qquad \text{.... (E4)}$$

$R^2 = 0.73$; Residual S.D. = 0.442 cm

Diameter growth below crown:-

$$i_{u1} = -1.176 + 2.945(HR2) + 0.02913(\Delta GS) \qquad \text{.... (E5)}$$

$R^2 = 0.64$; Residual S.D. = 0.419 cm

Diameter growth within crown:-

$$i_{u2} = 15.43 - 2.664(CI) \qquad \text{.... (E6)}$$

$r^2 = 0.38$; Residual S.D. = 3.157 cm

The following regressions relate diameter growth to GS at the lower two stem levels:-

$$i_{dbh} = 0.6894 + 0.04963(GS) \qquad \text{.... (E7)}$$

$r^2 = 0.69$; Residual S.D. = 0.463 cm

$$i_{u1} = 1.423 + 0.04517(GS) \qquad \text{.... (E8)}$$

$r^2 = 0.52$; Residual S.D. = 0.470 cm

At the highest level within the crown the relation between growth and GS was not significant, though it was with ΔGS:-

$$i_{u2} = 10.85 + 0.1855(\Delta GS) \qquad \text{.... (E9)}$$

$r^2 = 0.33$; Residual S.D. = 3.270 cm

GS, ΔGS and CI used in all the above regressions were calculated using regression CR2 (Table 3) and a weighting cooefficient of a = 2 (see Appendix 1). See Table 5 for a comparison with the regression of diameter growth at 1.3 m over three growing seasons on growing space.

5.4 Crown parameters and growth

5.4.1 Total weight of branchwood and foliage

The total weight of branchwood and foliage at each whorl was related to branch sectional area of the whorl by a simple logarithmic function. The values of the coefficients obtained are given in Table 7. Over 90% of the variation in weight is accounted for by the linear regression suggesting that branch area can be used to estimate branch weight. Actual weights and regressions are shown in the top part of Figures 9-14 for the subject trees and ten other trees from block 2.

Table 7. Total branchwood and foliage weight in relation to branch sectional area by whorls
Coefficients of function: Weight = a.(br area)^b

Tree	a	b	r^2%
1	25615	1.38	91
2	31906	1.49	92
3	33957	1.46	97
4	39223	1.64	95
5	17719	1.21	96
10 others	22374	1.27	97

5.4.2 Foliage weight

Total crown weight, including both wood and foliage was not expected to be as useful a parameter in growth prediction as foliage alone. The weight of foliage is however partly dependent on the light received in different parts of the crown and is affected by the presence of neighbour crowns. Below the level of the crown exposed to full vertical light at mid-day the quantity of foliage for a unit of branch sectional area falls with increasing shade to the point at the base of the crown where all foliage is shaded out. Distribution of foliage is shown in part (b) of Figures 9-14. The relation of foliage weight to branch sectional area was not close for the unthinned trees as expected, though the logarithmic relationship for thinned trees explained over 80% of the variation in weight. See Table 8.

Table 8. Total foliage weight in relation to branch sectional area by whorls.
Coefficients of function: Weight = a.(br area)^b

Tree	a	b	r^2%
1	7480	1.21	66
2	12333	1.53	91
3	20131	1.66	86
4	10938	1.58	81
5	6768	1.22	86
10 others	21590	1.88	43

Measurements were made three years after thinning and it is unlikely that crowns have become fully adapted to their new growing space during this period so total foliage weight is not easily predicted from branch and crown parameters. The foliage weight in the 'light' crown only should however be more easily predicted and also be related more closely to growth. Steinhübel (1971) used the relations between shoot characters to estimate the photoassimilating crown surface of young Pinus nigra trees. A similar hypothesis was used by Beauregard (1976) in developing a crown view factor index for uneven-aged mixed hardwoods assuming a geometrical model. In our data the crown geometry is strongly influenced by treatment and the problem is to define the base of the light crown. It is not easily observed in dense stands and in this study the stratification had to be done on the data after the termination of field work. Foliage weight is related closely to branch area in the top part of the crown down to level of maximum crown width, at least for the trees growing in dense stands. Height of maximum crown width is the simplest criterion for the base of the 'light' crown. The proportion of young, first year, foliage to the total foliage weight was observed to decrease in a regular manner from the top to the base of the crown in unthinned trees and tended to be ≃ 25% at the widest part of the crown. This is used as a criterion for defining the base of the 'light' crown. It is defined here as the level in the crown below which branches carry less than 25% of their foliage weight as first-year foliage. See Table 9.

Table 9. Crown length and length of 'light' crown of five subject trees in block 2

Tree No.	Total height (h)	Crown length (cl)	Base of 'light' crown as % of h	cl	Length of 'light' crown	No.of whorls in whole crown	'light' crown
1	16.6	11.7	33	54	5.0	17	12
2	11.2	7.4	34	51	3.8	14	10
3	12.2	7.0	33	57	4.0	10	6
4	13.2	9.5	67	83	8.4	16	8
5	13.8	9.2	62	94	8.6	15	11

Note: Crown length is the distance from tip to lowest whorl containing two or more live branches.
'Light' crown includes whorls on which more than 25% of the foliage weight is contributed by first-year foliage.

Two further sets of regressions were then calculated, one relating foliage weight in the 'light' crown to branch sectional area (Table 10) and the second considering only the weight of first-year foliage for the same part of the crown (Table 11).

Table 10. Foliage weight in 'light' crown in relation to branch sectional area by whorls
Coefficients of function: Weight = a.(br area)^{b}

Tree No	Number of whorls from base of crown	a	b	r^2%
1	(6-17)	17854	1.55	90
2	(5-14)	16318	1.63	96
3	(8-13)	29437	1.61	98
4	(10-17)	24100	1.73	94
5	(3-15)	8022	1.19	96
10*	above 7.5 m	12456	1.33	94

*10 sample trees from surrounding stand

Table 11. First-year foliage weight in 'light' crown in relation to branch sectional area by whorls
Coefficients of function: Weight = a.(br area)^{b}

Tree No	Whorls	a	b	r^2%
1	(6-17)	3641	1.17	95
2	(5-14)	3011	1.26	91
3	(8-13)	9321	1.39	96
4	(10-17)	6701	1.44	92
5	(3-15)	1703	0.84	85
	(5-15)	1451	0.84	92
10*	above 7.5 m	3041	1.06	91

*10 sample trees from surrounding stand

5.4.3 Crown parameters in relation to bole parameters and diameter growth

The crown parameters in Table 12 were obtained from the regressions in the previous section. Tree volume was obtained from the second regression (V2) in section 5.2. From this overview certain relations of interest were derived and the regressions are listed at the foot of Table 12. Crown weight was found to be approximately proportional to the cube of diameter at 1.3 m times a constant. Foliage weight also had a cubic relationship to diameter, though first-year foliage increased in proportion to diameter to the power of 4.

A

Table 12. Summary of bole and crown parameters for 15 trees felled in block 2: 1978

Tree No.	Dbh cm	Total height m	Volume ob m^3	Crown length m	Dry weight: 1st year foliage 'light' cr. kg	Dry weight: All foliage 'light' cr. kg	Dry weight: All foliage kg	Dry weight: Branch wood kg	Dry weight: Total crown kg	i_{dbh} 1976-78 cm
1	26.9	16.6	0.388	11.7	6.96	22.04	30.18	55.11	85.29	1.9
2	17.4	11.2	0.145	7.4	3.13	9.17	11.27	17.99	29.26	1.5
3	12.4	12.2	0.068	8.4	1.10	2.04	6.84	7.90	14.74	1.3
4	19.7	13.2	0.192	10.0	3.43	7.94	21.94	34.75	56.70	3.2
5	21.5	13.8	0.234	9.6	6.26	18.09	22.20	25.08	47.29	3.2
19	10.9	11.4	0.047	6.1	0.84	1.05	3.03	3.75	6.78	0.4
22	14.0	12.8	0.082	7.9	2.14	4.04	7.10	8.65	15.77	0.8
60	10.5	10.1	0.044	5.1	0.61	0.74	1.92	2.69	4.61	0.0
115	10.9	11.3	0.047	6.2	1.50	3.16	3.78	4.31	8.09	1.2
162	21.8	14.2	0.221	9.9	7.70	21.80	35.60	33.00	68.60	2.2
164	8.3	9.5	0.026	4.9	0.44	0.74	2.67	3.14	5.81	0.0
180	21.5	14.6	0.215	10.8	5.46	16.18	30.98	28.84	59.82	1.5
185	23.0	15.2	0.249	11.8	7.64	22.01	37.65	35.66	73.31	2.6
192	14.5	11.7	0.089	8.5	1.85	4.28	7.42	7.80	15.22	0.9
219	6.6	6.5	0.016	3.5	0.02	0.04	0.29	0.47	0.76	0.0

Relations between crown and bole parameters:-

Crown weight = $0.004(\text{dbh})^{3.13}$; $r^2 = 0.95$ .... (E10)

" " = $490.45(\text{bole volume})^{1.4}$; $r^2 = 0.95$ .... (E11)

Tot. foliage weight = $0.0016(\text{dbh})^{3.17}$; $r^2 = 0.93$ .... (E12)

Light crown foliage = $0.0001(\text{dbh})^{4.02}$; $r^2 = 0.90$ .... (E13)

Relations between crown parameters and diameter growth:-

i_{dbh} = $0.0055(\text{total foliage weight})^{1.96}$; $r^2 = 0.48$ .... (E14)

= $0.0001(\text{total crown weight})^{2.50}$; $r^2 = 0.58$ .... (E15)

= $0.0133(\text{'light' crown foliage})^{1.96}$; $r^2 = 0.63$ .... (E16)

From this small sample of felled trees the relation between crown parameters and growth was not close. As judged by the values of the coefficient of determination slightly less variation in i_{dbh} is explained by crown parameters than by growing space (section 5.31) although this sample contains 10 trees from the unthinned stand and is not directly comparable to the 25 subject trees being considered in the earlier section. Two trees in this set are showing anomalous behaviour. Tree No. 1, a large tree without thinning of the surrounding stand, has grown less than the average in relation to crown weight. Strict comparison with tree No. 185 of similar foliage weights is difficult as the latter was at the edge of the assessment plot and no growing space data are available. Tree 115 is an edge tree which may explain the relatively large diameter growth for its size. Obviously many factors beside the crown dimensions are affecting diameter growth. Some are discussed below.

