AN ABSTRACT OF THE THESIS OF

Fiona C. Hamilton   for the degree of   Master of Science   in   Forest Management   presented on   April 9, 1984.

Title: Contagious Distributions in Even Aged Forest Stands:

Dynamics of Spatial Pattern and Stand Structure

Abstract approved:

David W. Hann

Six stands of Eucalyptus regnans and E. delegatensis with significantly contagious or clumped spatial patterns, were observed between either ages 4 and 12 or ages 30 and 41 years. The effects of aggregation on the development of these stands are described. The prediction of growth and mortality responses of individual trees is demonstrated in these stands where average stand density measures are not good indicators of the competitive conditions which individual trees face.

Results show that clumping intensifies competition, producing a high proportion of suppressed stems and substantial mortality even in regions of low average density. Average tree size is reduced. The bimodal diameter distribution illustrates the distinct separation of the suppressed class from the dominants and codominants. Individual tree growth differs significantly between crown classes. Basal area

growth of the suppressed stems which survive averages near zero. In all crown classes variables which reflect competitive conditions such as distance to the nearest neighbouring tree and the basal area in larger trees are more successful predictors of individual tree growth than average stand density variables. Mortality is largely confined to the suppressed class and within any stand can be predicted by tree size and local density variables. The concentration of mortality in the densest parts of the stands is changing the spatial pattern, so that the degree of contagion is decreasing through time. A high degree of contagion results in increased variability of conditions within a stand and high local densities around some trees. The associated intensification in competition in these areas of the stand produces responses which are similar to those we would expect under an increase in general density.

Contagious Distributions in Even Aged Forest Stands:
Dynamics of Spatial Pattern and Stand Structure

by

Fiona C. Hamilton

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed April 9, 1984

Commencement June 1984

APPROVED:

Signature redacted for privacy.

Professor of Forest Management in charge of Major

Signature redacted for privacy.

Head of Department of Forest Management

Signature redacted for privacy.

Dean of Graduate School

Date thesis is presented _____ April 9, 1984

Typed by _____ Fiona C. Hamilton

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF TABLES

CONTAGIOUS DISTRIBUTIONS IN EVEN AGED FOREST STANDS :

DYNAMICS OF SPATIAL PATTERN AND STAND STRUCTURE

INTRODUCTION

In recent years spatial pattern of plant communities has
received considerable attention in ecology (Greig-Smith 1979),
forestry (Askew 1983, Daniels 1978) and biometrics (Cox and Lewis
1976). Although some degree of aggregation apparently occurs in most
plant communities (Greig-Smith 1979), observations of the development
of real populations with markedly non-random patterns have been
limited, perhaps due to the inherent complexity of their structure.
Kent and Dress (1979) stressed the importance of the dynamics of
spatial pattern to forest production and provided a theoretical model
describing the development of an initially random pattern over time.
Pielou (1960) modelled the development of a range of spatial patterns
which could occur in uneven-aged stands under a variety of conditions
of competition. Stiell (1982) discussed the effects of aggregation
on tree growth but his studies were confined to planted stands with
very regular patterns of aggregation.

Some more recent growth models simulate the growth of plants in
stands with a variety of spatial patterns (e.g. Daniels et al. 1979,
Wyszomirski 1983, Mead 1971). The patterns have been generated from
theoretical distributions or observed in planted populations and
subsequent development has been determined by the assumptions of the
models. Only limited observations have been made of the interactions

which occur during stand development. For example, Daniels et al. (1979) generated a variety of spatial patterns by assuming a Pearson type XI distribution of the squared distances from random points to the nearest plant and then used plantation data to predict tree growth and stand development in these clumped stands.

In the stands in this study there is a continuous variation in the spacing between neighbouring trees. The nonrandomness may have developed at stand initiation as a result of either an uneven distribution of propagules or variation in the site factors which limit establishment. In this environment individual trees will experience widely different degrees of competition throughout their lives as a result of the local density around them. Variations in individual tree growth and vigour will be marked and hence variations in the probability of mortality for individual trees will result. As mortality occurs spatial pattern will change and hence the competition experienced by individual trees will also change.

This dynamic process is described in detail and the necessity of accounting for this variation in local competition (by use of crown class, or other indicators of competitive position or measures of intertree distances) in both stand description and the prediction of individual tree and whole stand growth and development is demonstrated.

STUDY AREA AND DATA

The stands in this study are all in Victoria, Australia, within the region of "ash" type eucalypts, dominated by either Eucalyptus regnans or E. delegatensis . All the stands are even-aged, arising from either natural seedfall following wildfire or aerial seeding after clearfalling and burning. Marked heterogeneity in the spatial distribution of the stems, which prevents the consideration of the stands as fully stocked, occurs over about 13% of this forest type in Victoria (W.D. Incoll, pers. comm.). The stands were selected for the apparent homogeneity of site conditions within them so that the combination of the distribution of seed and the occurrence of suitable seedbed are the probable causes of the spatial heterogeneity. These species require mineral soil and the absence of competing vegetation for successful regeneration (Cremer et al. 1978).

The stands are all unthinned and either sapling stage (4 - 12 years) or pole or spar stage (30 - 41 years) (Ashton 1975). A summary of the stands' characteristics is given in Table 1.

Analysis of the spatial pattern and competitive conditions faced by each tree is based on records of spatial coordinates for each tree, measured to the nearest .0786 m in the younger stands and the nearest .3048 m in the older stands. Data on individual tree characteristics were collected at 2 to 3 year intervals over a period of 8 years in the younger stands and 11 years in the older stands.

TABLE 1: Stand characteristics at the first measurement in each stand.

STAND	Initial age	Stand area (ha)	Dominant[1] height (m)	Number of trees (ha^{-1})	Basal area (m^2ha^{-1})	Diameter at breast height min-mean-max (cm)	Crown[2] ratio mean	Principal species
DOWEY'S SPUR	4	.08	12.9	3842	15.2	1.1 6.4 14.4	.386	95% E. delegatensis
STARVATION CREEK	4	.08	11.3	6906	11.8	0.3 3.8 13.4	.614	71% E. regnans
BUNYIP	4	.08	9.5	4472	6.0	0.3 3.4 12.4	.686	87% E. regnans
ACHERON	30	2.02	45.9	380	39.9	10.3 34.0 72.6	.534	100% E. regnans
HARDY'S CREEK	30	2.02	35.0	324	30.2	8.3 32.4 73.5	.500	100% E. regnans
MT. MONDA	30	2.02	30.8	220	25.4	5.8 35.1 78.7	.707	100% E. regnans

(1) Dominant height is the mean height of the 50 trees of largest diameter at breast height per ha.

(2) Crown ratio for young plots is based on a sample of trees of all sizes, biased toward larger trees. For the old plots it is based on samples of dominant trees only.

At the first measurement in the older stands the crown class of each tree was recorded. The diameters at breast height (DBH) of all the trees were recorded (to the nearest 0.1 cm) at each measurement. Heights of a sample of (predominantly larger) trees were recorded less frequently. The species of each tree was also recorded.

METHODS

Spatial pattern

A great variety of statistics are available to classify and quantify spatial patterns, (for reviews see Pielou (1969), Payandeh (1970)). A map of one of these stands demonstrates that a description of the pattern is not trivial (Fig 1).

Statistics based on distance from a tree to its nearest neighbour (eg. Clark and Evans 1954), measure the intensity of the smallest scale of pattern present (Pielou 1959) and hence detect the degree of aggregation on the scale most critical to the growth of individual trees. We use Pielou's statistic (Pielou 1960):

$$\alpha_i = \Pi \rho \, \bar{\omega}_i \qquad\qquad (1)$$

where ρ is the density in number of trees per unit area

$\bar{\omega}_i$ is the mean squared distance to nearest neighbour

The statistic has a distribution related to the χ^2 distribution (Pielou 1969) and since the density of the plots is known a test of its significance is available. It has an expected value of $(n-1)/n$ (where n is the number of sample trees) in a random population, and smaller values in aggregated populations. In each stand the statistic was determined using measurements for all trees excluding those in a buffer zone wide enough to contain any trees which were
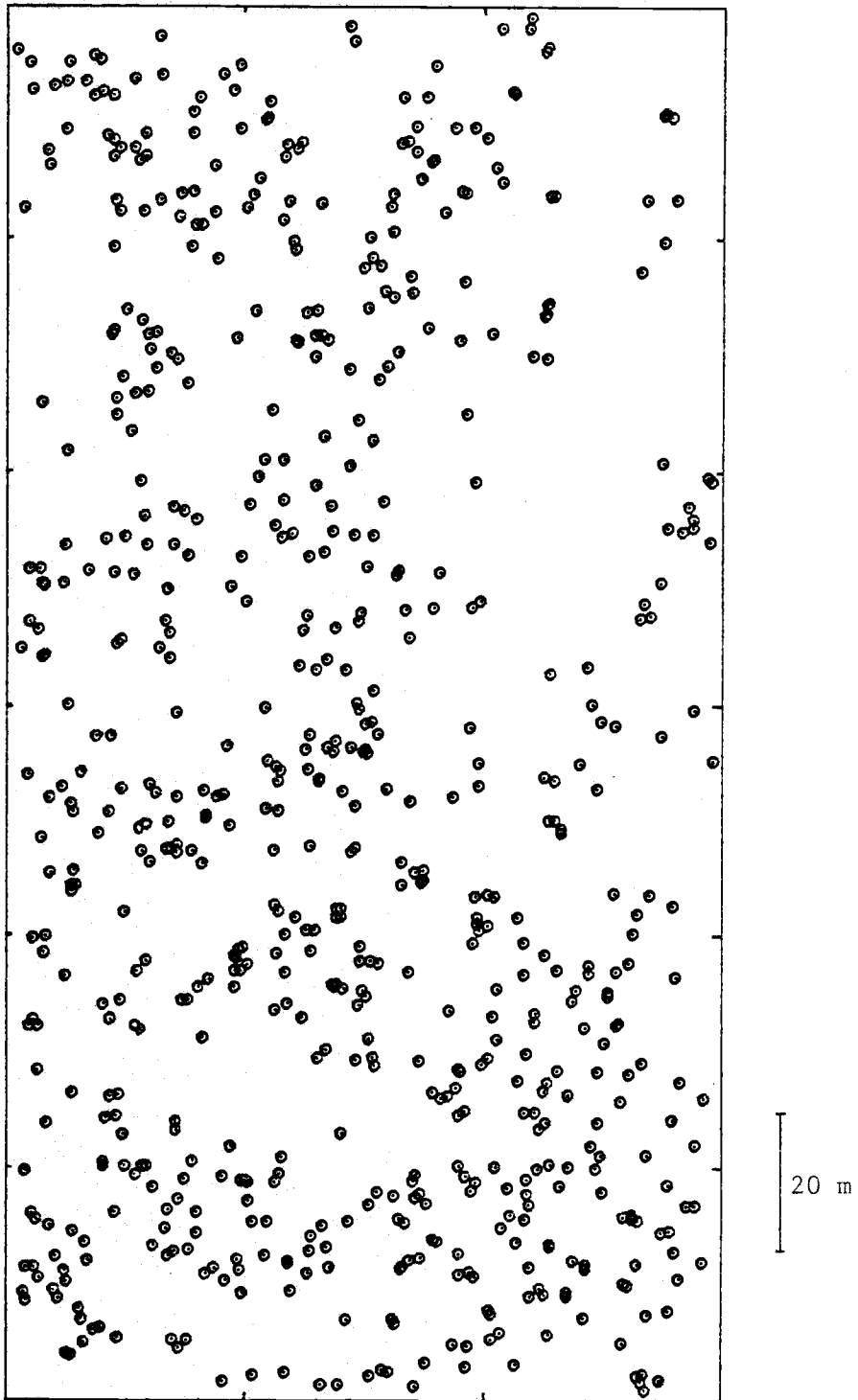
Fig. 1: Map of Hardy's Creek at age 30 showing the location
of each tree (●). Tick marks on the stand border
indicate the boundaries of eighteen .11 ha plots used
to describe the variation in characteristics
throughout the stand.

closer to the boundary than their nearest neighbour within the plot.

Pielou's (1959) and Mountford's (1961) point to plant distance index is another measure of aggregation:

$$\alpha_{\scriptscriptstyle P} = \Pi \, \rho \, \bar{\omega}_{\scriptscriptstyle P} \tag{2}$$

where $\bar{\omega}_{\scriptscriptstyle P}$ is the mean squared point to plant distance

The statistic is "affected by most, if not all the levels of non-randomness in the population", (Pielou 1959). It was computed for each stand based on a maximum of 120 random points and excluding the same border defined for the previous test. It has an expected value of $(n-1)/n$ in random populations but takes higher values in aggregated populations.

