NOTE

DIAMETER GROWTH OF *EUCALYPTUS GRANDIS* UNDER CONDITIONS OF EXTREME SUPPRESSION

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ABSTRACT

Investigation of *Eucalyptus grandis* Maiden stands under conditions of extreme suppression indicated that diameter growth of dominant individuals continues even when that of suppressed individuals ceases altogether and mean diameter growth of the stand is minimal. An increase in the mean diameter of the suppressed stand is due to a real increase in the size of the mean tree and is not merely an artifact of mortality amongst the lower size classes.

Keywords: spacing; correlated curve trend; diameter growth; stand density; tree competition; suppression; *Eucalyptus grandis.*

INTRODUCTION

Diameter growth (as represented by the quadratic mean calculated from all live trees) in very dense stands of *Eucalyptus grandis*, is very rapid during early years and then the rate of increase slows, as is characteristic of most species. After competition-induced mortality makes additional growing space available, the rate of diameter growth increases again. In the most dense treatments of a spacing trial in *E. grandis*, the rate of increase appeared to have essentially ceased before resumption. The subsequent acceleration implied a second inflection in the growth curve. Scrutiny of the mean diameters of three replications of the experiment showed that diameter growth had ceased for all practical purposes by the end of the twelfth growing season (Fig. 1). Mean dbh for those treatments was 139 mm, and the Chapman-Richards model indicated an approximate asymptotic dbh of 167 mm. By contrast, the "free-growing" trees in another treatment had already attained a mean dbh of 519 mm. Stand density in the very dense plots represented an extreme stocking and the relative spacing had reached 0.05, this being the asymptotic minimum recorded for the

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species at Langepan by Bredenkamp & Burkhart (1990). The extreme stocking resulted in competition-induced mortality of 49.8% by the twelfth year (Fig. 2). An investigation was undertaken to ascertain whether dbh growth of trees which survived really had ceased for a period between the twelfth and fourteenth growing seasons and, if not, how such growth was distributed.

THE STUDY

The data emanate from a correlated curve trend (C.C.T.) experiment in *E. grandis* established at Langepan on the coastal plain of Zululand in 1952. The database provided by these trials has been described by Bredenkamp (1984). For this study the data from the most dense treatments (which had been planted at 6726 stems/ha and left unthinned) from the measurements of July 1964 and November 1968 were selected to test the hypothesis that the small (c. 17 mm) measured increase in quadratic mean dbh between the ages of 11 years 10 months and 16 years 2 months in *E. grandis* planted at extremely dense stocking levels was a real increase in the population mean and not merely an artifact of mortality in the smaller dbh classes. Truncation of the lower part of the diameter distribution would, by definition, result in an increase in mean dbh. A second associated null-hypothesis was that there was no increase in variation of dbh over the interval. The null hypotheses thus imply that there was neither a positive location shift in mean dbh nor an increase in dispersion of dbh for the 4 years between measurements. In the normal course of events both the mean dbh and the variance of the dbh distribution would be expected to increase over time.

It must be noted for purposes of statistical analysis that the data are not independent. Under conditions of extreme suppression the smaller trees will be more adversely affected than the larger trees. Between-tree competition is asymmetric and the growth of the smaller of any pair of adjacent trees is depressed more than the growth of the larger. As asymmetric competition intensifies, the smaller trees lose vigour and the size inequality expands (Brand & Magnussen 1988). Further sources of lack of independence in the data include repeated measures on the same trees, environmental or site variables, and genetic correlations. Considerable dependence can thus be assumed, and this imposes a need for use of distribution-free methods.

The investigation used paired samples, where the pair was made up by matching the dbh of the i^{th} tree at the beginning of the interval with dbh of the i^{th} tree at the end of the interval; thus, pairs were formed on a per-tree basis. This means that those trees which succumbed during the interval between measurements were excluded from the sample. The distribution of differences between matched pairs was highly skewed to the right (Fig. 3). The very pronounced peak at zero indicated that a large proportion (138/357) of the trees did not grow in girth over the interval. A scatter plot of the data (Fig. 4) clearly indicates that only the larger trees increased in size and thus deviated from the zero-growth line of the null hypothesis. Use of Kolmogorov-Smirnoff (Hollander & Wolfe 1973) provided very strong evidence (DNS=3.37) against the null hypothesis of a Gaussian distribution. This was reinforced by the distribution-free test for symmetry (U=0.44) of Randles *et al.* (1980) and it was apparent that normal parametric procedures would be inappropriate for the study.