5.5 Relative efficiency of individual tree crowns

The ratio of basal area increment to the product of foliage weight and growing space was calculated for the thirteen felled trees for which sufficient information was available. If i_g is the basal area increment for the three-year observation period

$$\frac{i_g}{\text{(foliage weight)} \times \text{(growing space)}}$$

can be taken as a measure of individual tree efficiency for the felled sample trees (omitting two 'edge' trees for which GS could not be calculated). The results are given in Table 13.

The value for tree 3 is unreliable since the actual GS of this tree at the centre of a cluster is probably underestimated as explained above. However if the index of 30 is taken as an arbitrary maximum, the relative efficiency of the remaining trees can be expressed as a percentage of this value. This indicates that smaller trees with small GS tend to be more efficient and that above a GS of 11 m^2 the values of the index are more or less constant. Trees less than 10 cm dbh have not grown at all but those still growing above this size have high index values. This observation is not easy to explain.

Table 13. Relative efficiency of felled sample trees

Tree No.	Dbh	GS	Fol. wt.	i_{dbh}	i_g	$\frac{i_g}{\text{wt x GS}}$	%
1	26.9	12.8	22.0	1.9	0.774	2.7	9
2	17.4	15.8	9.2	1.5	0.392	2.7	9
3	12.4	4.0	2.0	1.3	0.239	30.0	100
4	19.7	35.5	7.9	3.2	0.910	3.2	11
5	21.5	32.0	18.1	3.2	1.161	2.0	7
19	10.9	2.7	1.0	0.4	0.067	24.8	83
22	14.0	5.8	4.0	0.8	0.171	7.4	24
60	10.5	2.4	0.7	0.0	0.0	0.0	0
162	21.8	8.2	21.8	2.2	0.715	4.0	13
164	8.3	2.4	0.7	0.0	0.0	0.0	0
180	21.5	11.3	16.2	1.5	0.489	2.7	9
192	14.5	7.2	4.3	0.9	0.199	6.4	21
219	6.6	1.6	0.02	0.0	0.0	0.0	0

The influence of neighbours is reflected more strongly in diameter growth at 1.3 m than at upper stem levels - compare regressions E4 to E6 in section 5.3.2. Growth near the base of the 'light' crown was not correlated closely with any index of LSD and over 60% of the variation in diameter growth was unexplained, see regressions E6 and E9. This fact may have little significance in terms of forestry production of saw timber where the yield of most value is obtained from the first 6 to 8 m of the bole. Apart from indicating, however, how crown structure is influenced by LSD it suggests one explanation for the growth variation not explained by the growing space or point density measures. The upper crown growth is almost as great for a dominant or codominant tree of given size whether it is influenced by neighbours or not.

The crown weight estimates are unfortunately restricted to a single part of the experiment - block 2. Of the 5 subject trees the largest tree happened to be the treatment control, tree No. 1. This was a strong dominant that had established its own appreciable growing space of 12.8 m^2 by the beginning of the period of observations and was the second largest subject tree in the experiment. Nevertheless the influence of growing space is striking in that its growth at 1.3 m was only 1.9 cm in 3 years compared with increments of twice the value on smaller trees with larger growing space after thinning.

6. DISCUSSION

Previous studies have not provided convincing evidence of a close correlation between growth of individual trees and their position in the stand. van Laar (1969) could only account for 40% of the variation in radial increment at various heights in the stem of Pinus radiata by reference to dbh, crown length and point density. Johnson (1973) investigated the effect of various procedures for measuring point density in explaining diameter and basal area growth of individual trees of southern Pines in Alabama. He concludes that a new approach to the problem of evaluation of competitive pressure on individual trees may have to be developed. A previous application of growing space measures to explain growth of coniferous plantations in East Africa (Adlard, 1974) was unsatisfactory. The Flaxley thinning experiment was prompted by the desire to investigate the role of growing space in relation to other measures of competition, or LSD, under controlled conditions.

The main conclusion from the analysis is that only some 70% of growth variation at breast height, and less at higher levels in the stem can be explained by spatial indices of LSD in 20-year-old Douglas Fir on one site in the Forest of Dean.

The difference between the efficiency of the various indices tested was not great. The coefficient of determination varied from 0.54 to 0.69 when relating i_{dbh} to GS estimated by the various weightings and crown projection area regressions. At the upper stem level within the crown i_{u2} was related to one mean basal area measure within an r^2 of 0.30 (the poorest fit) and to an overlap-zone index with an r^2 of 0.38 (the best). Slightly better fits were obtained using several independent variables. i_{u2} was related to tree volume, tree class, growing space, change of growing space after thinning, and an overlap-zone index with an R^2 of 0.49 but all the variables except the overlap-zone index were non-significant and were rejected by a step-wise regression procedure.

The absence of a relationship between growth and tree size at the beginning of the period is notable. In an undisturbed stand the larger trees are growing faster on average than the smaller trees. Tree size reflects the competitive advantage that a tree has been exercising within the stand. In the experiment the subject trees were all dominants or codominants and the observed effect is mainly due to the degree of release, or increase in growing space afforded each tree and not to past behaviour. Response to release from competition is dependent on the size of the subject tree relative to the size of its neighbours but independent of absolute tree size. Response was more closely related to increased growing space created by removal of immediate neighbours than to the average density of the surrounding stand. But treatment 3 - thinning of the second row of trees leaving the subject tree surrounded by a group of close neighbours - has resulted in relatively large i_{dbh} for growing space (Tables 5 and 13) suggesting that the subject tree is benefitting to some extent from growing space created outside the cluster. The clusters of treatment 3 were not all 'closed' since some trees had died before the thinning and advantage can have been taken of gaps in the cluster of which account has not been taken in the construction of the growing space polygons.

The best correlation of i_{dbh} was found to be with the foliage weight of the upper part of the crown. The determination of the number of whorls to be included in the 'light' crown was, though, the most subjective parameter used in the study. Further, the small sample on which regression E14 was based does not justify its general application. Further work is needed to investigate the interaction between foliage weight and growing space and its relation to growth. On the other hand the static relations within the crown were more precise. Total crown weight and foliage weight were closely related to the sum of branch sectional area in a whorl. This was considered to be the level of investigation at which crown structure could be derived from observations practical to measure on standing trees in the field. In older trees of Douglas Fir it becomes difficult to distinguish whorls where internodal shoots develop into branches of considerable size. Though time consuming and requiring some climbing the numbers and sizes of branches in each whorl can be estimated on standing trees. The method used here could be applied to trees on different sites, and of different species with monopodial branching habit, for developing functions to predict crown weight from dbh with the same order of precision as for prediction of bole volume widely used in practice. Relations within single branches have not been discussed here as not being essential for the development of predictive functions on a whole tree basis. A close relationship found between branch diameter and length justified the use of the single parameter of sectional area at the base of the branch when developing branch size and weight relations. Foliage weight was highly variable within and between whorls as expected from previous work on Pines (e.g. Gary, 1976), but problems caused by this variation are largely avoided by use of branch sectional area per whorl as the single independent variable in crown weight prediction functions.

The data on foliage weight for the subject trees show that thinning response is due to greater crown efficiency rather than to an increase in crown weight or size itself; see for instance the data for trees 1, 4 and 5 in Table 12. A conclusion is that some measure of 'efficiency' must be assessed if a better method of evaluating competitiveness of an individual is to be devised.

The reduction in the proportion of first-year foliage borne by successive whorls from the top of the base of the crown appears as a smooth quadratic curve in an unthinned control tree (Figure 9(b)). Thinning resulted in an increase in the proportion of first-year foliage at lower levels in the crown in approximate proportion to the intensity of release (Figures 10(b) - 14(b)). The proportion at about half tree-height increased from 5% in the unthinned control to 35% on the released trees. The response to light has been rapid and illustrates how these Douglas Fir crowns are able to adapt to changing conditions at this age.

The foliage illumination model of Monsi and Saeki (1953) and developments of it (see Verhagen et al., 1963) are helpful in understanding the behaviour of foliage in the lower canopy where light intensity falls to levels where respiration losses are greater than photosynthetic gains - the compensation point. It is accepted that a simple geometrical crown model, even if confined to the photosynthetically active part of the crown, cannot easily take account of alteration in the form and function of leaves in different levels of the canopy. The low correlations found in our data between foliage weight and i_{dbh} (regressions E14-E16 in Table 12) are to be expected as the model is too simple. Besides possible physiological changes in leaf behaviour in different parts of the crown, the changes in crown form induced by the extreme thinning treatments render it unrealistic to fit the same model to trees growing in such a wide range of LSD.

Comparison of foliage weights of the unthinned control tree in block 2 with the fully released trees (see Figures 9b, 12b and 13b) does not take account of the changes in crown form. First-year foliage percentage declines in a regular manner from tip to crown base in the dominant tree growing in a dense stand. New crown growth on the other hand has occurred at deeper levels in the crown on the released trees. The abrupt increase in the first-year foliage percentage at different crown levels in trees 2 to 5 is evidently associated with treatment. These trees are adapting to their new light environment and the crowns have not stabilized within the three-year observation period. At least some of the foliage on the released trees appears to be assimilating more efficiently than on the control tree. Further conjecture on very limited data may be valueless but the evidence presented suggests possible approaches to future research. Efficiency of the individual crown has to be balanced by considerations of the efficiency of the canopy of the stand. From the results of many thinning experiments in coniferous stands it has been shown that the maximum yield of cellulose is obtained at maximum or near maximum stand densities. Maximum efficiency of a stand could be defined as one composed of trees with high basal area increment for minimum foliage weight and growing space.

Hamilton (1969) found that narrow crowned trees of Sitka Spruce were most efficient producers of increment and that trees of larger dbh were better producers if other factors were kept constant. Our evidence suggests that, after thinning, increment is related to GS up to a certain value above which further increase in growth is only achieved by larger amounts of foliage so that efficiency does not increase. The implications of this for thinning theory, by providing an objective measure of a 'marginal' density, are obvious but further work on devising measures of efficiency is needed. It is believed that this approach can have applications in the evaluation of provenance and progeny trials where the early recognition of individuals with small crowns but high potential growth is important for tree improvement programmes. Sakai and Mukaide (1967), after partitioning the phenotypic variation in Cryptomeria japonica stands into environmental and competitive components, concluded that effective selection of genetically superior trees would be difficult. Closer study of crown structure and efficiency in relation to growing space is considered to be one approach to solving this difficulty.