Where spatial pattern is random the number of individuals found in quadrats of fixed area follows a Poisson distribution. The parameter λ, corresponds to the population mean and variance, measured in terms of the plot density (Pielou 1969). In a uniform population the variation in density between quadrats is reduced and so is less than the mean while in an aggregated population the ratio of the variance to the mean density is significantly greater than one. The statistic, the variance to mean ratio (Var/Mean) is dependent on the size of the quadrats used. Eighteen plots of 0.11 ha each were used to compute this statistic in the older stands and eight 0.01 ha plots were used in the younger stands. Plots of similar size are routinely used for stand description in stands of

each age and will be used for illustrating the variability in characteristics within the stands. Pielou (1969) states that the Var/Mean statistic should not be used as a test statistic where we have no reason to assume a random pattern.

In a number of the plots in the older stands, measures of distance to nearest neighbour were available for all trees (none of the trees were affected by the boundary condition), and so it was possible to compute the α_i statistic on a plot basis. The plots were too small for reliable determination of the α_r statistic (Pielou 1959).

Stand Structure

The relationship between spatial pattern, the variability in local density and individual tree characteristics was analyzed by studying the variation between small plots in each stand. The same system of plots used to test the spatial pattern was used to study the stand characteristics.

The coefficient of variation (the ratio of the standard error to the mean value of a variable) was used to study the variability in a range of stand parameters. It allows the variability in parameters of different absolute magnitude to be compared. Variability within stands is an important consideration in sampling stand characteristics.

An analysis of the frequency distribution of plant size, and in

the older stands, of the numbers and proportion of trees in each dominance class was used to compare stand structure in different regions of the spatial pattern. The spatial distribution and characteristics of the dominant class alone were also investigated. A test of the Var/Mean ratio (Greig-Smith 1952) of the number of dominants per plot was used to test for randomness in their distribution.

Mortality

Where mortality is competition induced the proportion of trees dying on a plot increases with increasing density. We tested the dependence of the rate of mortality on stand density and then used logistic regression, (as used by Hamilton 1974) to identify the variables which are significant predictors of individual tree mortality. A stepwise approach, available in the BMDP statistical software system (BMDP 1983) was used for variable selection. The form of the model was:

$$P = (1 + \exp (\beta X))^{-1} + \varepsilon$$

(3)

where P is the probability of mortality for a tree

β is a matrix of regression coefficients

X is a matrix of significant explanatory variables

ε is the random error term

In each case, tree species and size (measured by diameter at breast height), plot density variables, site index, distance to the nearest neighbouring tree (a measure of local competition), and where available, crown class, were tested as potential predictors.

Individual Tree Growth

Regression models were developed to explore the relationship between tree growth and tree and stand characteristics in each stand. Models predicting the growth over the full measurement period, 8 years in the younger stands and 11 years in the older stands, were fitted to seven subsets of the data.

The two age classes of trees were treated as separate data sets. Among the older trees, graphical analysis suggested a difference in the response between crown classes, so models were fitted to each of the three crown classes separately as well as to all three combined. The value of using a different equation in each crown class was then tested.

Data on crown dimensions was only available for a subset of trees in both the young and old stands, so models were fitted separately to these subsets. Both the young and the old crown data sets were biased toward larger trees, i.e. the data from the older trees contained only the largest of the old dominants and the data from the young stands, though it covered the range of sizes in the younger trees, had a greater proportion of the larger trees. To test

the value of crown ratio as a predictor for these subsets it was, therefore, necessary to fit models to these trees both with and without crown ratio.

This approach allowed testing of all available variables and comparison of the equations for the different subsets of the data. The variables considered as potential predictors were: site index, total plot basal area and the density of trees on the plot, basal area in trees larger than the subject tree and basal area in trees smaller than or equal in size to the subject tree, diameter at breast height, crown ratio, species and distance to the nearest neighbouring tree.

Two model forms were considered; the nonlinear exponential form:

$$Y = \beta_0 + \beta_{0i} X_{1i}^{\beta_{1i}} X_{2i}^{\beta_{2i}} \cdots e^{\beta_{1j} X_{1j} + \beta_{2j} X_{2j} \cdots} + \varepsilon \tag{4}$$

with the errors weighted by $1/(\text{diameter at breast height})^4$, and :

$$Y = \beta_0 + \beta_{0i} X_{1i}^{\beta_{1i}} X_{2i}^{\beta_{2i}} \cdots e^{\beta_{1j} X_{1j} + \beta_{2j} X_{2j} \cdots + \varepsilon} \tag{5a}$$

which can be linearized by log transformation to give:

$$\ln (Y - \beta_0) = \ln \beta_{0i} + \beta_{1i} \ln X_{1i} + \beta_{2i} \ln X_{2i} \cdots + \beta_{1j} X_{1j} + \beta_{2j} X_{2j} \cdots + \varepsilon \tag{5b}$$

where Y is the periodic individual tree growth

β is a parameter estimate

X is an explanatory variable

To fit the linear model prior estimates of the parameter, β_0, were necessary, since they are not obtained from the least squares fit.

Furnival's index of fit (Furnival 1961) was used to compare the performance of regression models with different dependent variables.

RESULTS

Spatial Pattern

The smallest scale of spatial pattern (as measured by Pielou's nearest neighbour statistic) was contagious in all the stands at the first measurement (Table 2). The large values of Pielou's (1959) and Mountford's (1961) point to plant distance index of aggregation confirm that there is significant aggregation in all the stands (Table 2).

Using a 0.11 ha plot in the older stands and a 0.01 ha plot in the younger stands the high values of the Var/Mean ratio of the plot densities also show the distributions of trees in all the stands are apparently contagious (Table 2).

The extreme values for all three indices at Bunyip reflect the very high intensity of contagion there, where the majority of the trees were clustered in a few small groups of very high density. By comparison, in the other young stands the trees were more scattered and these very high densities did not occur even within clusters.

The difference in ranking of the three older stands for the nearest neighbour statistic as compared to the other two statistics results because each one measures a different aspect of the spatial pattern. For example while the clumps at Mt. Monda are well defined,

TABLE 2: Spatial pattern statistics computed in each stand at the first measurement, and tests of the significance of their departure from the random condition.

STAND	Distance to[3] nearest neighbour			Point to plant[4] distance			Variance to mean[5] ratio
	α_i	n	P	α_p	n	P	
DOWEY'S SPUR	.830	203	.006	1.520	68	<.0001	7.82
STARVATION CREEK	.903	465	.017	1.353	102	.0005	7.52
BUNYIP	.618	157	<.0001	2.881	62	<.0001	53.30
ACHERON	.678	603	<.0001	1.418	96	.0001	2.99
HARDY'S CREEK	.764	541	<.0001	1.519	84	<.0001	5.80
MT MONDA	.715	301	<.0001	2.063	83	<.0001	12.90

(3) The expected value of α_i in random populations is $(n-1)/n$ and is smaller than this value in contagious populations. The value $2n\,\alpha_i$ is distributed according to χ^2_{2n}, where n is the number of sample trees. P is the probability that the spatial pattern is random, given the computed value of the α_i statistic.

(4) The expected value of α_p in random populations is $(n-1)/n$ and is larger than this value in contagious populations. The value $2n\,\alpha_p$ is distributed according to χ^2_{2n}, where n is the number of sample points. P is the probability that the pattern is random, given the computed value of the α_p statistic.

(5) The expected value of the variance to mean ratio is 1 in random populations and larger than this in contagious populations.

(as measured by the point to plant and Var/Mean statistics) the trees are apparently not as intensely aggregated within the clumps (as measured by the nearest neighbour statistic) as those at Acheron.

The Var/Mean ratio of plot densities was computed at each stand measurement (at 2-3 year intervals) and in all stands the ratio is decreasing over time (Figs. 2 and 3). The very rapid decrease in the contagion at Bunyip is the result of the rapid reduction in density which naturally occurred in the intensely aggregated clumps there. The trends in the older stands suggest that significantly non-random patterns will be maintained for many more years. In the younger stands this small scale pattern (measured by the variability between 0.01 ha plots) is approaching randomness, but larger scale heterogeneity may still exist.

Calculations of the pattern statistic based on distance to the nearest neighbour for individual plots show that the degree of aggregation varies within a stand and is not determined solely by plot density, although plots with lower stocking tend to have more extreme values of the aggregation index (Fig. 4).

Stand Structure

There is great variability between the characteristics of individual plots in both the young and old stands. In the young stands, the variation in basal area at age 4 is greater or approximately equal to the variation in density, while in the older

Fig. 2: Change in spatial pattern with age in the young stands
as measured by the ratio of the variance of the number
of trees on 8 small (.01 ha) plots to the mean number
of trees on these plots. The expected value of this
ratio in a random population is 1.0.

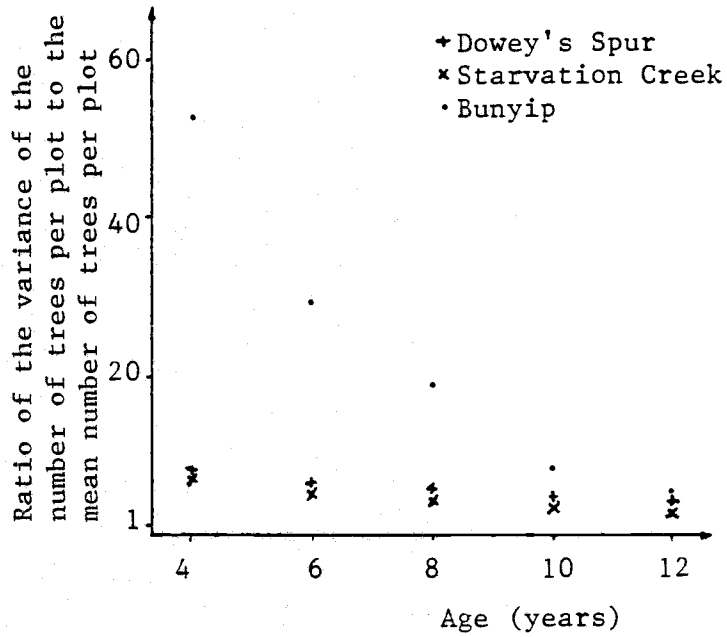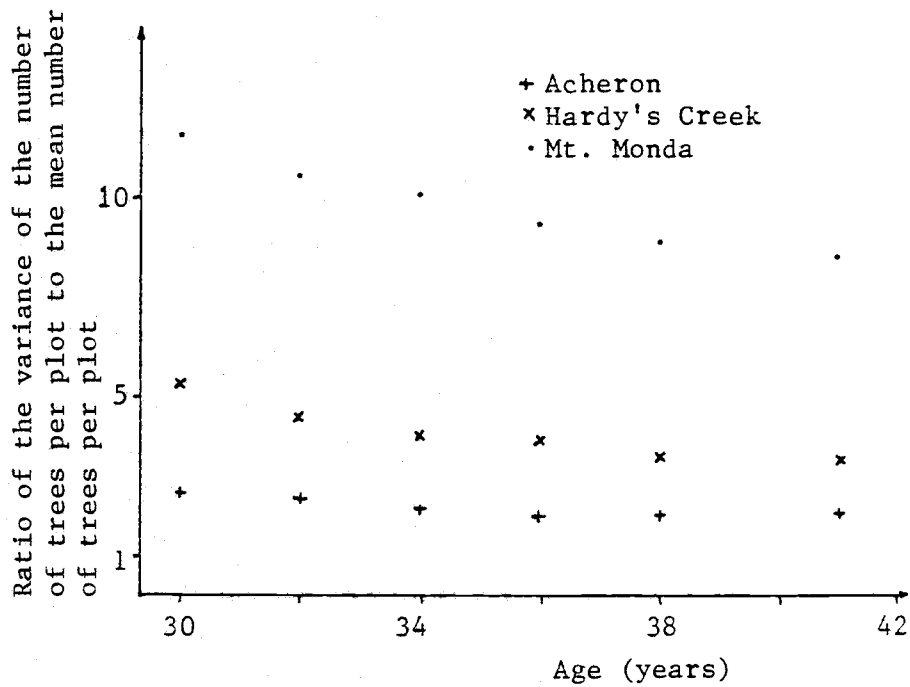Fig. 3: Change in spatial pattern with age in the old stands as measured by the ratio of the variance of the number of trees on 18 small (.11 ha) plots to the mean number of trees on these plots. The expected value of this ratio in a random population is 1.0.
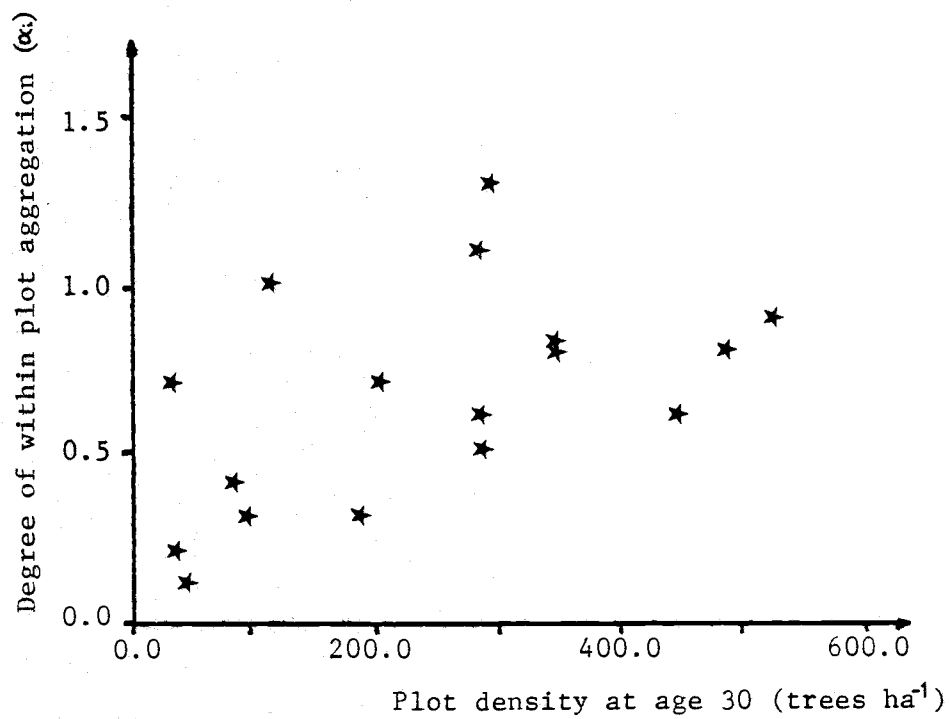
Fig. 4: Relationship of the degree of within plot aggregation (α_i) to the number of trees per ha for individual plots at age 30.