The sign test and Wilcoxon's signed rank test (Hollander & Wolfe 1973) provided the means to strongly reject the null hypothesis that the median difference between the 1964 and

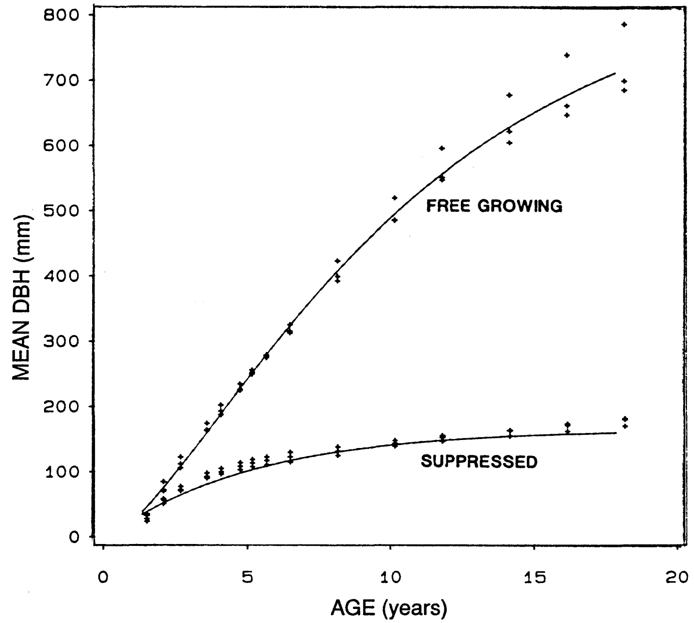

FIG. 1–Diameter development of free-growing and suppressed stands of *Eucalyptus grandis* in Zululand.

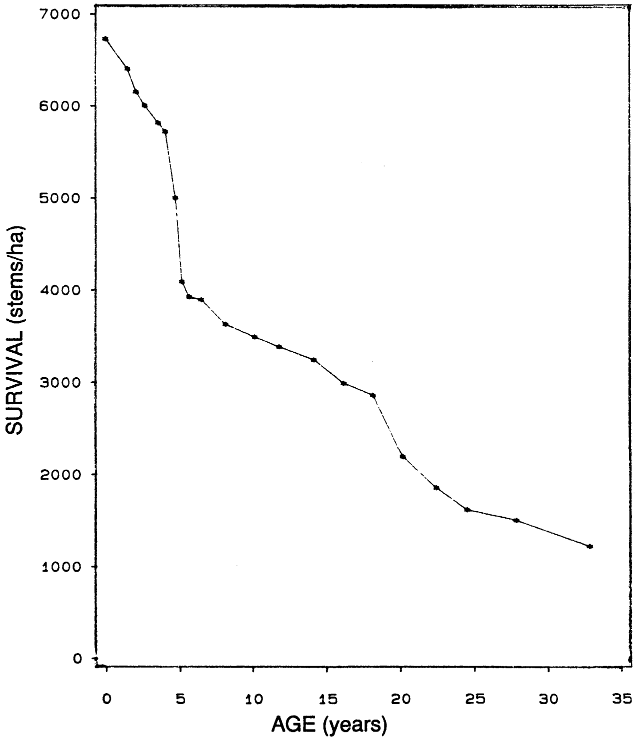

FIG. 2–Survival in suppressed stands of *Eucalyptus grandis* in Zululand.