7. CONCLUSIONS

Up to 70% of tree variation in the growth response at breast height of individual trees released, or partially released, from neighbour-tree interference was accounted for by a measure of growing space based on Thiesson polygons. This measure explained slightly more variation than the other competition indices referred to in section 2. A small increase in the variation explained was found using the height of the subject tree relative to the height of the surrounding stand plus the change of growing space on thinning as independent variables.

Diameter growth response was not significantly related to tree size at any of the three stem levels at which diameter growth was monitored when growing space was one of the independent variables.

The influence of neighbour-tree competition on diameter growth was strongest at breast height and less significant at the highest point of measurement within the crown.

Foliage weight distribution on one tree from each treatment showed an increase in the proportion of first-year foliage in the parts of the crown exposed to light. This effect reached down to the lowest whorls of living branches on the trees released most strongly. Foliage weight in the part of the crown exposed to direct sunlight for part of the day (though this was arbitrarily defined in section 5.4.2) was the predictive variable that best explained diameter growth at breast height.

A close relation was found between branch and foliage weight and the sectional area of the branch base was used to predict foliage and total crown weight from size and number of branches.

A measure of tree efficiency based on the ratio of basal area increment to foliage weight times growing space suggested (Table 13) that trees growing under the influence of strong lateral competition (GS = 4-8) were more efficient in the use of ground area as indicated by basal area production than trees with a larger growing space at this age. No change in the measure of efficiency used here occurred with GS of 10 or more. The largest dominants growing over 3 cm in diameter in the three growing seasons are shown to have been less efficient in their use of space and crown weight than smaller trees that grow only 1.5 cm in the same period.

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Appendix 1. The weighting method used in the calculation of growing space

The coordinates of the vertices of a polygon enclosing the growing space of a tree are determined by

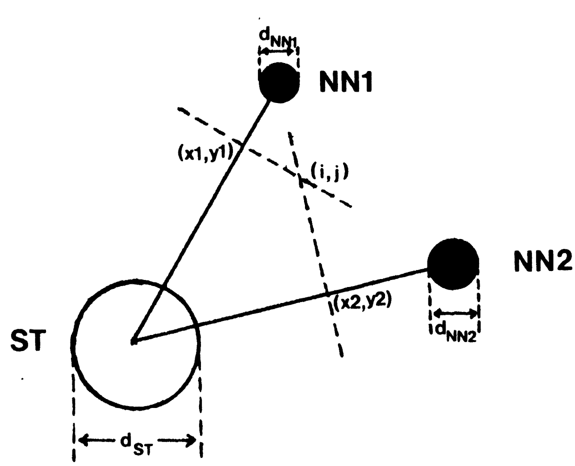
(a) points lying on the lines drawn from the subject tree, ST, to successive neighbours, NN, whose position (x1, y1) (x2, y2) .... are determined by the relative sizes of ST and NN1, NN2 ...., using a weighting factor

$$w = \frac{d^a_{ST}}{d^a_{ST} + d^a_{NN}}$$

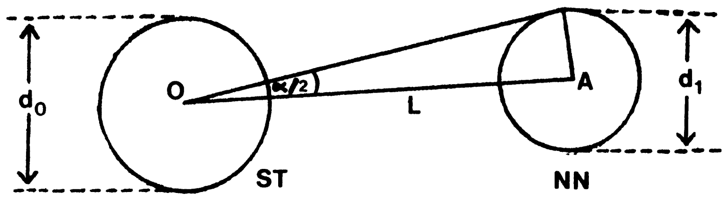
where d_{ST} is dbh of the subject tree
d_{NN} is dbh of a near neighbour

and a is a weighting coefficient that may be varied arbitrarily ($1 \leqslant a \leqslant 3$) depending on whether the weighting is to be in proportion to d, d^3 or some intermediate value. If a = 2 weighting is proportional to basal area; if a = 2.5 weighting may be considered to be roughly proportional to tree bole volume, and

(b) the points of intersection (i,j) of lines drawn at right angles from (x1, y1), (x2, y2) ....



Appendix 2. Calculation of net basal area stress



Distance from subject tree (ST) to the nearest neighbour (NN),

$$L = \frac{d_1}{2 \sin (\alpha/2)} \quad \text{.... (1)}$$

The basal area factor, K, that relates the actual basal area of NN to the basal area per ha at the sample point O depends on the angle α that NN subtends from point O:

$$\alpha = 2 \arcsin \sqrt{K.10^{-4}}$$

$$\text{or } K = 10^4 \sin^2 (\alpha/2) \quad \text{.... (2)}$$

Angle α is dependent on the ratio of tree diameter (d_1) and L and, in practice, is observed using a gauge placed at a fixed distance (x) from O such that the width of the gauge, y

$$\simeq \frac{x.d_1}{L}$$

From (1) and (2) above:

$$K = \frac{10^4 . d_1^2}{4.L^2}$$

If K_{10} is the basal area factor describing the basal area density represented by NN at O and K_{01} is the density represented by ST at A, then the net basal area stress is

$$K_{10} - K_{01} = \frac{d_1^2 - d_0^2}{4\ L^2}$$

where d is in centimetres
and L is in metres

Net basal area stress for n neighbours is then

$$\text{Net } G = \sum_i^n (K_{10} - K_{0i})$$

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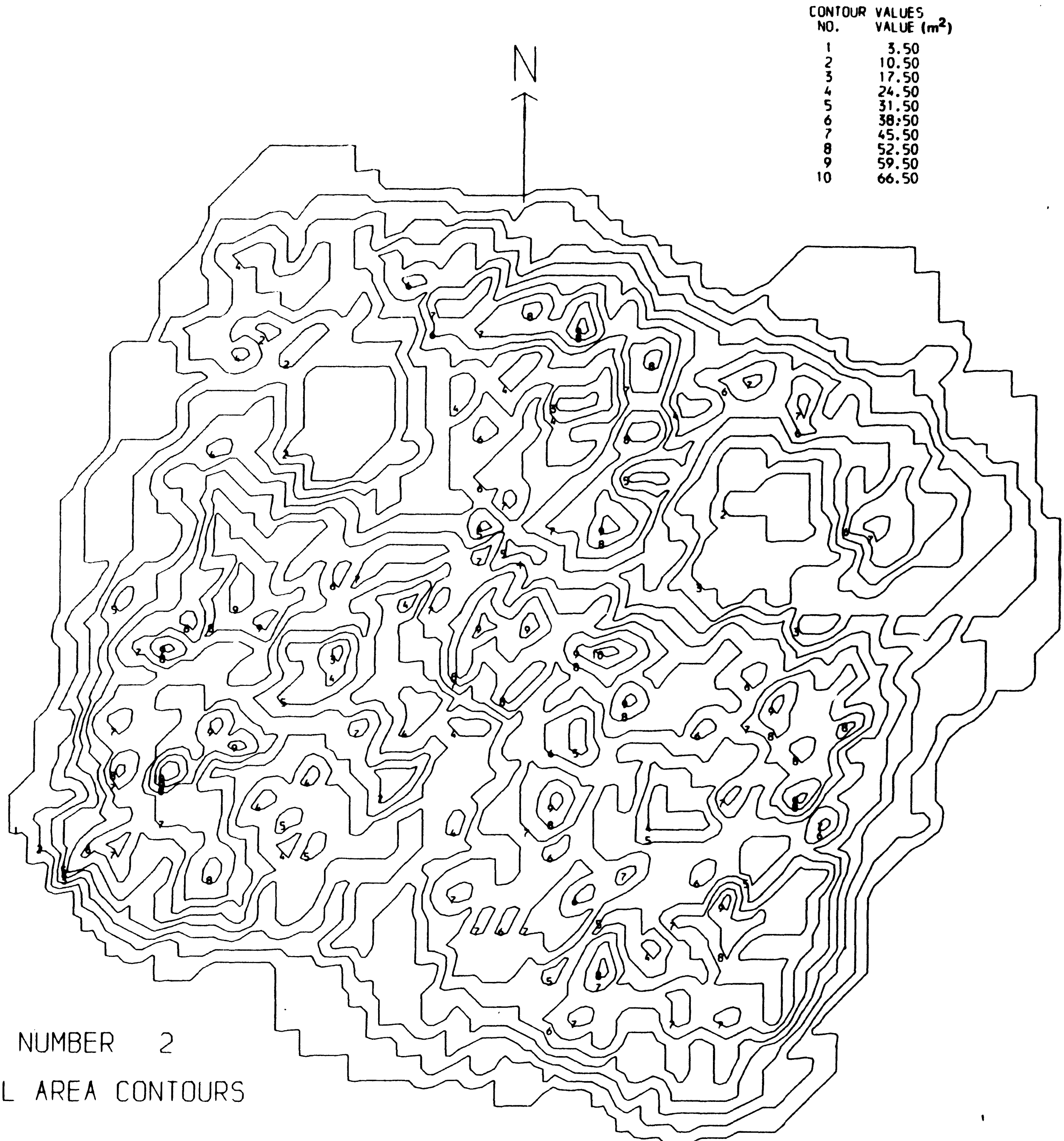