stands at age 30 basal area variation is consistently less than
density variation (Table 3). By age 30 mean tree basal area is
greater on the lower density plots. Variation in dominant height
between plots is minimal. When sampling in these stands large sample
sizes will be necessary to estimate stand characteristics.

At age 4 the frequency distributions of tree diameters on the
young plots are all strongly positively skewed (Fig. 5). On the two
lower quality sites the modal class is the smallest diameter class.
In the stand with the highest site and lowest average stand density,
dominated by E. delegatensis rather than E. regnans, (Dowey's Spur)
mortality has already reduced the number of trees in the smallest
diameter class. As a result the modal class has shifted to the
right, i.e. skewness is decreasing. The size of the largest trees on
each plot is not related to plot density. The proportions of trees
in each diameter class are similar regardless of plot density. By
age 12 the distribution on almost all of the small plots shows some
evidence of a second peak in the larger size classes.

At age 30 the range of diameters is similar in all the plots
within each of the older stands (Fig 6). The frequency distributions
on the older plots all show clear bimodality and a distinct
separation between trees in each crown class. There is one modal
class among the dominant and codominant trees and a second in the
suppressed class. The variability in plot density can be attributed
to variation in the numbers of codominant and suppressed trees (Fig.
6). The number of dominants does not vary with local plot density

TABLE 3: Variability in characteristics between plots in each stand at
the first measurement, as measured by coefficients of
variation (the ratio of the standard error to the mean).

PLOT VARIABLE	COEFFICIENTS OF VARIATION FOR PLOTS WITHIN A STAND					
	AGE 4				AGE 30	
	DOWEY'S SPUR	STARVATION CK	BUNYIP	ACHERON	HARDYS CK	MT MONDA
STOCKING	.450	.328	1.085	.262	.407	.723
BASAL AREA	.527	.420	1.073	.175	.274	.504
DOMINANT [6] HEIGHT	*[7]	*	*	.023	.037	.078
TOTAL VOLUME	*	*	*	.183	.282	.535

(6) Dominant height is mean height of the 50 trees of largest diameter
at breast height per ha.

(7) Plots contained too few trees to estimate dominant height or
volume.
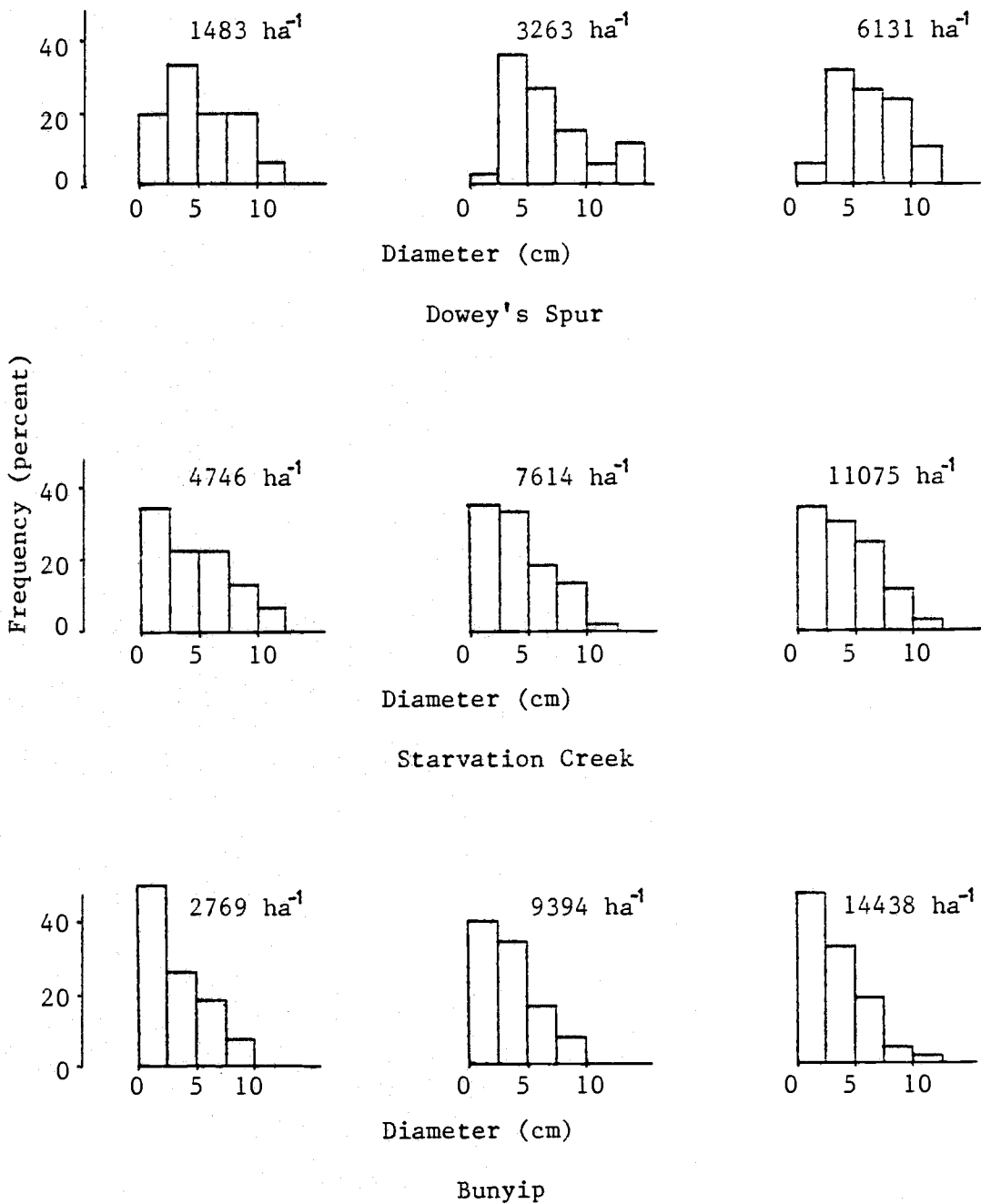
Fig. 5: Frequency histograms of the percent of trees in each
2.5 cm diameter class at age 4 for low, medium and
high density plots in each stand.
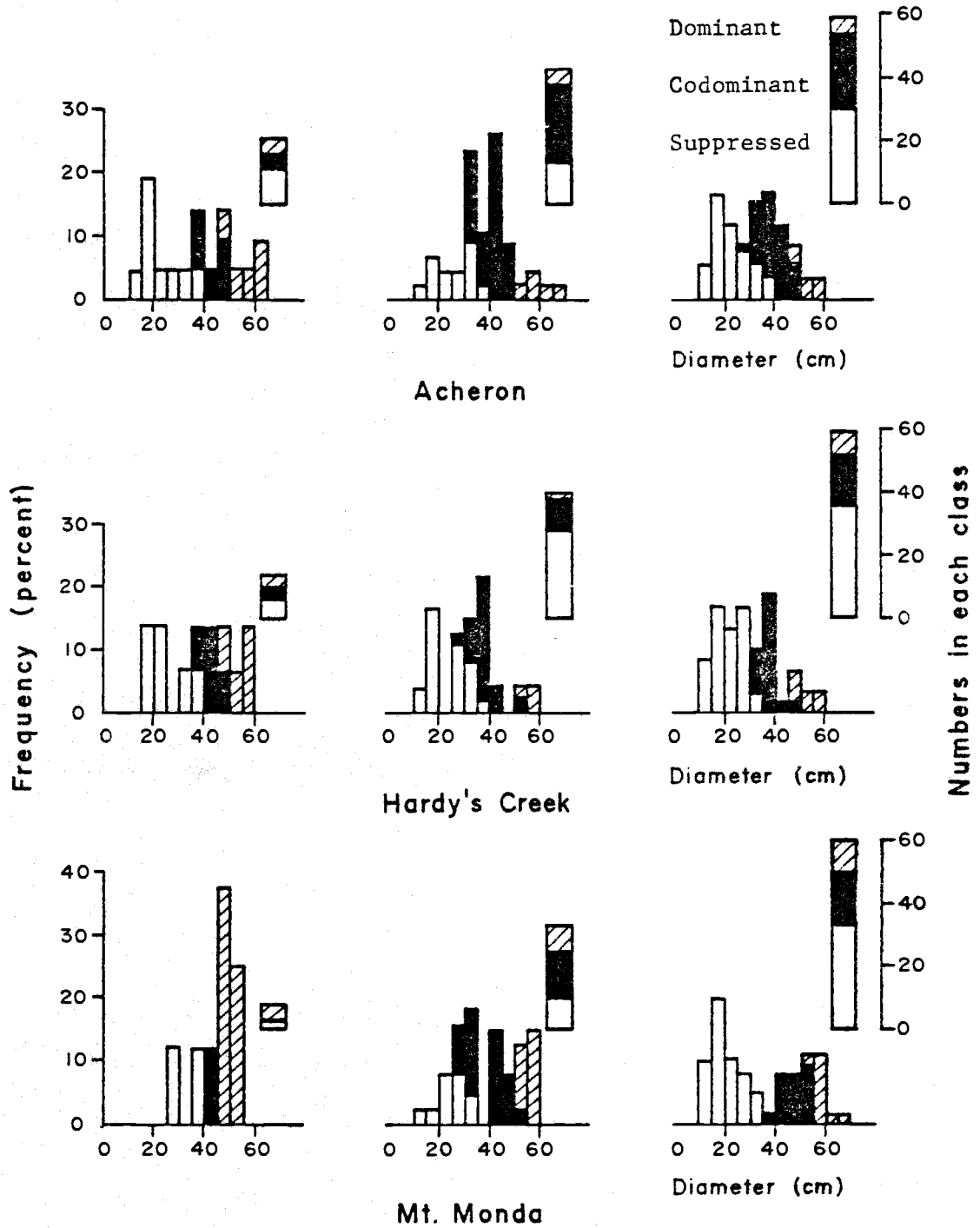
Fig. 6: Frequency histograms of the percent of trees by crown
class in each 5 cm diameter class at age 30 for low,
medium and high density plots in each stand. Also shown
is the total number of trees per plot in each crown
class.