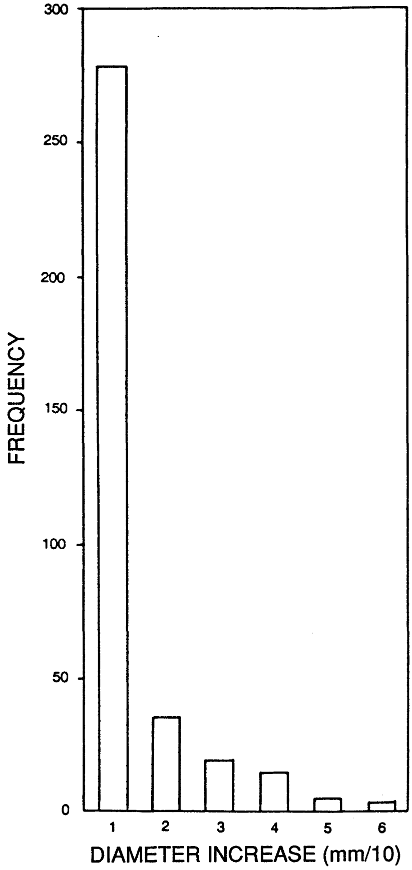

FIG.3–Frequency distribution of differences in dbh measured over the interval in question. The first column includes 138 zero values.

1968 measurements was zero and it was concluded that mean dbh did indeed increase significantly over the interval. The Hodges-Lehman (Hollander & Wolfe 1973) estimate of the median increase is 26 mm which is enclosed by a 95% confidence interval of (25.5, 27.5) mm, with this confidence interval being estimated nonparametrically. The large sample thus made possible the specification of an extremely narrow confidence interval for the increase. Note that the median increase is 50% more than the mean increase of 17.3 mm. As only surviving trees were included in the sample, the recorded increase in mean dbh is based on net stems, and this indicates a real increase in the population mean dbh, and not merely a manifestation of variation change within a population where the mean has remained constant or changed very little. The tests above, together with the scatter plot of differences (Fig. 4) illustrate this argument.

Dispersion changes, as well as location differences, are important as this has a major influence on the product mix from a stand of trees. The Moses rank-like test (Hollander & Wolfe 1973) for equal dispersion in paired samples provided very strong evidence ($p=0.0002$) that the variance in dbh increased over the specified interval.

These results indicate that real diameter growth did occur, at least among the larger trees, under conditions of extreme suppression. During the interval of interest, stand density dropped from 3377 to 2982 stems/ha on average across replications (Fig. 2). This is an 11.7% loss in stems. Growth under such conditions results in very steep slopes of Reineke's SDI and Yoda's self-thinning line for *E. grandis* (Bredenkamp & Burkhart 1990). However, the smaller trees did not increase in size and as a result variability in the diameter distribution increased. This provides additional evidence against too-high stocking rates for *E. grandis* for crops other than pulpwood (Bredenkamp & Schutz 1984), which result in stands being less uniform in terms of diameter distribution.

A second question concerning diameter growth under conditions of intense competition is the apparent surge in diameter growth after significant mortality within the densest stands. This precluded use of the Chapman-Richards model to describe the further diameter development with age when dbh growth continued beyond an ostensible asymptote (Bredenkamp & Gregoire 1988).

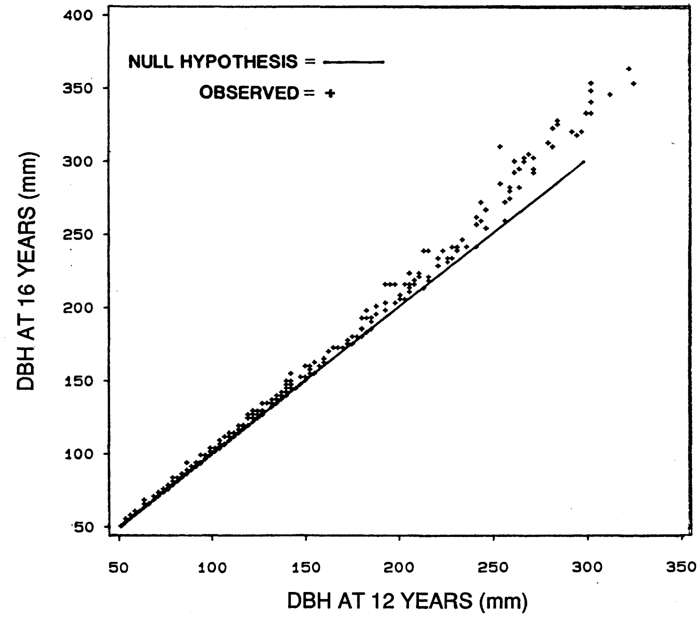

FIG. 4—Plot of dbh at the beginning of the interval against dbh at the end of the interval. The diagonal indicates the null hypothesis of zero growth.