FIGURE 1

CONTOURS OF POINT DENSITY

BLOCK 2 : 1978

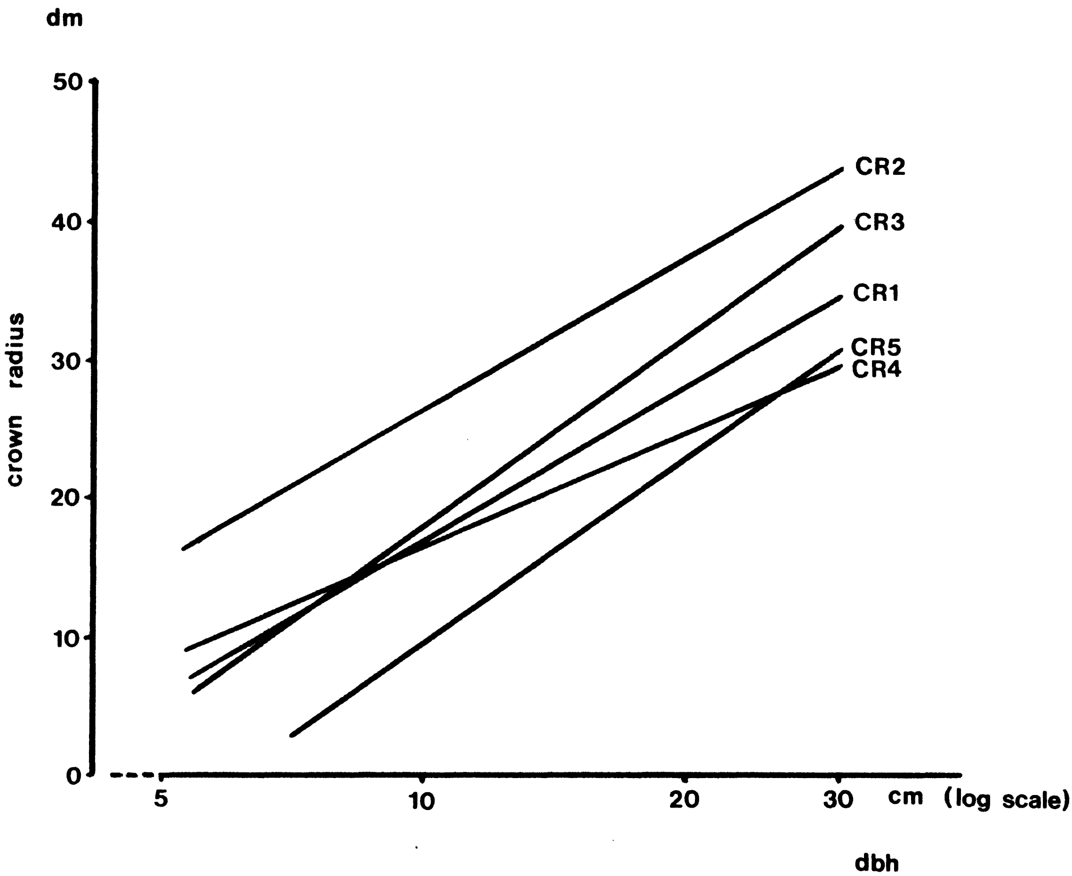


FIGURE 2

CROWN RADIUS REGRESSIONS

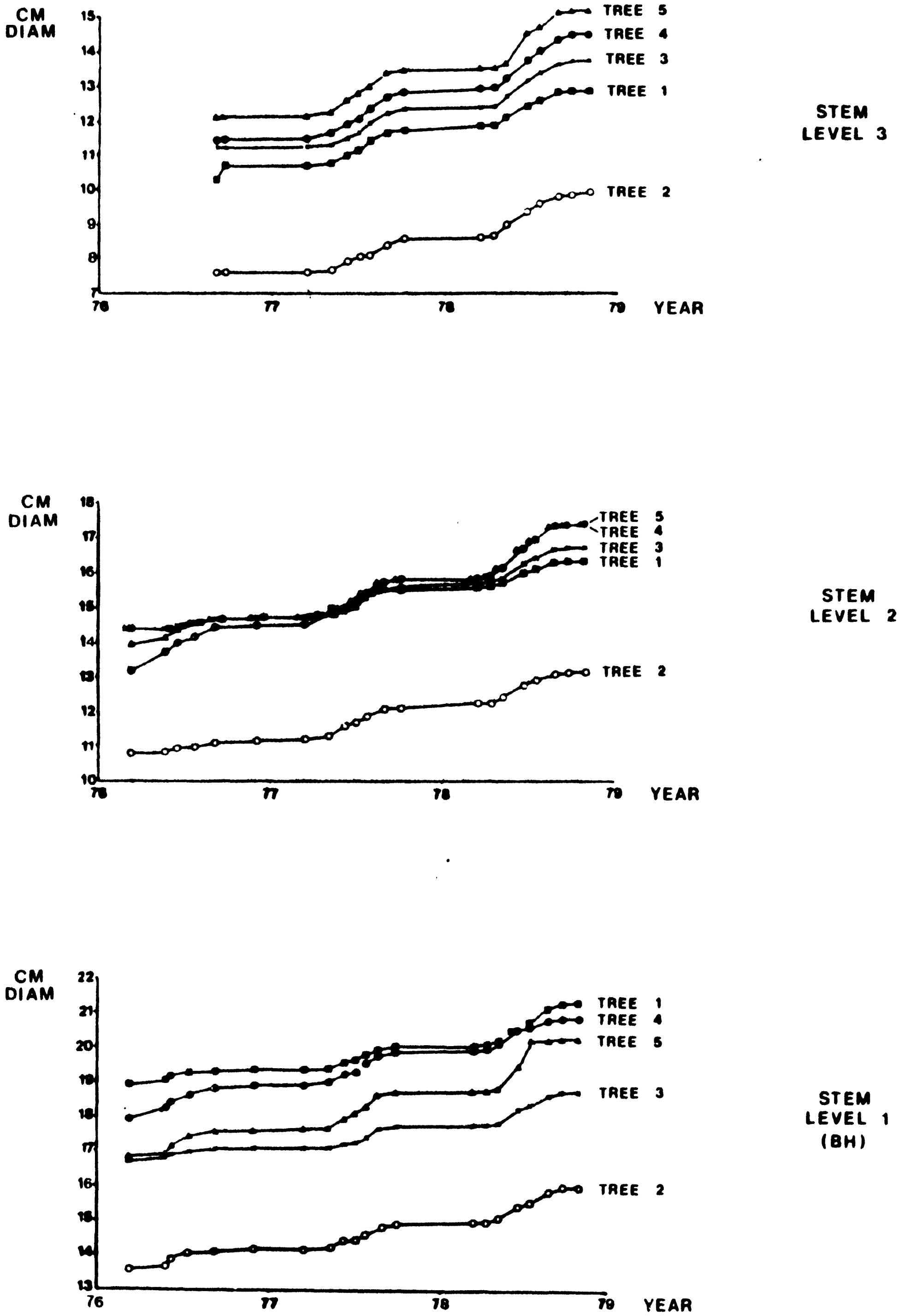


FIGURE 3

DIAMETER GROWTH AT THREE STEM LEVELS, BLOCK 1

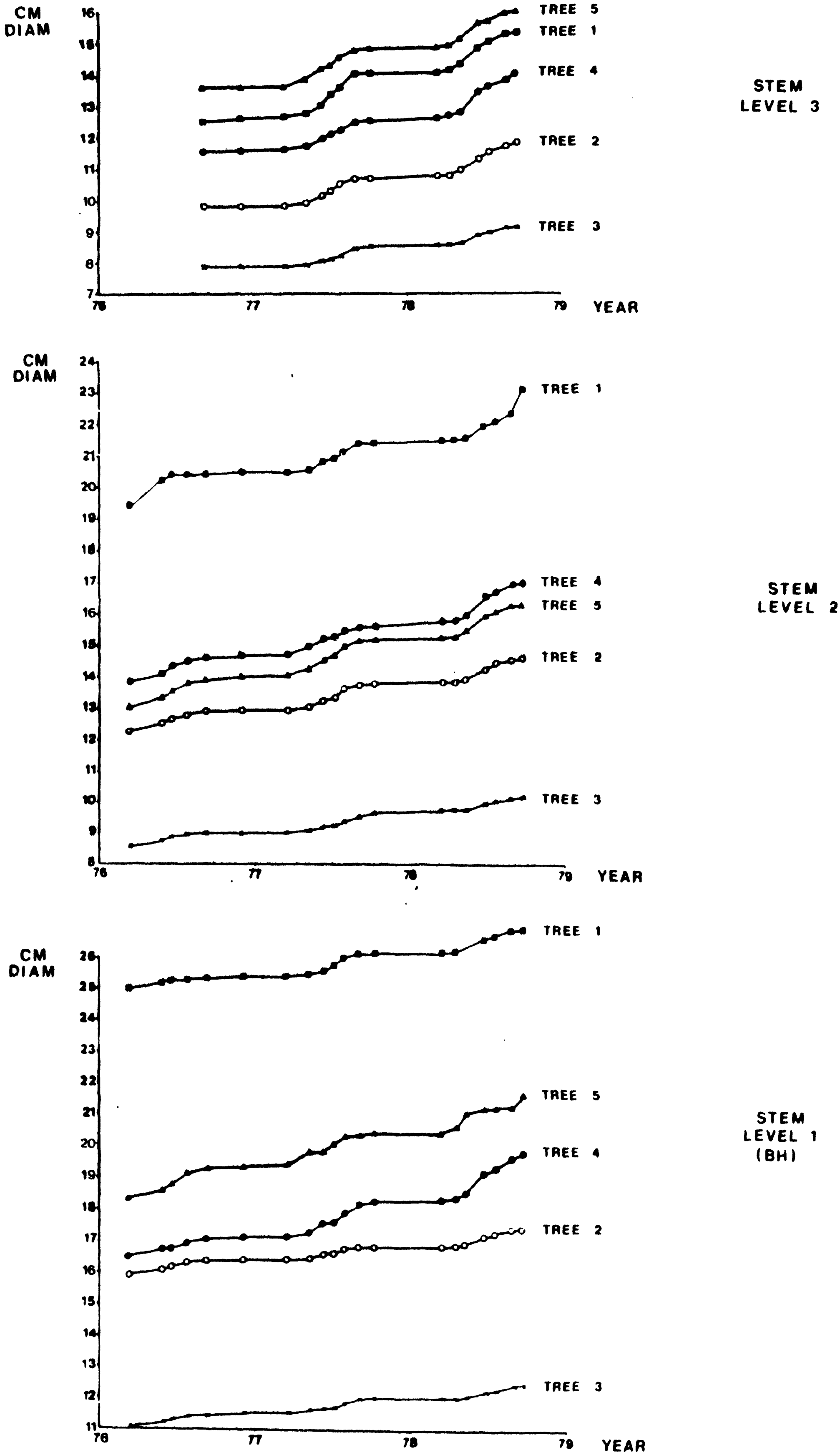