(Fig. 7). A Var/Mean ratio test of their distribution confirms that they are randomly distributed between plots in all the older stands (Table 4). The values of the statistic are not significantly different from its expected value (P = .05) in a random population (1.0 with s.e. of 0.34) in any of the stands. Similarly, Ford (1975) found that the large trees in plantations of Picea sitchensis of several spacings and ages tended to be more regularly distributed than the population as a whole.

The size of the dominants (in terms of both height and diameter) is similar throughout each stand (Fig. 6) regardless of the local plot density or the proximity of neighbouring trees. The proportion of dominant E. regnans in each of the older stands is considerably less than the proportion reported by Ashton (1976) in fully stocked stands of the same age. The stands are apparently less than fully occupied, while high densities are attained in the occupied parts.

Skewness, bimodality and a high coefficient of variation for tree size are all recognized as being indicators of competition within a population (Mead 1979). A lognormal distribution of trees across diameter classes, seen in these stands at age 4, is proposed to be the direct consequence of an exponential distribution of plant growth rates. A reduction in the skewness of this distribution as the population ages, as between 4 and 12 years here, is the result of mortality of the most suppressed stems (Mohler et al. 1978). Ford (1975) showed how bimodality results from a disjunct distribution of relative growth rates under competition, whereby relative growth

25
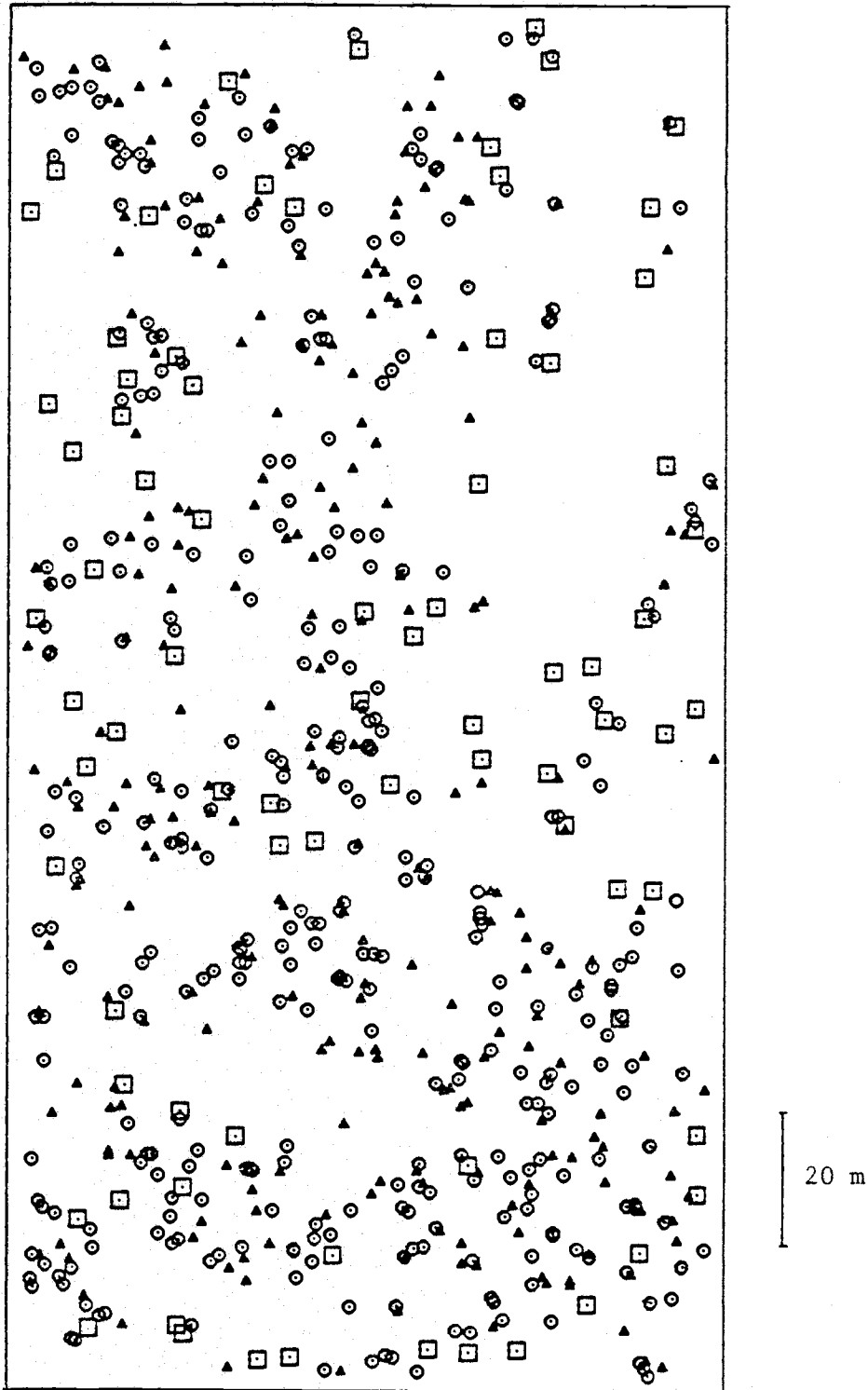
Fig. 7: Map of Hardy's Creek at age 30 showing the spatial
distribution of trees in the three crown classes;
dominant (⊡), codominant (▲), suppressed (☉).

TABLE 4: Tests for randomness in the spatial distribution of the dominant trees in the older stands using the Var/Mean ratio of the number of dominant trees per 0.11 ha plot.

STAND	VARIANCE TO MEAN RATIO	
	AGE 30	AGE 41
ACHERON	0.978 n.s.	1.155 n.s.
HARDY'S CK.	1.059 n.s.	1.046 n.s.
MT. MONDA	1.217 n.s.	1.217 n.s.

rates in a class of smaller plants are consistently low and do not increase appreciably with increasing plant size. Ford (1975) notes that 10 or more size classes are necessary to reveal the secondary maximum in frequency histograms of plant size, and so bimodality may have been masked in some of the distributions. The occurrence of a distinct suppressed class indicates that competition is affecting plant growth even on the least dense plots in these stands.

Variation in tree size can be partly attributed to the degree of aggregation on a plot (Fig 8). At high levels of aggregation the variability in total stem volume increases as competition and hence the proportion of suppressed trees increases. This result also explains the low proportion of dominant trees on the stands as a whole. Wyszomirski (1983) predicted a similar result for variations in plant weight in a theoretical competition model for populations with different degrees of spatial irregularity. In the absence of experimental data he proposed that responses to increasing competition could be expected to parallel responses to increasing density, since clumped spatial distributions are associated with high local densities.

Between age 30 and 41 many suppressed trees and a few larger trees died, while the largest trees grew most rapidly. As a result the primary peak in the histograms decreased and the coefficient of variation for diameter increased. The dominants remained randomly distributed throughout the stands (Table 4).
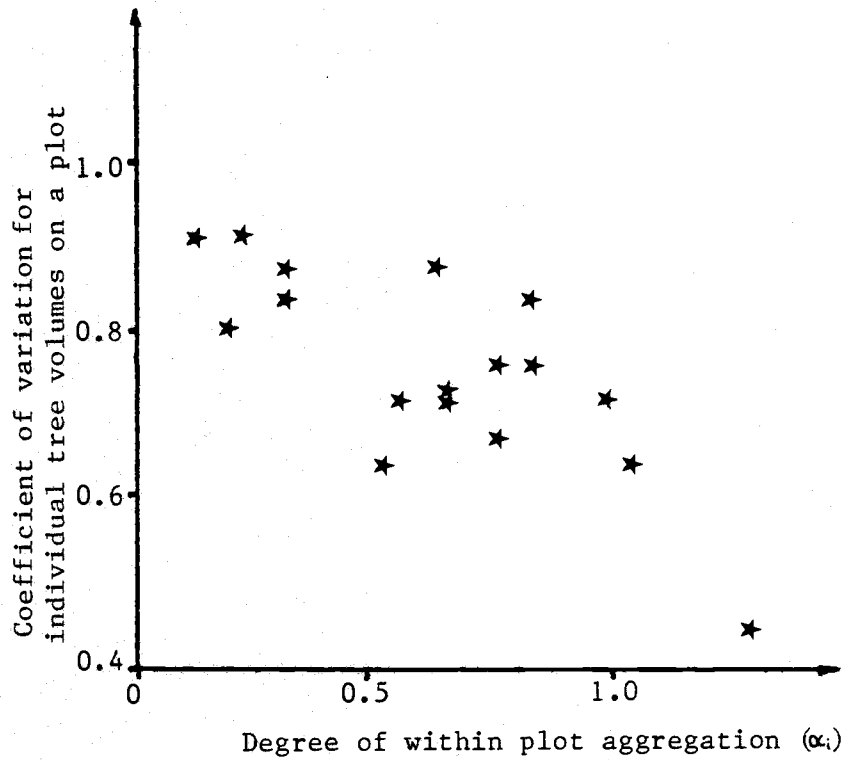
Fig. 8: Relationship of the coefficient of variation for
individual tree volumes on a plot and the degree of
within plot aggregation (α_i) for plots at age 30.

Mortality

The proportion of trees dying over the measurement period is greatest at the highest densities in all the stands, so at least some of the mortality is density dependent or competition induced. There is a linear relationship between percent mortality and density in all the stands. In all the young stands the relationship is:

$$\text{Mortality \%} = 32.73 + .00332\ N \qquad R^2 = .463$$
$$\phantom{\text{Mortality \%} = } (4.63)\ (.00076) \qquad\qquad (6)$$

where Mortality % is the total percent of trees dying over 8
years

N is initial stocking density on a plot in trees ha^{-1}

The standard errors of the parameter estimates are shown in parentheses.

There is a significant difference in the level of mortality between the older stands which cannot be explained by site index and may be attributable to the localized occurrence of severe drought conditions:

$$\text{Mortality \%} = k_1 + 0.0326\ N \qquad R^2 = .615$$
$$\phantom{\text{Mortality \%} = k_1} (0.0084) \qquad\qquad (7)$$

where k_1 is 15.81 (2.98) at Acheron,

10.66 (2.80) at Hardy's Creek,

2.36 (2.65) at Mt. Monda

The pattern of occurrence of mortality in one of the stands is shown in Fig. 9. Since mortality is concentrated in the regions of highest density, the intensity of aggregation is decreasing through time and the pattern is tending towards random, as demonstrated by the trends in the Var/Mean ratio (Figs. 2 and 3).

In the young stands, tree species, size and plot density variables and distance to the nearest neighbouring tree are significant predictors of the eight year periodic mortality rate (probability of death over the measurement period) for individual trees, giving a fitted model:

$$P = (1 + \exp (k_2 - .880 D + 8.4 \times 10^{-9} N^2 + .0024 BA^2 - .0061 DNN))^{-1}$$
$$(.057) \quad (2.3 \times 10^{-9}) \quad (.0008) \quad (.0016)$$