Quadratic mean dbh is by definition determined with stem count of the sample in the denominator of the equation. Mortality in the smallest degree must reduce the denominator and, by the mere definition of the parameter, increase mean dbh (obviously the numerator is also reduced but mortality is concentrated in the lower quartile of the diameter distribution and the trees which die are typically smaller than the mean tree).

Whether there was an upswing in dbh growth over and above this artificial increase was investigated by comparing the trends of mean diameter growth from a single population defined in two different ways. The bench-mark was provided by the quadratic mean dbh, determined in the normal fashion, based on all trees found alive at each measurement. By contrast, the second set of quadratic mean dbh estimates was based solely on those trees which survived until the most recent measurement. This means that the denominator in the definition formula is a constant through the life of the stand in the second set. The population of diameters in both calculations consisted of the arithmetic means across replications of quadratic mean diameter for each measurement (Fig. 5). The means based on the surviving trees were consistently higher but the difference diminished with time as the samples on which the means were based became increasingly more similar. Mean dbh continually increased but there was no indication of an upswing which could be ascribed to anything over and above normal diameter growth. The dbh/age trend was virtually linear with a small bulge at 22 years. This deviation from the linear occurred at a time when there was an exceptional amount of mortality (*see* Fig. 2) which followed nearly a decade of below-average rainfall.

There is no evidence that rate of diameter growth was related to the increase in growing space resulting from mortality, and the development of stand basal area did not show a marked decrease in rate of growth over the interval in question.

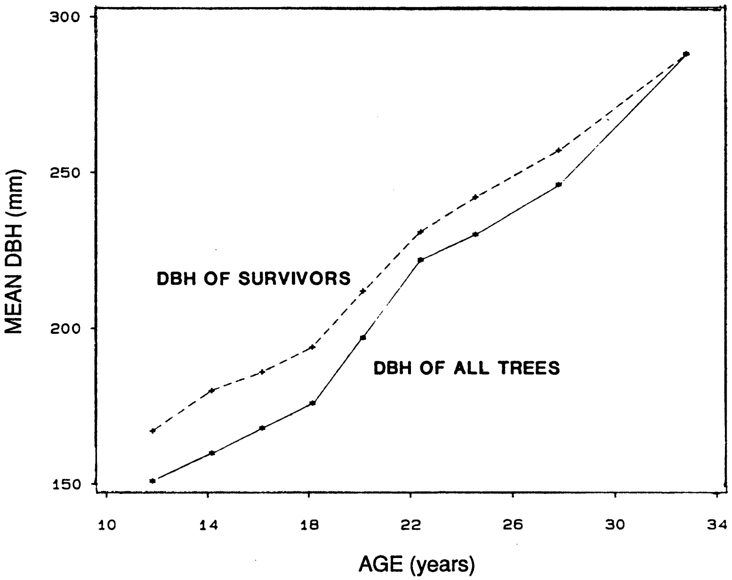

FIG. 5–Mean diameter development under conditions of extreme suppression. The upper line shows means based only on those trees which survived until the most recent measurement. The lower is based on all trees alive at each measurement.

CONCLUSION

It is concluded that mean diameter growth of dominant trees continues despite very high degrees of competition and the rate of growth of the dominant trees is not markedly affected by increased growing space made available through the mortality of suppressed trees. With severe competition the smaller trees cease diameter growth altogether, although they need not all succumb. Increased mean diameter can thus be attributed to growth of dominant trees alone. The result is an increase in the spread of diameters together with an increase in mean dbh of the stand.

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