FIGURE 4

DIAMETER GROWTH AT THREE STEM LEVELS, BLOCK 2

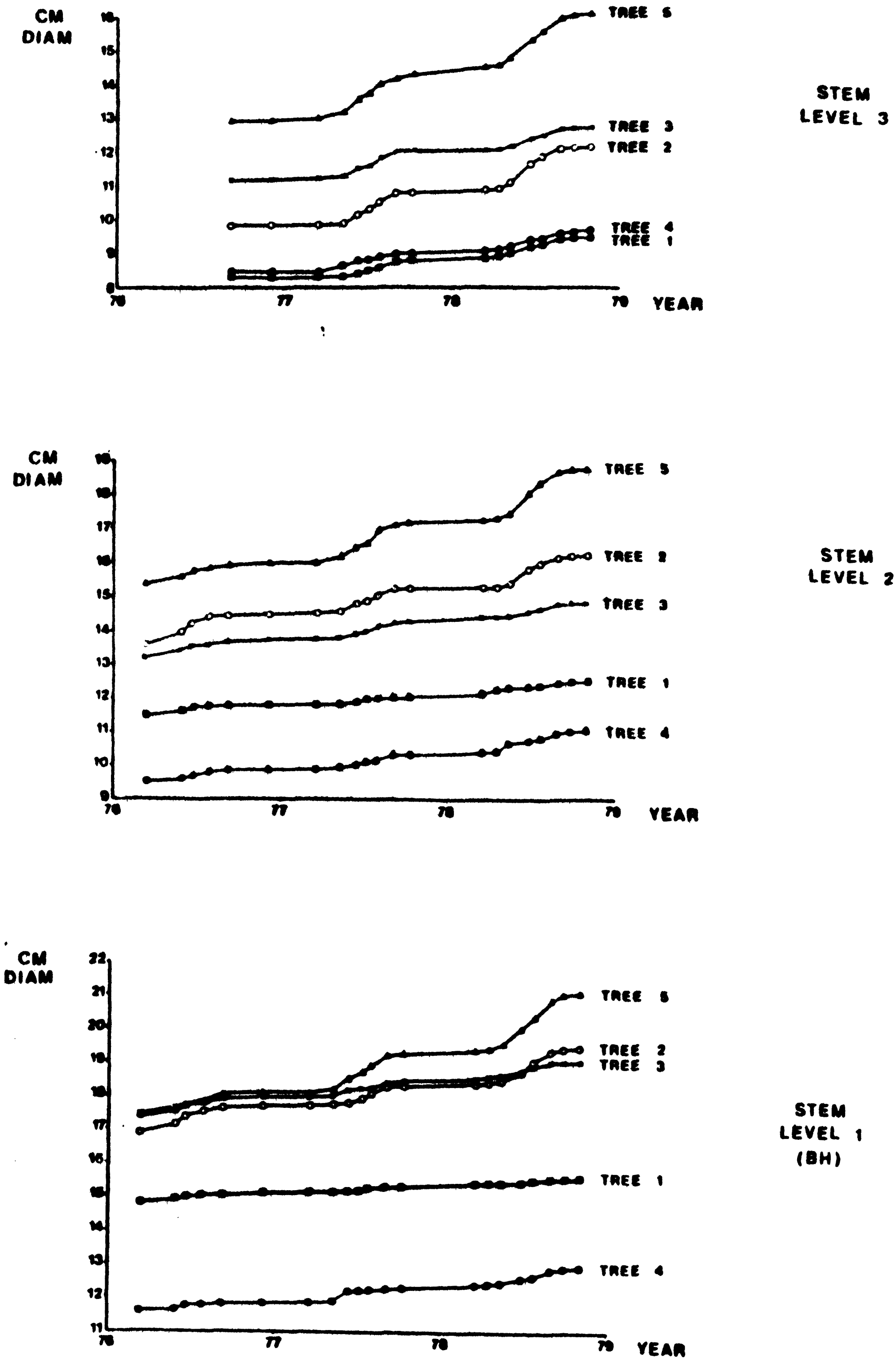


FIGURE 5

DIAMETER GROWTH AT THREE STEM LEVELS, BLOCK 3

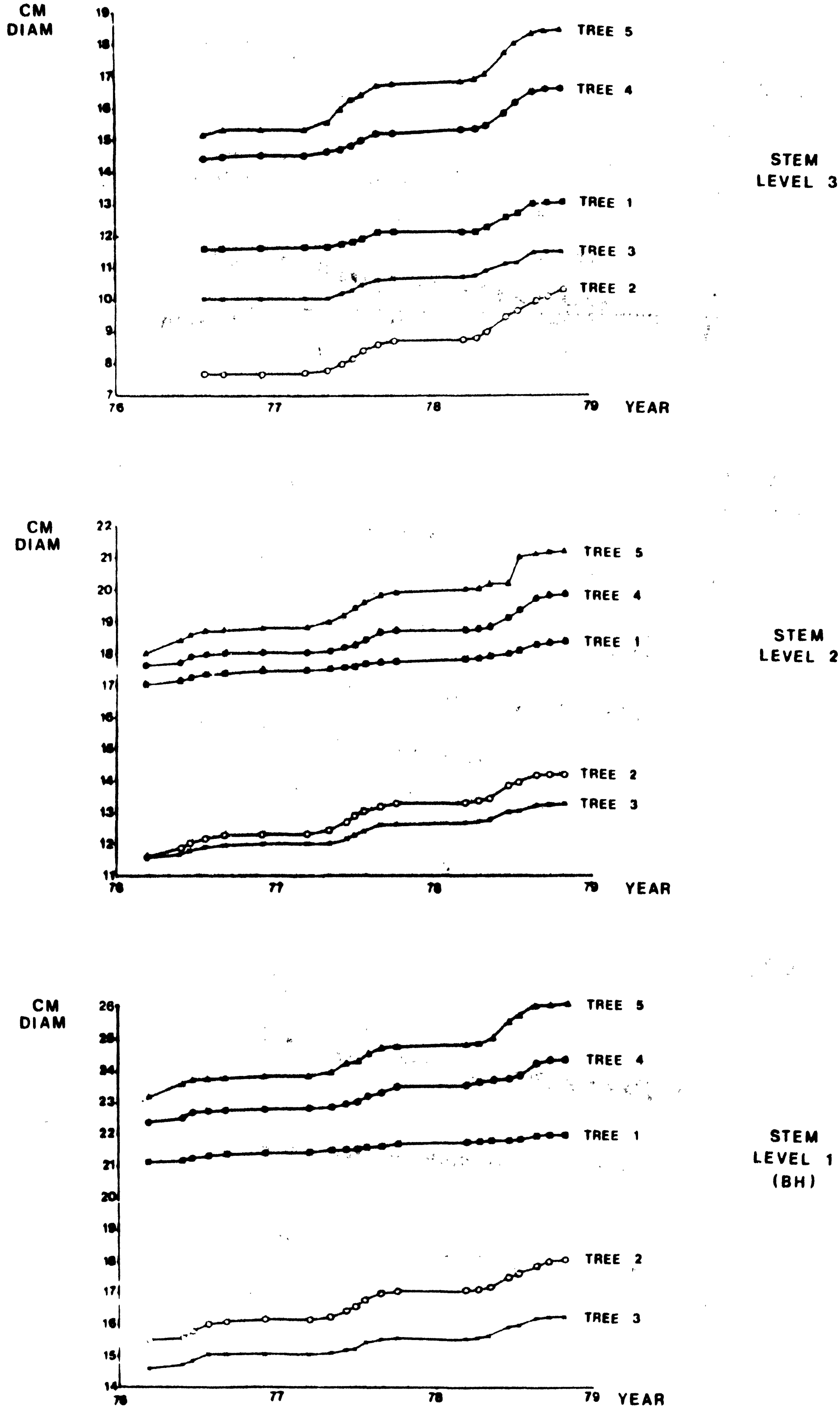


FIGURE 6

DIAMETER GROWTH AT THREE STEM LEVELS, BLOCK 4

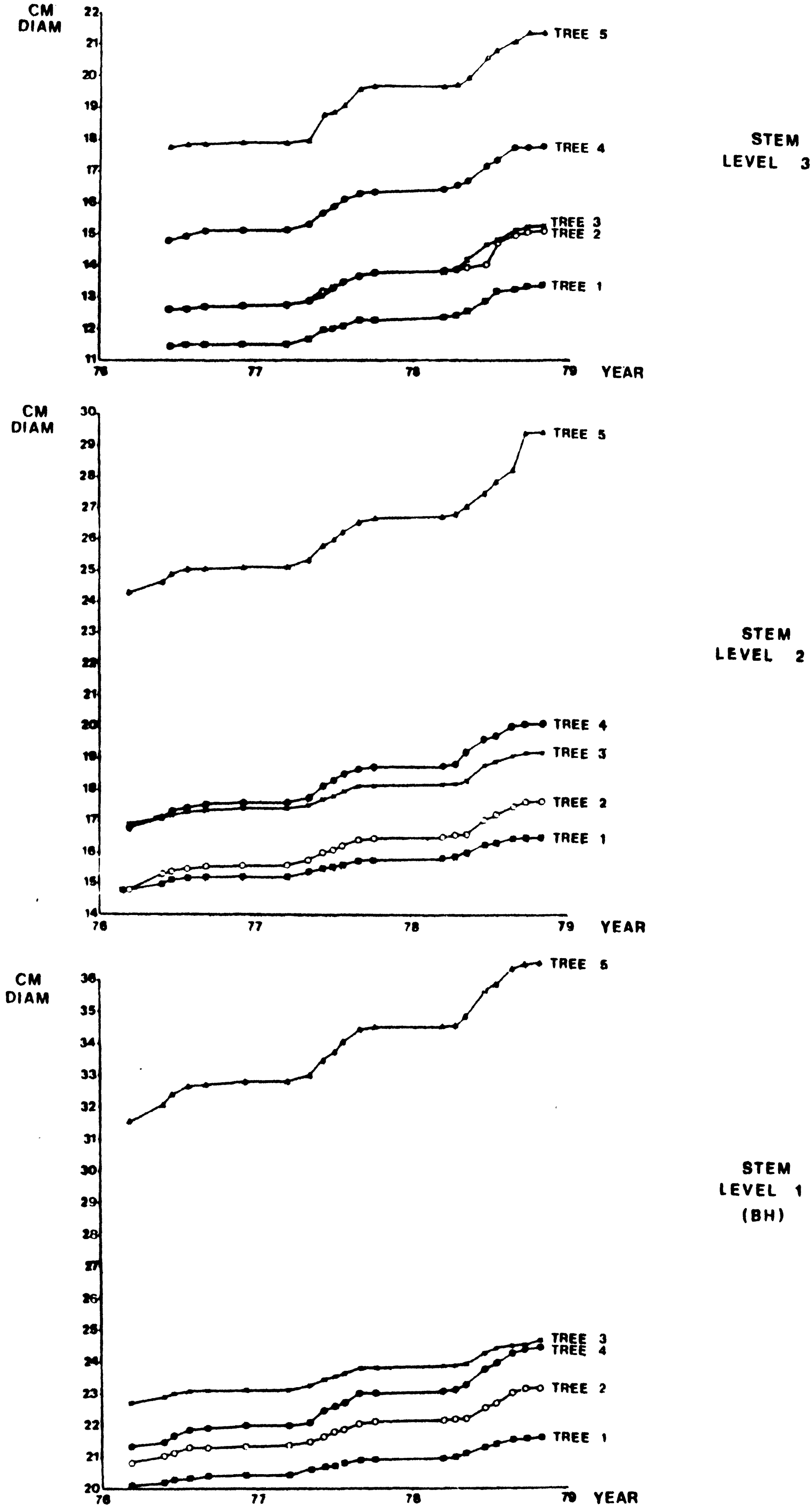