(8)

where k_2 is 0.873 (.305) in E. regnans,

0.456 (.596) in E. delegatensis,

3.261 (.742) in E. nitens,

−0.201 (.363) in E. cypellocarpa

D is midpoint diameter at breast height of a 2 cm diameter class

BA is initial basal area of plot in $m^2 ha^{-1}$

DNN is initial distance to the nearest neighbouring tree in
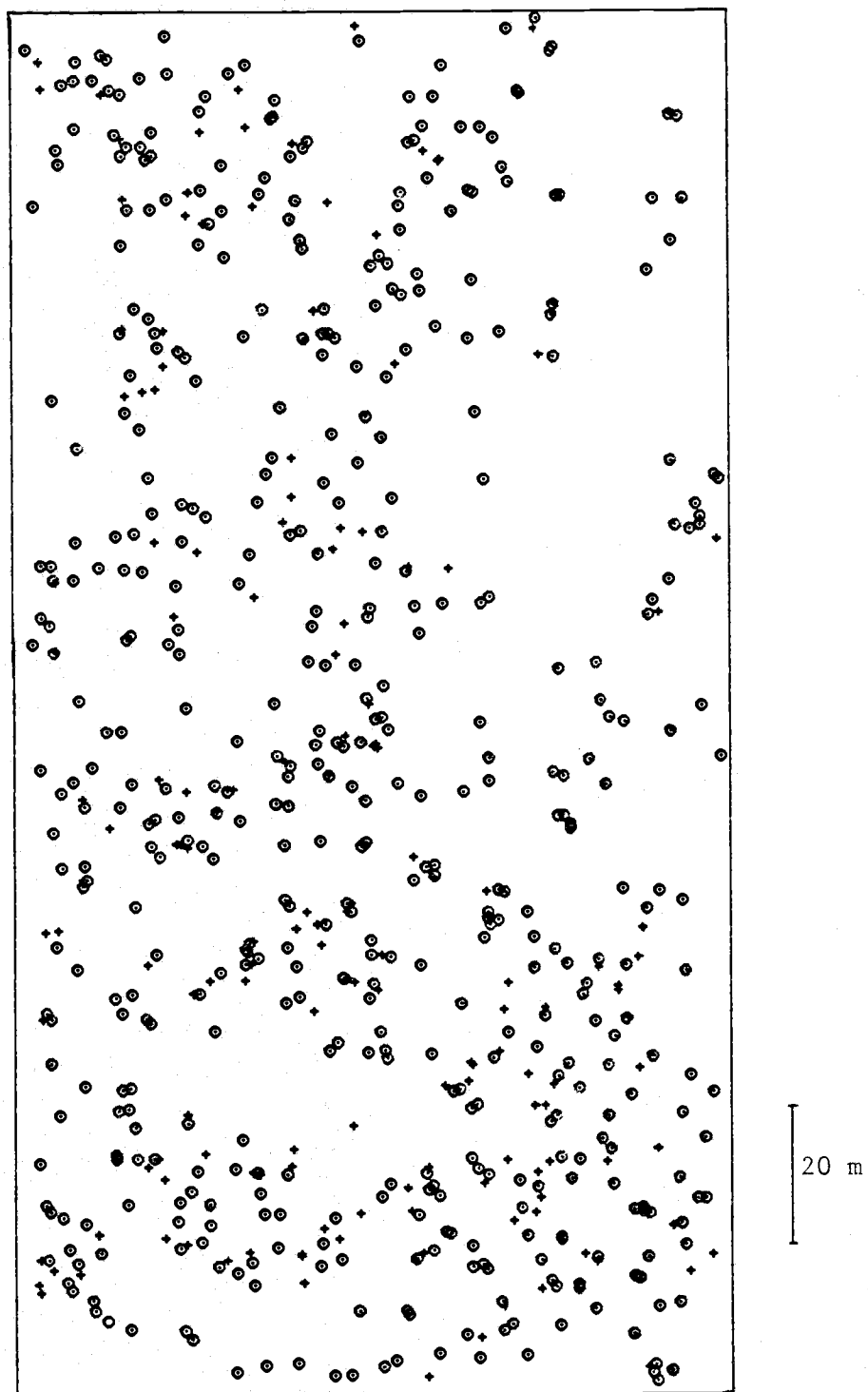
m.

The percent mortality is, as expected, highest in the small diameter classes and at low values of distance to nearest neighbour. The agreement of the model with the observed response is very good (Fig. 10). An approximate χ^2 test of the goodness of fit does not allow us to reject the null hypothesis that the predicted and observed numbers of trees dying in each diameter class are the same.

In the older stands the only variables selected for predicting eleven year periodic mortality rate across all crown classes were tree size and site index:

$$P = (1 + \exp (0.922 - .228 D + .137 SI))^{-1}$$
$$(0.567) \quad (.013) \quad (.019)$$

$$(9)$$

where SI is site index, the mean height of the 50 trees of
       largest diameter at breast height per ha on the plot
       at age 20

Allowing for the difference in the probability of mortality between crown classes the model became:

$$P = (1 + \exp (k_3 - 0.222 D + .135 SI))^{-1}$$
$$(0.016) \quad (.020)$$

$$(10)$$

Fig. 10: Observed and predicted (using equation 8) eight year periodic mortality rate, in percent, for the four year old trees by initial 2 cm diameter classes.

where k_3 is   2.523 (.642) in the dominant class,

0.299 (.724) in the codominant class,

0.443 (.589) in the suppressed class.

Equations (9) and (10) both predict a distribution of mortality across the diameter classes which is not significantly different from the observed mortality (Fig. 11), but the addition of crown class markedly improves the fit of the predicted to the observed distribution. A χ^2 test of the logarithm of the maximum likelihood ratio of the two models shows that the improvement is significant (P = .002). Suppressed trees account for 94.5% to 98.4% of the deaths in these stands.

For trees of the same diameter equation (10) predicts a higher probability of mortality for the dominant trees than for the codominant or suppressed trees. Other models have predicted an increase in the probability of mortality for extreme values of age (West 1981) or mean tree diameter at breast height (Hamilton 1974). In both these instances the mortality of the larger trees could be attributed to their relative maturity. In the present study the proportion of trees dying in both the dominant and codominant classes is very low and the difference may be spurious. The result suggests that some agent of mortality, other than competitive stress, is present which affects larger trees.

The significance of distance to nearest neighbour and stand density variables as predictors of mortality in the young stands but

35

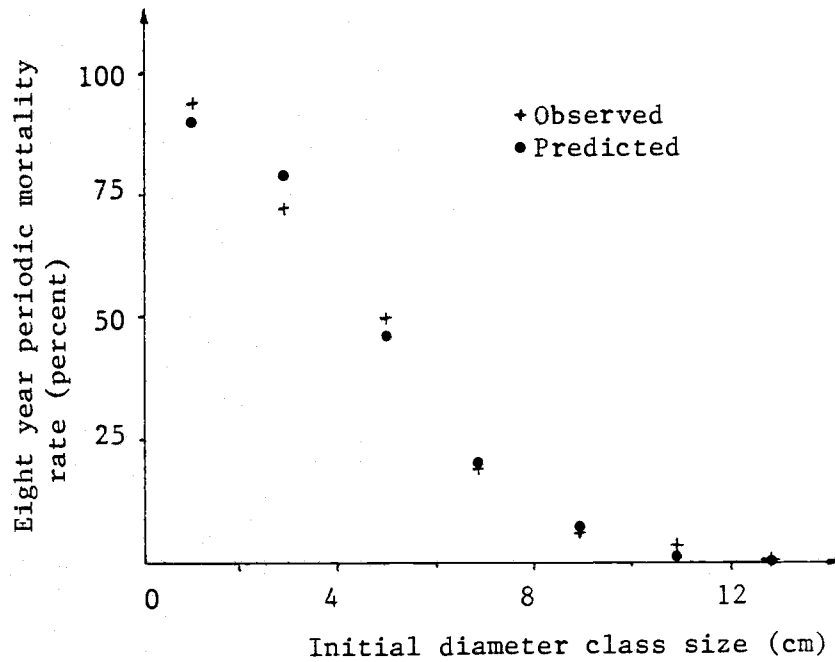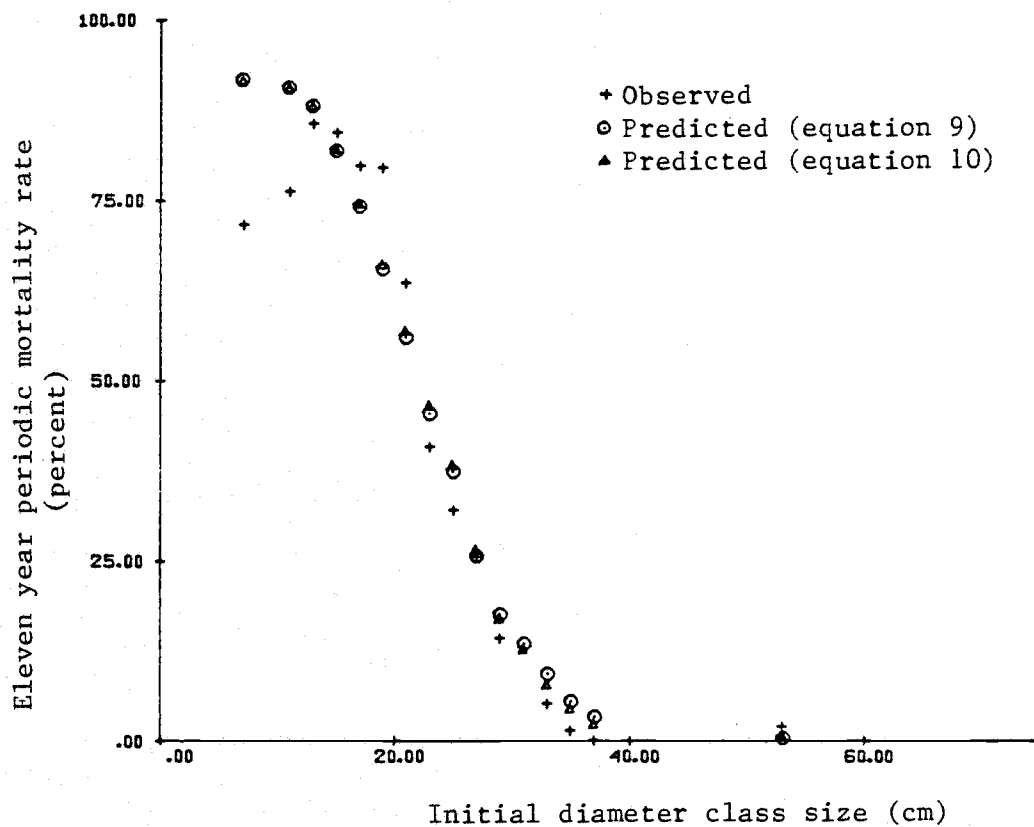

Fig. 11: Observed and predicted eleven year periodic mortality
rate, in percent, for the thirty year old trees by
initial 2 cm diameter classes. Equation 9 is without
crown class while equation 10 includes crown class.
Where the observed or predicted number of trees dying
in a class was less than five, adjacent classes were
combined.

not in the older stands is indicative of the nature of competition at
each stage of stand development. In the young stands contagion is
still intense and neighbouring trees are a source of competitive
stress, which reduces vigour and leads to suppression and mortality.
Daniels (1978) stated that "early spatial relationships are most
pertinent to tree and stand growth models". By age 30, in
E. regnans, competitive positions and hence susceptibility to
mortality have largely been established. E. regnans will only move
into less dominant positions through time (Ashton 1976). The early
pattern of contagion has broken down under competition so that the
spatial positions of remaining competitors are less indicative of a
tree's competitive position and chance of survival. West (1981)
suggested that a period of intense early mortality among seedlings in
regrowth eucalypts is followed by a period when mortality declines as
crown classes are delineated and then a period, which he identified
to be between 24 and 59 years, when the suppressed trees die. In
stands with more uniform spatial patterns, where there is less
variability in spacing, the distances between competing trees may not
be as good a predictor of likely survival. It is, however, a very
simple measure of the competition from surrounding trees. Many more
sophisticated measures, incorporating distance to a number of
competitors and their size have been proposed (for reviews and
examples see Mead 1971, Noone and Bell, 1980).

Individual Tree Growth

In the old stands, preliminary analysis suggested there were

marked differences in the growth rates of trees between crown classes. The average basal area growth of suppressed trees on any plot is near zero in all the older stands (Fig. 12). Many individual trees had records of near-zero or slightly negative diameter increments between each remeasurement over the whole measurement period. The persistence of suppressed stems of E. regnans has been noted elsewhere (Ashton 1976, West 1981), as has the seasonal shrinking of their stems in response to drought (Hopkins 1968).