FIGURE 7

DIAMETER GROWTH AT THREE STEM LEVELS, BLOCK 5

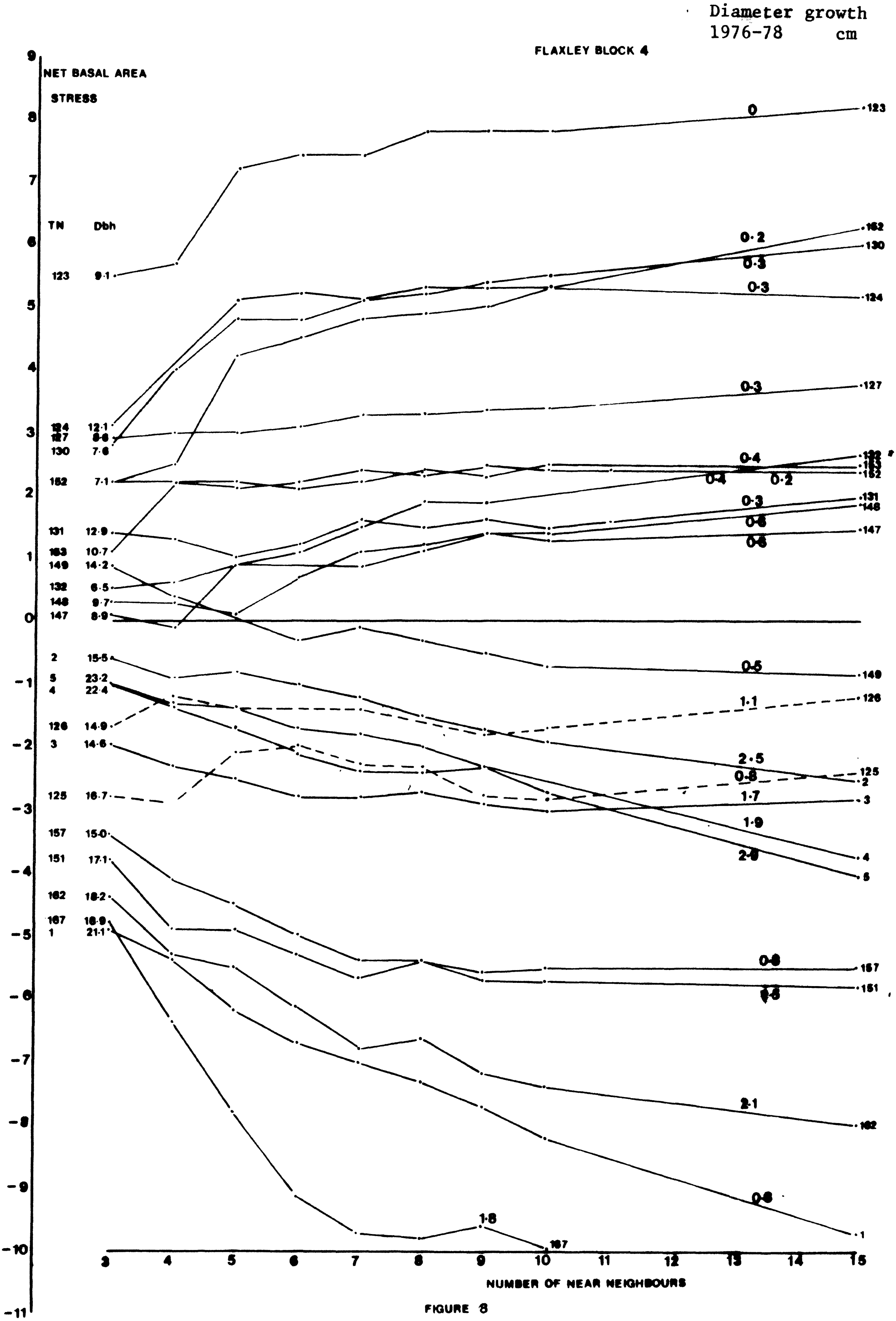


FIGURE 8

NET BASAL AREA STRESS FOR SELECTED TREES IN BLOCK 4

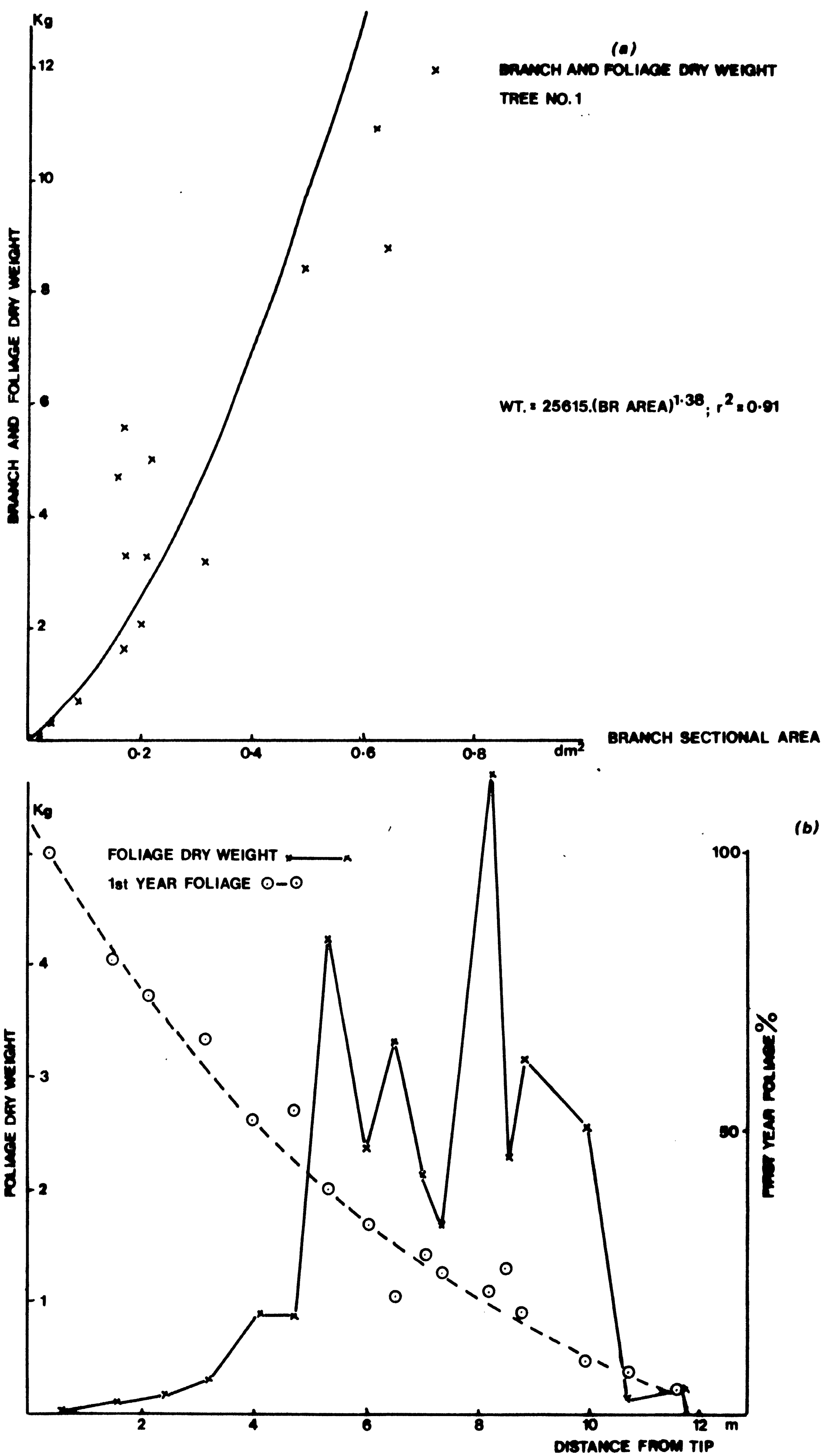


FIGURE 9

BRANCH AND FOLIAGE WEIGHTS : TREE 1 OF BLOCK 2

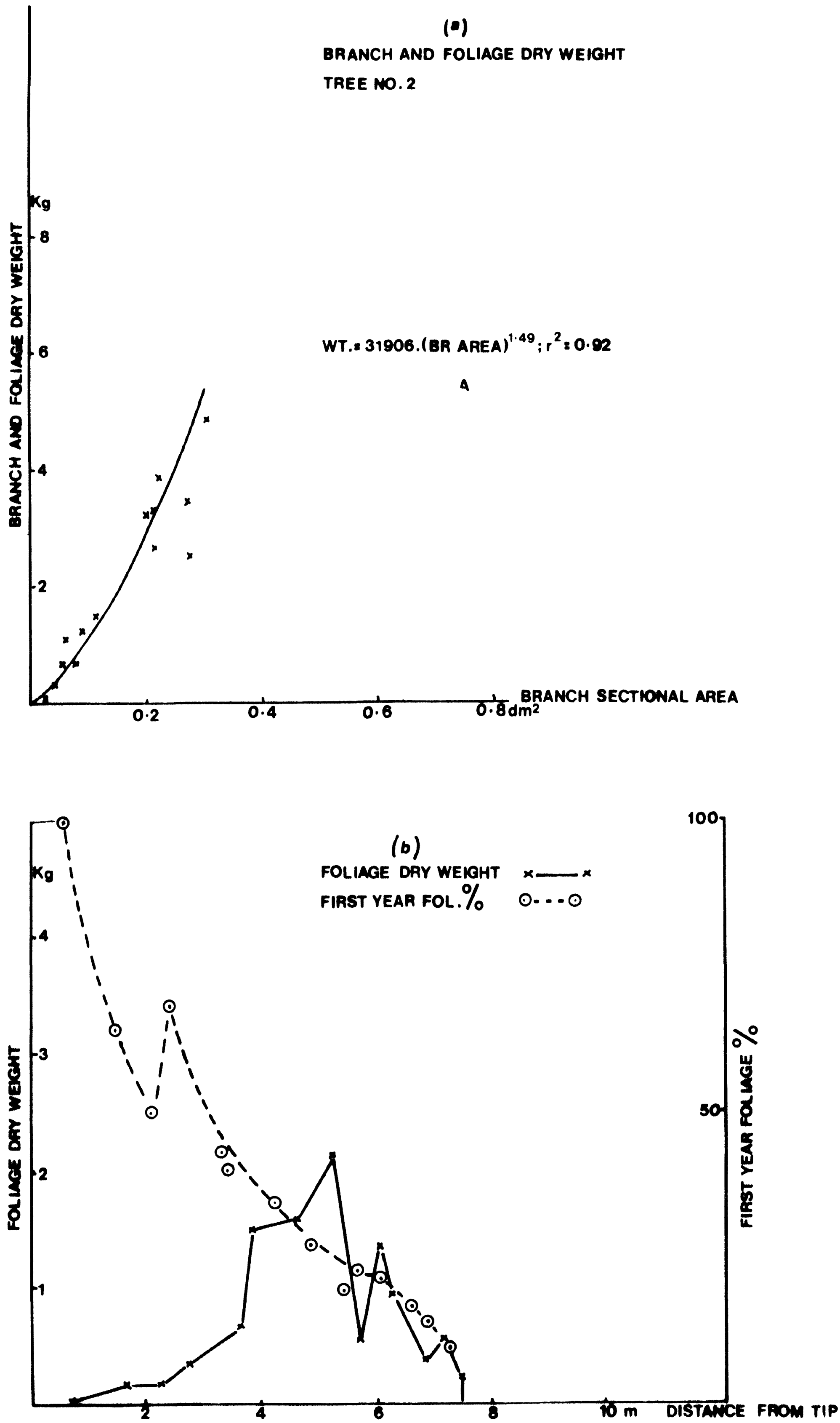


FIGURE 10

BRANCH AND FOLIAGE WEIGHTS : TREE 2 OF BLOCK 2

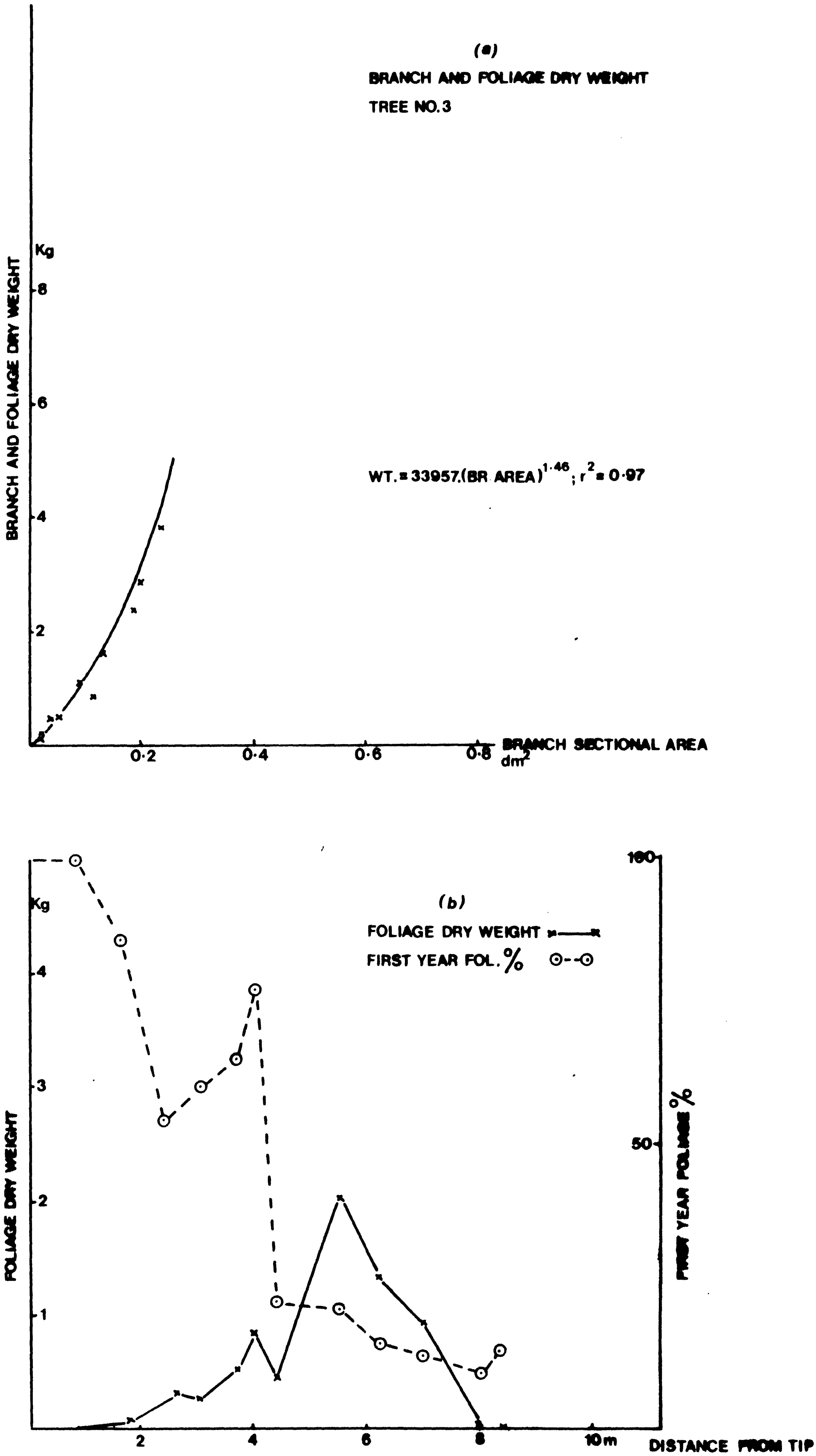


FIGURE 11

BRANCH AND FOLIAGE WEIGHTS : TREE 3 OF BLOCK 2

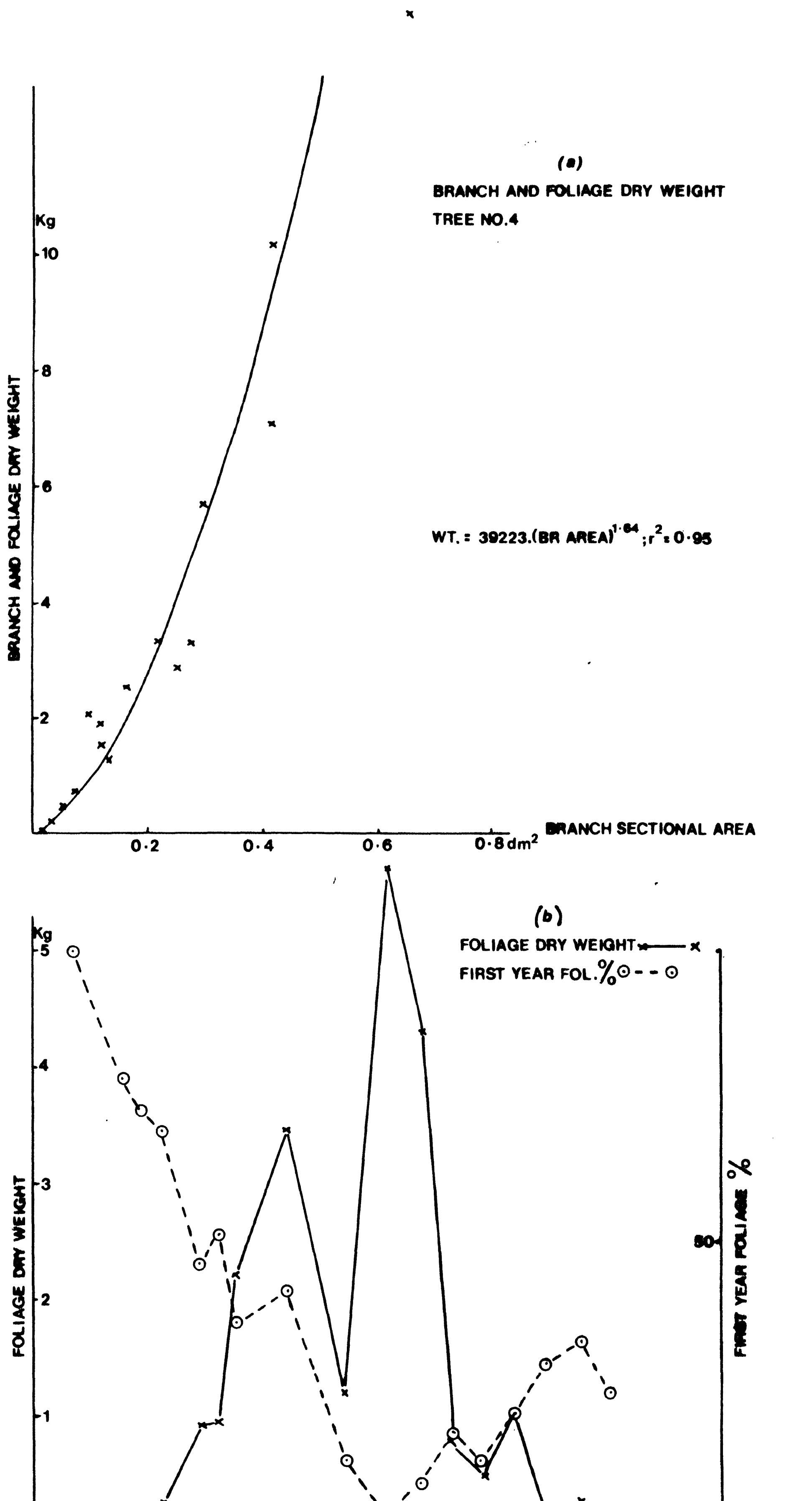
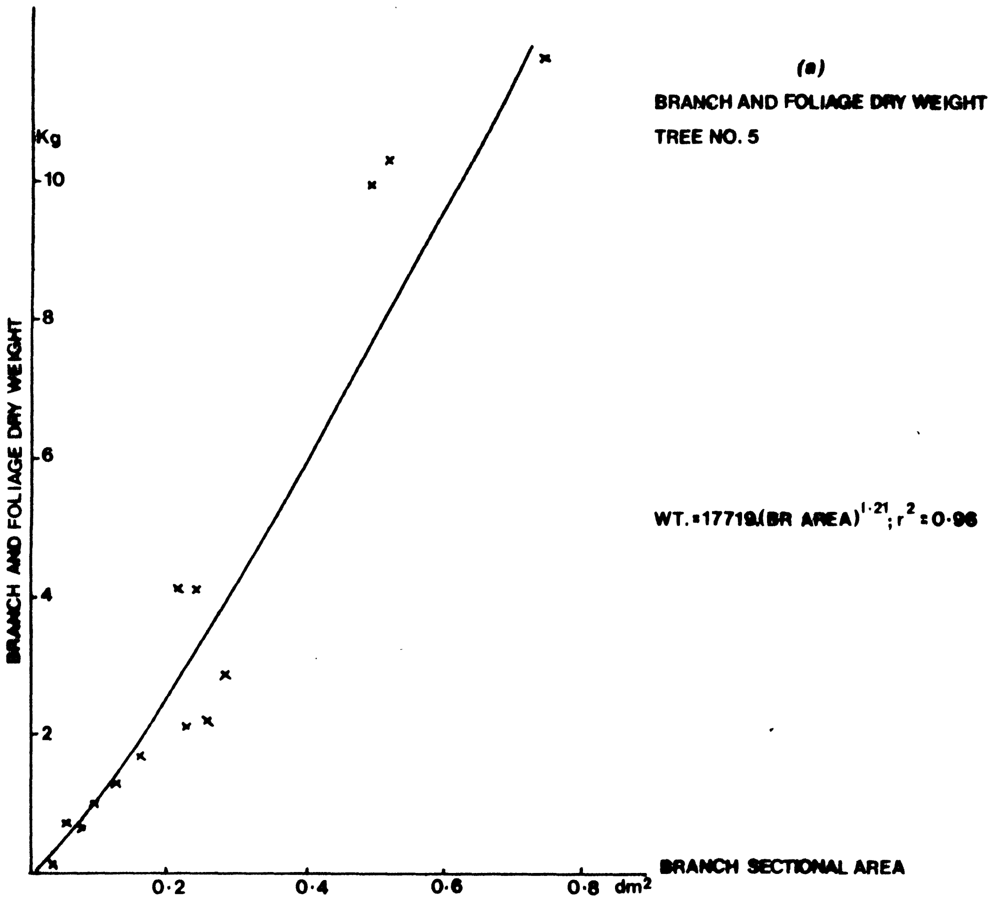