Despite the large variation in the number of trees on small plots in each stand, mean gross basal area growth of trees within any crown class in the older stands is almost independent of density (Fig 12). Very similar trends were apparent for estimated volume growth. In the dominant and codominant classes, mean growth increases with decreasing stand density only at the lowest levels of density. The size of the dominants and codominants is also greater only on these very low density plots. This suggests that in most of the plots the local density has been high enough to limit tree growth. Although trees in some of the most open plots, where there are as few as 45 stems ha^{-1}, were clumped, in others they were scattered and hence would have experienced much lower levels of competition than trees throughout the rest of the stands. This suggested that other measures of competition, apart from average plot density variables, would be necessary to explain individual tree growth. In addition to the number of trees and basal area density on a plot, the basal area in trees larger than the subject tree, BALT, and in trees smaller than or equal in size to the subject trees, BAST, (both in m^{2}ha^{-1}) and
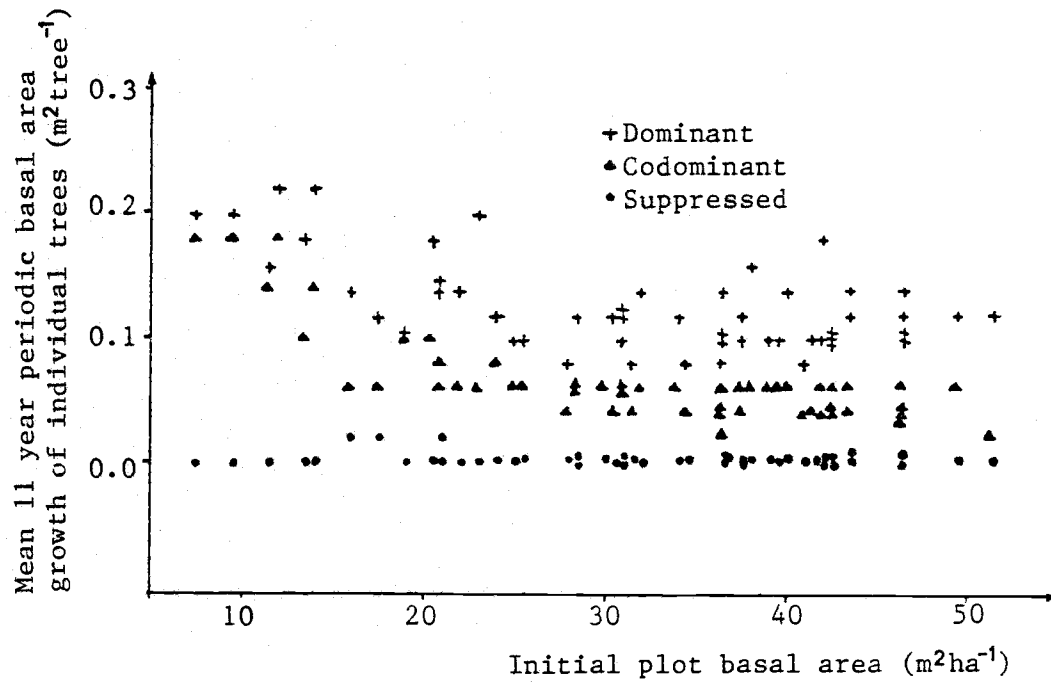
Fig. 12: Mean 11 year periodic basal area growth of individual
trees by crown class over initial plot basal area at
age 30.

the distance to the nearest neighbouring tree were tested as predictors.

All of the stands in this study are less than fully stocked and this has influenced stand development. At Acheron (SI = 35.6 m) and Mt. Monda (SI = 23.9 m), for example, mean tree size is similar but average growth is greater on the stand with the lower site index. Since the initial density at Acheron was considerably higher than that at Mt. Monda, but we expect mortality to be greater on better sites, the trees at Acheron must have developed under considerably higher densities than those at Mt. Monda. The difference in the average crown ratio of the dominant trees at each site (Table 1) indicates that the trees at Acheron are now less vigorous than those at Mt. Monda despite the higher site quality. The data do not cover enough of the range of possible stand structure and site quality conditions to fully specify their individual contributions to tree growth. In trees of the same age we expect basal area growth to increase with increasing site index but, in both the young and old data sets, initial parameter estimates for site index were negative. To allow for the expected contribution of site index, this variable was forced in to the models (4 and 5) as one of the set of X_i variables without an exponent.

In the linear models (model 5) the exponent on diameter at breast height, DBH, was estimated to have values close to 2.0, implying that basal area growth is proportional to tree basal area. In the nonlinear model (4) the high correlation between β_{0i}, the

multiplier on DBH, and its exponent β_{1i}, led to very unstable estimates for these two parameters. Replacing $DBH^{\beta_{1i}}$ with DBH^2 had very little effect on the fit of either the linear or non linear models, so the latter form of the model was used throughout.

The remaining variables entered the models as exponential terms, giving the following model forms for final parameter estimation :

$$Y = \beta_0 + \beta_1 SI\ DBH^2\ e^{\beta_2 BALT + \beta_3 BAST + \beta_4 DNN + \beta_5 CR + \beta_6 SP + \beta_7 N} + \varepsilon \tag{11}$$

$$\ln((Y - \beta_0)/(SI\ DBH^2)) = \ln \beta_1 + \beta_2 BALT + \beta_3 BAST + \beta_4 DNN + \beta_5 CR + \beta_6 SP + \beta_7 N + \varepsilon \tag{12}$$

where CR is crown ratio, the ratio of the length of the crown to the total tree height

SP is an indicator variable for any of the species

The contributions of a single basal area term and, in its place, BALT and BAST together, were tested independently.

Initially both basal area growth and diameter growth were tested as potential dependent variables. Furnival's (1961) index indicated basal area was a better dependent variable in both the linear and nonlinear models and so the best predictors of basal area growth were sought in subsequent models. The parameter estimates and their standard errors for nine equations fitted to models (11) and (12) are shown in Table 5.

TABLE 5: Parameter estimates and their standard errors (below) for nine individual tree basal area growth
equations. Also presented are the length of the growth period, the sample size and the mean squared
error for each equation.

Equation number	Data[a] set	Growth period (years)	Sample size	PARAMETER ESTIMATES AND THEIR STANDARD ERRORS (BELOW)								Mean squared error
				β_0 10^2	β_1 10^6	β_2 10^{-2}	β_3 10^{-2}	β_4 10^{-2}	β_5	β_6 10^{10}	β_7 10^{-5}	
Linear model (12)												
(13) YOUNG TREES	8	425	0.00[b]	5.71	-14.33	-2.41	0.123		0.693	–	0.614
					.80	.81	.77	.055		.084		
(14) YOUNG TREES (with CR)	8	192	0.00	8.49	-16.73	-4.05	–		0.71	–	0.547
					1.27	1.28	.98			.11		
(15) YOUNG TREES (with CR)	8	192	0.00	2.08	-11.80	-2.61	–	2.61	0.35	5.47	0.497
					.83	1.76	.58		.57	.15	2.65	
Non-linear model (11)												
(16) OLD TREES	11	1130	-0.193	2.05	-4.38	-1.03	5.43			–	1.35×10^{-4}
				.035	.15	.24	.18	.81				
(17) OLD DOMINANTS	11	242	5.34	1.58	-5.94	-2.05	6.11			–	1.79×10^{-6}
				.98	.23	1.57	.35	.15				
(18) OLD CODOMINANTS	11	520	1.48	2.88	-5.71	-2.74	8.72			–	3.35×10^{-6}
				.33	.44	.76	.41	1.81				
(19) OLD SUPPRESSED	11	368	-0.032	0.98	-4.15	–	–			–	1.44×10^{-6}
				.031	.23	.88						
(20) OLD DOMINANTS (with CR)	11	174	5.50	1.69	-4.88	-2.26	4.78			–	1.94×10^{-6}
				1.39	.29	1.84	.43	1.73				
(21) OLD DOMINANTS (with CR)	11	174	5.38	0.72	-3.63	-1.63	4.76	1.10		–	1.87×10^{-6}
				1.38	.29	1.62	.42	1.62	.43			

TABLE 5: (continued)

FOOTNOTES:

(8) Each set includes only those trees which survived to the end of the measurement period and were not within the buffer zone which included all trees which were closer to the boundary than their nearest neighbour within the plot. A description of each data set follows:

DATA SET	DESCRIPTION
Young trees:	All the trees in the younger stands
Young trees (with CR):	All trees in the younger stands for which records of crown ratio were available.
Old trees:	All the trees in the older stands.
Old dominants:	All the trees in the older stands which were classified as dominants at the first measurement.
Old codominants:	All the trees in the older stands which were classified as codominants at the first measurement.
Old suppressed:	All the trees in the older stands which were classified as suppressed at the first measurement.
Old dominants (with CR):	The dominant trees in the younger stands for which records of crown ratio were available.

(9) Not a least squares estimate.

(10) E. regnans had the only significant indicator variable

41a

Furnival's index of fit indicated that the nonlinear model (model 11) gave a better fit than the linear model to the data from the individual crown classes among the older trees. The size of the mean squared error from the nonlinear model varied greatly between crown classes (Table 5) and so when a model was fitted to the data from all the old trees (equation 16) the errors were weighted in proportion to this variability, as well as to DBH^4. The log-transformed linear model (model 12) provided a much better fit to the data from young trees, in which the trees were from all classes but no records of crown class were available.

Where the data include records from small and suppressed trees we expect the value of the intercept term, β_0 , to be zero or slightly negative. Since no negative basal area growth was recorded for any of the young trees, a value of zero seemed most appropriate for fitting the log model to these data sets.

The total basal area on a plot was not a significant predictor of growth in any of the subsets of the data. The number of trees on a plot was significant only for the subset of young trees for which crown data was available, and then only when crown ratio was also included in the model (equation 15). Basal area in larger and smaller trees proved to be better predictors of growth than basal area and density alone in all the data sets. These average density variables reflect average competitive stress and are constant for all the trees on a plot. In contrast, basal area in larger trees and smaller trees reflect a tree's relative competitive position. They

have the same value as the total basal area only if the parameter
estimates of the two variables are equal. In all the equations here
a unit of basal area in larger trees has a stronger impact on growth
than a unit of basal area in smaller trees, as indicated by the
magnitudes of the coefficients, e.g. -4.38 for basal area in larger
trees and -1.03 for basal area in smaller trees for old trees from
all crown classes (equation 16). The relative effects of competition
from large trees are much more severe for young trees than they are
for older trees. By comparison, for young trees from all crown
classes the coefficients were -14.33 for basal area in larger trees
and -2.41 for basal area in smaller trees (equation 13). Competitors
which have exerted their dominance by age 4 will be sources of
significant stress over the next 8 years. In contrast, many smaller
competitors will have become suppressed or died over the measurement
period, a period when dominance is being asserted.

Among the old suppressed trees, neither distance to the nearest
neighbour nor basal area in smaller trees were significant predictors
of growth. Just as the proximity of competitors does not predict
which trees will die (equation 10), distance to nearest neighbour
does not predict which suppressed trees will continue to grow
vigorously. Many suppressed trees go through a period of near-zero
growth before succumbing to mortality. All the suppressed trees
experience significant competition. They are within the zone of
influence of larger trees, even where these are not their nearest
neighbours. Their tolerance of this competition is determined
largely by their relative size and competitive position, measured by

DBH and the basal area in larger trees.

In the dominant and codominant crown classes competition is more variable. A given level of competition may be produced by smaller or larger neighbouring trees. The size and number of these competitors relative to the size of the subject tree, measured by the basal area in larger and smaller trees, in combination with their distance from the subject tree, indicate the intensity of this competition.

The difference in the response between crown classes in the older stands is significant. There is a significant increase in the sum of squared errors when the three individual crown class equations (18 to 20) are collapsed into one equation ($P < .005$).

The subjective selection of the trees in the young "crown" data sets may serve to explain the nonsignificance of distance to nearest neighbour as a predictor here (equation 14) while it is significant, though not a strong predictor for the full young tree data set (equation 13). The addition of crown ratio significantly improved the fit of the model in the data sets where it was available ($P = .008$ in the old trees, $P < .005$ in the young trees). Crown ratio is a good indicator of the past competition experienced by a tree and hence its vigour. In the young trees, once crown ratio was added to the model, density, in trees ha^{-1}, was also a significant predictor in this data set.

Stand Growth and Development

Total gross production of basal area increased approximately linearly with increasing local density over the range of densities found on plots within each of the stands (Fig 13), but growth per tree declined at the higher densities. Since mortality was concentrated in the areas of greatest density, net plot growth had a weaker correlation with plot density (Fig 14). The decline in growth per tree with increasing density is indicative of stands in which the trees are competing. Since these species are intolerant of competition, as density increases a larger proportion of the trees move into lower crown classes and eventually die, rather than survive with reduced growth rates. Since, at least in the older stands, suppressed trees are not contributing significantly to stand basal area growth (Fig. 12) and the numbers of dominants and their growth are independent of average plot density, the increase in total basal area production with increasing density is related to the increasing numbers of codominant trees (Fig. 6).