FIGURE 12

BRANCH AND FOLIAGE WEIGHTS : TREE 4 OF BLOCK 2



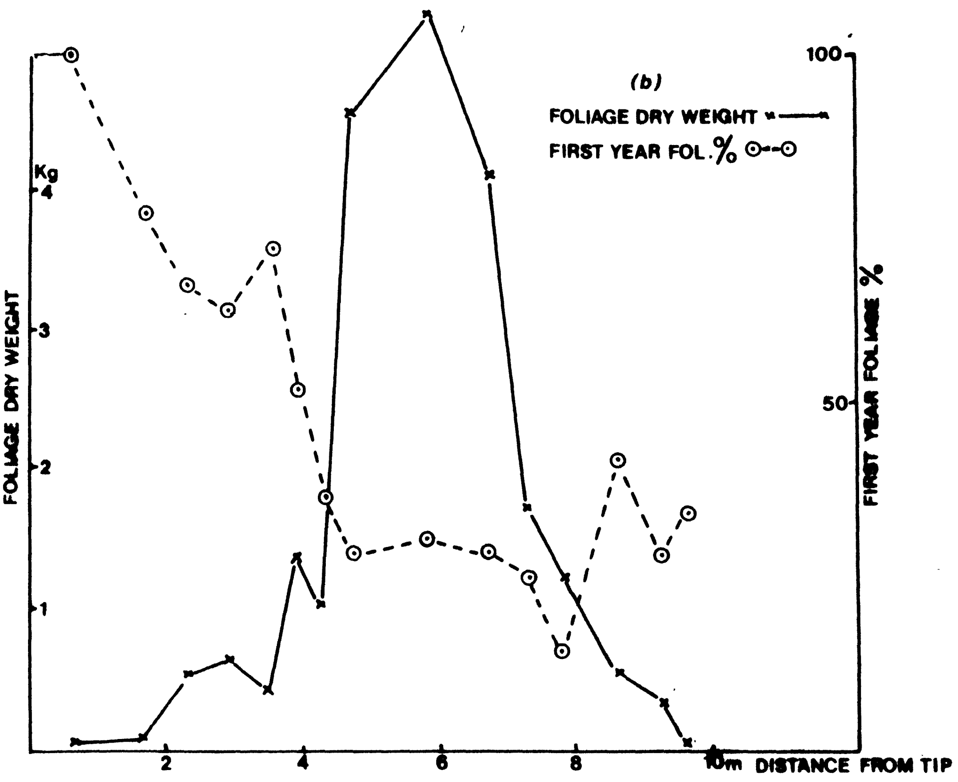


FIGURE 13

BRANCH AND FOLIAGE WEIGHTS : TREE 5 OF BLOCK 2

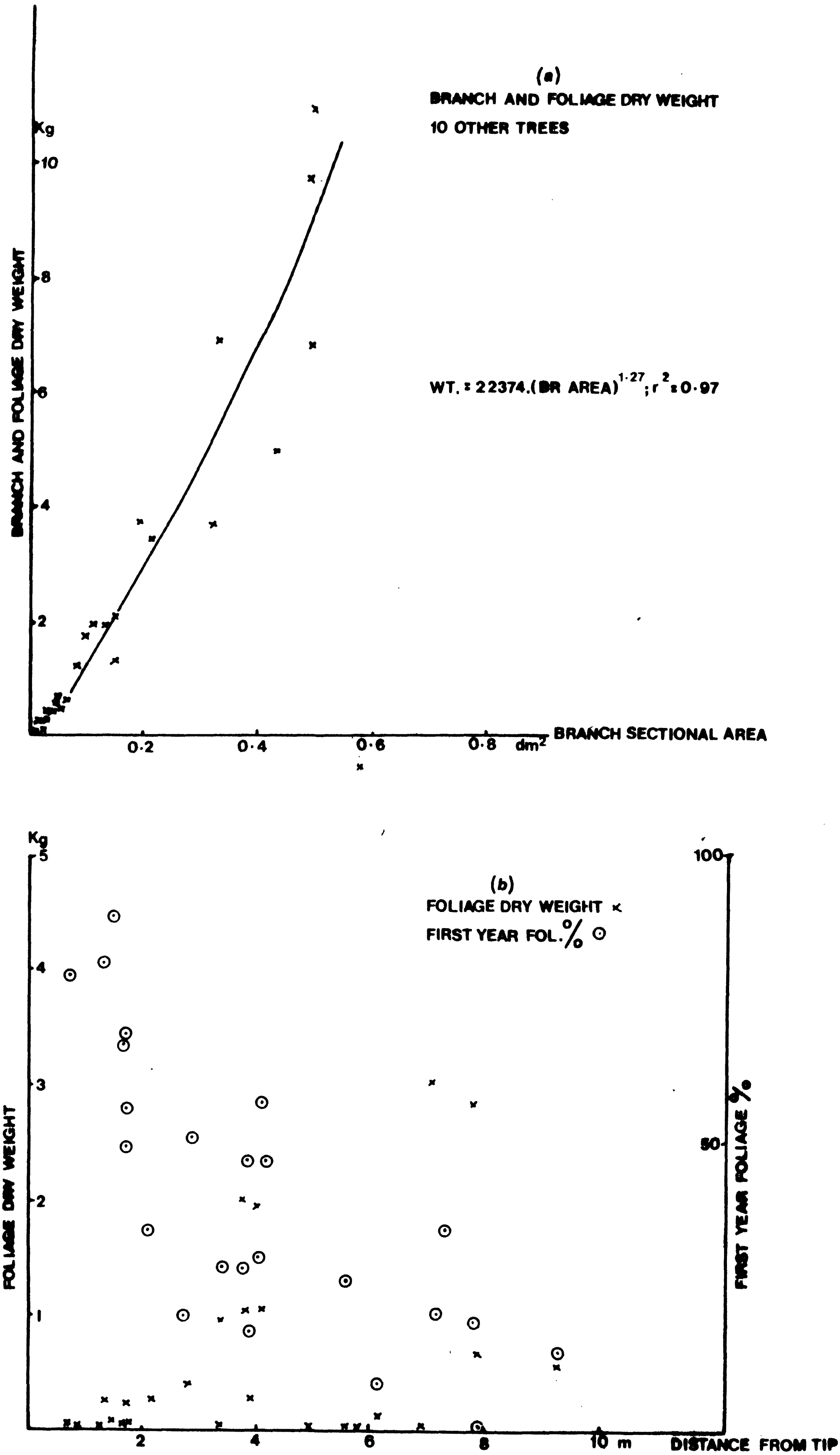


FIGURE 14

BRANCH AND FOLIAGE WEIGHTS : 10 OTHER TREES IN BLOCK 2