Among both the young and old stands, total basal area growth on individual small plots did not increase with increasing site index. This trend also applied to net volume growth. In both age classes the stand with the lowest site quality also carried the lowest stocking. For two plots with the same basal area, the plot on the lower site carried fewer and hence larger trees. The difference between plots in the two stands is the difference in the proportions of the crown classes. As we demonstrated in relation to individual
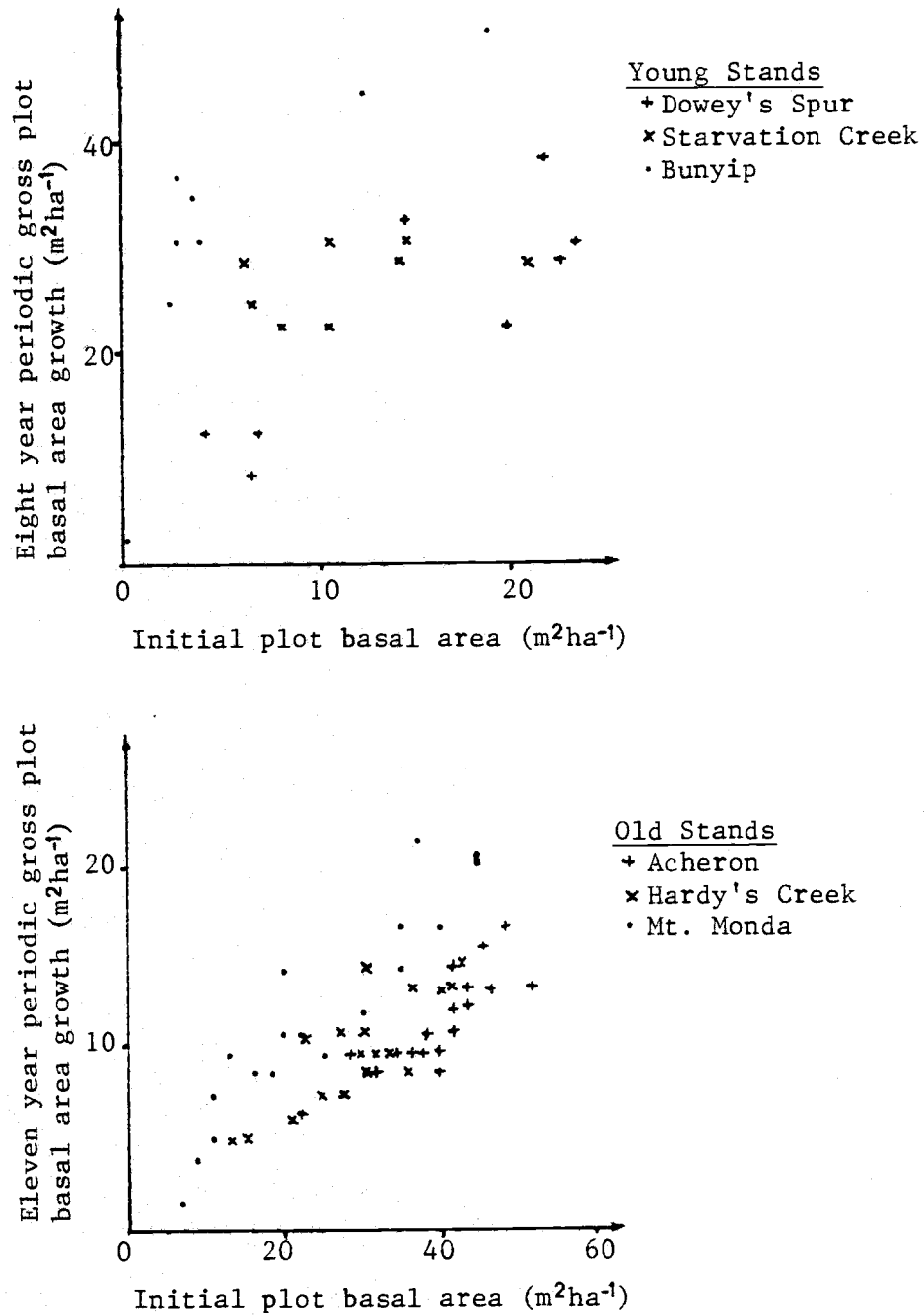
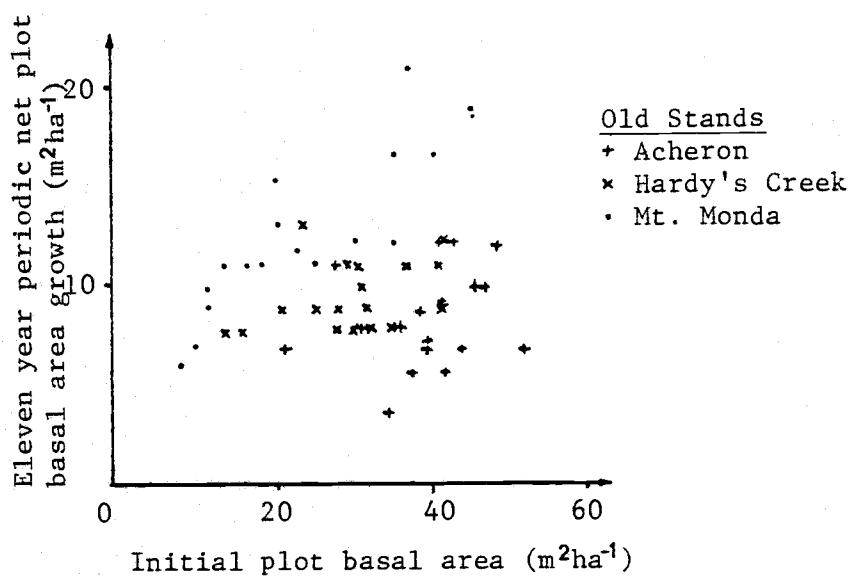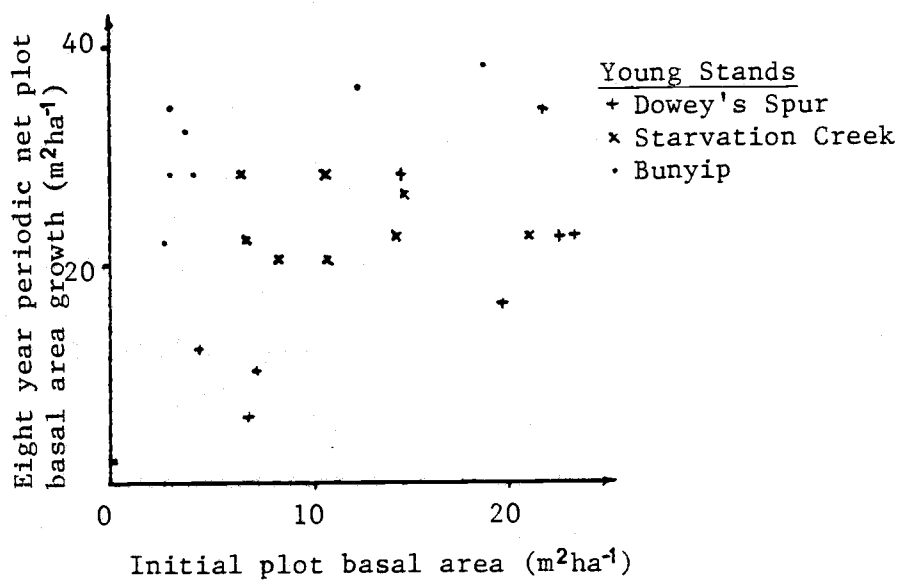Fig. 13: Periodic gross plot basal area growth over initial plot basal area.

Fig. 14: Periodic net plot basal area growth over initial plot basal area.

tree growth, recognition of past density conditions in these stands is important to explain growth. We have shown the value of crown ratio, an indicator of past density stress, in predicting growth in these stands.

Size-Density Relationships

White and Harper (1970) and Drew and Flewelling (1979) have demonstrated a consistency in the way plant size changes with density as stands develop. For any species there is a maximum mean tree size possible for any given level of stand density. The log of this maximum size increases linearly at a slope of -3/2 as the log of density decreases (White and Harper 1970). Mortality due to intraspecific competition occurs once this maximum condition is approached. Since spatial pattern apparently influences both tree growth and young tree mortality it is possible that spatial pattern also affects the trajectory of a stand's size-density development.

The change in estimated mean tree volume and plot density between the first and last measurements on each of the older plots is shown in Fig 15. The position of the maximum size-density line has not been determined for E. regnans, but data for production in a number of fully stocked stands (W.D. Incoll, pers. comm.) is also shown in Fig. 15. The consistency of the slope in these high density plots suggests that many have reached the maximum condition for these stands. In fully stocked stands of E. regnans density dependent mortality occurs from an early age. In contrast, many of the plots
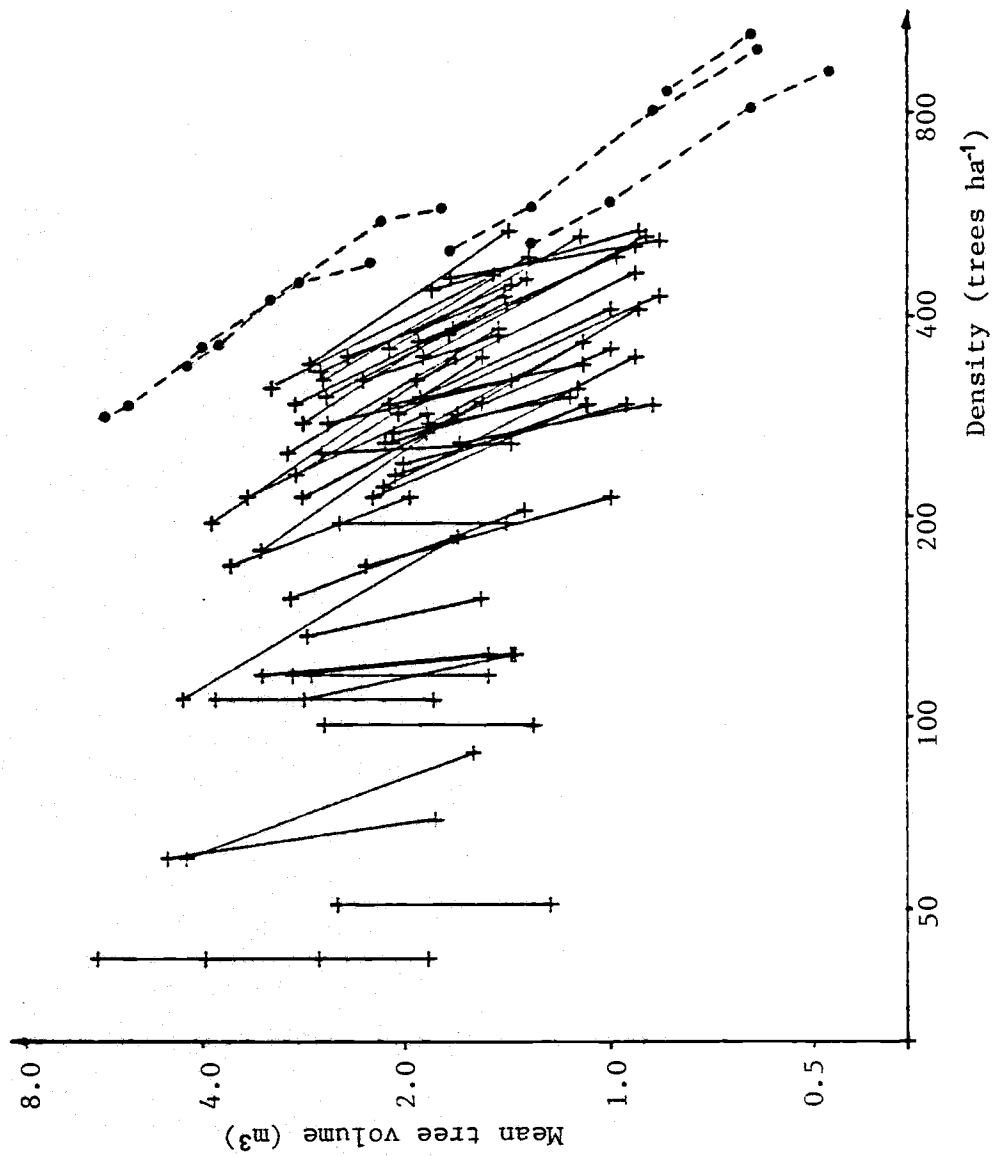
Fig. 15: Surviving mean tree volume for each plot over surviving
number of trees per ha, in both fully stocked (•) and
contagious, unevenly stocked (+) stands. For the plots
from the contagious stands, values are only plotted for
ages 30 and 41.

in this study are at much lower densities than the expected maximum
for their mean tree size. In some of the plots there was no decrease
in density over the measurement period. However in other plots, with
similarly low initial density, a significant degree of self-thinning
occurred. The slopes of the lines (Figure 15) represent the average
rate of thinning over the measurement period and may be the result of
a period of no change in density combined with a period of mortality.
This thinning even in low density plots suggests aggregation causes
thinning to begin at lower relative densities than it would in random
populations.

White and Harper (1970) present a derivation of the −3/2 power
law which defines the maximum size density relationship in terms of
the relationship between the distance from a subject plant to its
nearest neighbour and plant size. In the relationship :

$$W = k_4 \, \rho^{-3/2}$$

(22)

where W is mean plant weight, or some other measure of plant size

k_4 is a constant

The constant, k_4, is dependent on the space available to each plant
under competitive conditions and will be influenced by regeneration
pattern, density per unit area and the genetic properties of each
plant (White and Harper 1970). The relationship of k_4 to the
distance to nearest neighbour statistic, α_i, can be presented as

follows :

$$\alpha_i = \Pi \rho \ \bar{\omega}_i$$

(23)

where $\bar{\omega}_i$ is the mean squared distance to nearest neighbour.

Following White and Harper (1970) we assume that the volume of environmental space available to a tree, V, is directly proportional to $\bar{\omega}_i$, therefore:

$$V \propto \bar{\omega}_i^{3/2} = (\alpha_i \ / \ \Pi \ \rho \ )^{3/2}$$

(24)

and since plant weight, W, is proportional to the volume of environmental space:

$$W = k_5 \alpha_i^{3/2} \Pi^{-3/2} \rho^{-3/2} \qquad \text{or} \qquad W = k_4 \ \rho^{-3/2}$$

(25)

Therefore:

$$k_4 = k_5 \alpha_i^{3/2} \Pi^{-3/2}$$

(26)

where α_i is the pattern constant, which approaches one in random populations and decreases as aggregation increases

k_5 is a constant relating plant weight to the physical growing space.

In random populations α_i may remain relatively constant (Kent and Dress 1979). Plant size increases until the maximum k_4 value is approached and then thinning ensues. Plant size is then near the maximum for the space available. In aggregated populations spatial pattern tends toward random as thinning proceeds. In the populations of this study density will apparently begin to decrease in some parts of the stand long before the maximum k_4 value for the species is reached (Fig. 15). Since the space available varies between plants in an aggregated population, individual plants or small groups of plants reach the maximum size for the available space at widely different times. The resulting competition initially induces a plastic response, reducing mean plant size as we will demonstrate. Eventually competition induced mortality alters spatial pattern and hence the space available to the remaining plants.

The size-density relationship in a stand and its development are a product of the initial stand density, growth conditions and stand age. At the first measurement, at age 30, there was a variation in mean tree size for a given density even among plots in the same stand. For the subset of 17 plots for which the pattern statistic is available, mean tree size at age 30 is predicted by the equation:

$$\ln(V) = k_6 - .411 \ln(N) + .156 \ln(\alpha_i)$$
$$\quad\quad\quad\quad\quad (.075) \quad\quad\quad (.082)$$

$$R^2 = 0.81$$

$$(27)$$

where k_6 is 1.99 (0.30) at Acheron,

. -0.438 (0.091) at Hardy's Creek,

-0.52 (0.12) at Mt. Monda

V is estimated mean total stem volume in m^3

Within any stand, as aggregation increases (i.e. as α_i decreases) mean tree size decreases for a given density.

Under some conditions competition-induced mortality will result in a random or even uniform, spatial pattern and hence the general maximum size-density relationship will be reached. However in some stands the pattern may remain non-random (Fig 3). Where part of the stand is unoccupied due to extreme aggregation, the average plant size for the total space available will decrease. In this situation the maximum k_4 value, representing the maximum size-density condition will never be reached.

Evidence of the relationship between local competition and spatial pattern can be gained from a study of neighbouring trees. In all the stands in this study there was a significant positive relationship between the sum of the diameters of neighbouring trees and the distance between them (based on measurements at the start of the measurement period). As Pielou (1960) concluded, such a relationship between distance to the nearest neighbour and the sizes

of neighbouring plants strongly supports the hypothesis that the pattern results, in part at least, from competition between the individuals. We have already shown that, conversely, the growth of the trees is dependent on the distance to the nearest neighbour (see Table 5).

CONCLUSION

The individual tree and whole stand growth and development observed in this study are the result of intense but variable competitive stress. The responses are the product of the stand densities, the spatial patterns and the species and site characteristics.

Contagious spatial patterns result in a variable pattern of competition within a stand. One effect on some trees is to increase their chances of suppression and mortality. Much of our understanding of competition is based on the study of herbaceous plants under controlled conditions (Harper 1977). Even there, useful measures of interplant competition are generally lacking (Mead 1979). Ford (1975) has suggested that the mechanism of competition differs between forest crops and annual plants. He observed a distinct class of smaller plants, with uniformly low relative growth rates, in populations of Picea sitchensis but not in populations of the herbaceous species, Tagetes patula . This class of smaller plants is apparently made up of those plants which are overtopped but can maintain their crowns and continue production at a low level through their ability to replace their photosynthetic tissues. Suppressed trees of ash-type eucalypts can produce epicormic shoots which help them to maintain some foliage cover, useful with the canopy structure in these stands. The pendant leaves of these eucalypts, and the characteristic separation of their crowns allow high light intensities to penetrate even fully-stocked stands (Ashton 1976).

There are other trees which will remain open grown throughout their lives.

The rate of development of a population in terms of change in mean size and density is an indicator of the intensity of competition within it. It has been found, for example (Harper 1977), that stands on better quality sites begin thinning earlier and thin more rapidly than those on poorer sites. We suggest that for stands of the same density aggregation also speeds the onset of thinning. Ford (1975) proposed that the rate of change of mean plant size with change in density is dependent on "the dynamics of the competition mechanism". A steeper gradient indicates increased efficiency of growth per unit area. If aggregation is reducing this gradient i.e. causing thinning to start at lower densities, then aggregated stands are, as we might expect, less efficient. Dominant trees have been found to be the more efficient plants in a population (Ford 1975, Hamilton 1969). Considered alone they have a steeper size-density gradient. The lower efficiency of aggregated populations is obviously associated with the higher proportion of suppressed stems they produce. Since interplant distances vary greatly within an aggregated population it is characterized by great variability in tree survival and growth.

The high proportions of suppressed trees are associated with the high local densities in some regions of these stands. These high densities, in combination with the incomplete occupancy of the site, serve to reduce net production of stem volume. The roots of E. regnans have been observed to spread as far as 11.3 m into open

areas (Ashton 1975) but since the factor limiting growth is more often light than moisture (Ashton 1976), open patches result in reduced net production. The high proportion of suppressed stems and incomplete occupancy of the site result in stands which are understocked at least in terms of productive crop trees. Although average tree size is greater on the plots with lower densities (Fig. 15) these plots carry much less volume per unit area than the more densely stocked regions even at age 41. The reduction in yield with increasing intensity of aggregation has been demonstrated elsewhere (Braastad 1983) and attributed to these two factors.

The high densities common in ash stands in Victoria may be unusual in many managed forests. The distinct segregation into crown classes seen here may be characteristic of intolerant species, in which, nevertheless, the suppressed trees are persistent (Opie et al. 1978). However, Mohler et al. (1978) demonstrated some bimodality in the diameter distributions of both fast growing, successional pin cherry and strongly shade-tolerant balsam fir. Ashton (1976) observed bimodality in the diameter distributions of fully stocked stands of E. regnans which presumably had spatial patterns with little or no contagion.

Opie et al. (1978) propose that where suppressed trees comprise a significant proportion of the trees in a stand, stand descriptions for management purposes should focus on the upper crown classes. In stands with contagious spatial patterns the suppressed class is a significant but variable component. In contrast, the dominants show

little variability in terms of size or numbers. Detailed description of all the various stand components will therefore be of even more value in these heterogeneous stands. In making predictions of individual tree growth and mortality, a classification of the trees into crown classes, or other measures of the trees' competitive positions such as crown ratio and basal area in smaller and larger trees will be very useful.

BIBLIOGRAPHY

Ashton, D. H. (1975). The root and shoot development of Eucalyptus regnans F. Muell. Aust. J. Bot. 23, 867-887.

Ashton, D. H. (1976). The development of even-aged stands of Eucalyptus regnans F. Muell. in Central Victoria. Aust. J. Bot. 24, 397-414.

Askew, G. R. (1983). Two methods for evaluating spatial pattern in naturally regenerated loblolly pine stands. Forest Sci. 29(3), 514-518.

BMDP (1983). BMDP statistical software, 1983 printing with additions. University of California Press.

Braastad, H. (1983). (Yield level in Picea abies stands with low initial density and irregular spacing). Norwegian For. Res. Inst., Research Paper 7/83.

Clark, P. J., Evans, F. C. (1954). Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology 35(4), 445-453.

Cox, T. F., Lewis, T. (1976). A conditioned distance ratio method for analyzing spatial patterns. Biometrika 63(3), 483-491.

Cremer, K. W., Cromer, R. N., Florence, R. G. (1978). Stand establishment in "Eucalypts for wood production", Hillis, W. E., Brown, A. G., Eds., CSIRO, Australia.

Daniels, R. F. (1978) Spatial patterns and distance distributions in young seeded Loblolly Pine stands. Forest Sci. 24(2), 260-266.

Daniels, R. F., Burkhart, H. E., Spittle, G. D., Somers, G. L. (1979). Methods for modeling individual tree growth and stand development in seeded loblolly pine stands. V.P.I.S.U. Publication FWS-1-79. Blacksburg, Virginia.

Drew, T. J., Flewelling, J. W. (1979). Stand density management: an alternative approach and its application to Douglas-fir plantations. Forest Sci. 25(3), 518-532.

Ford, E. D. (1975). Competition and stand structure in some even-aged plant monocultures. J. Ecol. 63, 311-333.

Furnival, G. M. (1961). An index for comparing equations used in constructing volume tables. Forest Sci. 7(4), 337-341.

Greig-Smith, P. (1952). The use of random and contiguous quadrats in the study of the structure of plant communities. Ann. Bot. N.S. 16(62), 293-316.

Greig-Smith, P. (1979). Pattern in vegetation. J. Ecol. 67, 755-779.

Hamilton, D. A. (1974). Event probabilities estimated by regression. USDA Forest Service. Research Paper INT-152.

Hamilton, G. J. (1969). The dependence of volume increment of individual trees on dominance, crown dimensions and competition. Forestry 42, 133-144.

Harper, J. L. (1977). Population biology of plants. Academic Press, London etc., 892 pp.

Hopkins, E. R. (1968). Fluctuations in the girth of regrowth eucalypt stems. Aus. For. 32, 95-110.

Kent, B. M., Dress, P. (1979). On the convergence of forest stand spatial pattern over time: the case of random initial spatial pattern. Forest Sci. 25(3) 445-451.

Mead, R. (1971). Models for interplant competition in irregularly distributed populations. Statistical Ecology, Vol. 2. Penn. State University Press, College Park, Penn.

Mead, R. (1979). Competition experiments. Biometrics 35, 41-54.

Mohler, C. L., Marks, P. L., Sprugel, D. G. (1978). Stand structure and allometry of trees during self-thinning of pure stands. J. Ecol. 66, 599-614.

Mountford, M. D. (1961). On E. C. Pielou's index of non-randomness. J. Ecol. 49, 271-275.

Noone, C. S., Bell, J. F. (1980) An evaluation of eight intertree competition indices. Oregon State U., For. Res. Lab., Res. Note 66.

Opie, J. E., Curtin, R. A., Incoll, W. D. (1978). Stand management in "Eucalypts for wood production", Hillis, W. E., Brown, A. G., Eds., CSIRO, Australia.

Payandeh, B. (1970). Comparison of methods for assessing spatial distribution of trees. Forest Sci. 16, 312-317.

Pielou, E. C. (1959). The use of point-to-plant distances in the study of the pattern of plant populations. J. Ecol. 47, 607-613.

Pielou, E. C. (1960). A single mechanism to account for regular, random and aggregated populations. J. Ecol. 48, 575-584.

Pielou, E. C. (1969). An introduction to mathematical ecology. Wiley-Interscience.

Stiell, W. M. (1982). Growth of clumped vs. equally spaced trees. For. Chron. 58, 23-25.

White, J., Harper, J. L. (1970). Correlated changes in plant size and number in plant populations. J. Ecol. 58, 467-485.

West, P. W. (1981). Simulation of diameter growth and mortality in regrowth eucalypt forest of southern Tasmania. Forest Sci. 27(3), 603-616.

Wyszomirski, T. (1983). A simulation model of the growth of competing individuals of a plant population. Ekol. Pol. 31(1), 73-92.