

GROWTH AND SURVIVAL OF EUCALYPTUS GRANDIS — A STUDY BASED ON MODELLING LIFETIME DISTRIBUTIONS

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ABSTRACT. The objective of this study is to analyse the density-dependent dynamics of growth and mortality in an unthinned *Eucalyptus grandis* spacing experiment on a homogenous site in Zululand/South Africa. Specifically we propose models that describe how the (log) basal area develops in unthinned stands. Our data clearly indicate that mortality varies enormously with planting density. We therefore develop and investigate models that explicitly take mortality into account. To do so we first model the conditional distribution of log basal area as a function of age and the number of trees that are concurrently alive. The last of these covariates is generally unknown in advance, which would seem to render it inapplicable for the purpose of modeling the distribution of future basal area. We show how it is nevertheless possible to estimate the distribution of the number of surviving trees from the available data, and thereby to ‘integrate out’ the effect of this random variable in order to estimate the (unconditional) distribution of the log basal area for each planting density. This is achieved by fitting Weibull distributions to the lifetimes of the trees in the four available plots. A number of different models for the log basal area are compared.

Our estimates indicate that the distribution of the future basal area in an unthinned *Eucalyptus grandis* forest is not independent of the planting density, within the range of the experimental densities investigated in this study. Our results provide clear evidence that planting density has strong and long-lasting effects on basal area. Furthermore the estimates indicate that these effects persist for at least 40 years and that, even after length of time, the rate of convergence to a common condition is very slow.

Keywords: Planting density, spacing experiment, Weibull distribution, basal area growth

1 INTRODUCTION

The effect of planting density on the growth and survival of trees has been the subject of numerous studies. Neighbouring trees compete with their crowns as well as their roots for the available growing space. To survive in a competitive environment a tree must build up and maintain phytomass in order to access resources in the occupied growing space (Matyssek, 2003). Tree density affects the spatial distribution of light and temperature, and the availability of moisture and nutrients in a forest. Tree diameter growth is especially sensitive to changes in density. This effect was first demonstrated by Craib (1939) in an analysis of a South African *Correlated Curve Trend* (CCT)-spacing trial.

The CCT experiment is a classic spacing trial designed to predict the growth in plantations of various species of

pine and eucalyptus for a wide range of planting densities, varying between extremely dense (2965 stems per ha) and free growth (124 stems per ha). The majority of these CCT experiments were devised by O’Connor (1935) and initiated in 1936 and 1937. The typical CCT experiment consists of 18 plots, covering 0.04 ha each, some with up to four replications. Nine of the 18 plots were left unthinned, the other nine were subjected to various thinning regimes. Detailed descriptions of the design and analysis of the CCT studies were published by Marsh (1957), O’Connor (1960), Burgers (1976), Van Laar (1982), Bredenkamp (1984), Gadow (1987) and Gadow and Bredenkamp (1992). The effects of site quality and stand density on tree growth may be confounded. Thus, controlled experiments on a uniform site are useful if the aim is to study the effect of density on tree growth.

The objective of this study is to analyse the density-dependent dynamics of growth and mortality in four experimental plots planted at different spacings on a homogeneous site. Particular emphasis will be placed on estimating the (unconditional) distribution of stand basal area using a model that explicitly takes account of the probability of tree survival.

2 MATERIAL AND METHODS

This section presents the complete dataset used in this study and explains the modelling approach and the methods of model evaluation.

2.1 The dataset The material used in this study was derived from the *Eucalyptus grandis* spacing experiment “Langepan” which was established in September 1952 on the coastal plain of KwaZulu-Natal in South Africa, located at 28°36' S and 32°13' E. The altitude is about 60m above sea level. The mean annual rainfall on the experimental site is 1400mm, of which about 70% falls during the months of October to April. The coastal plain is an elevated marine platform, which consists essentially of a thick deposit of wind-borne sand. The sands are acidic and poor in organic matter due to rapid decomposition in the moist sub-tropical climate and the aerobic condition of the surface soils. The moisture storage capacity is very low, but this shortcoming is moderated by great rooting depth. The mean annual temperature is 21.8°C. Frost is virtually unknown along the coastal plain.

The design of the Langepan experiment is a modification of the standard CCT spacing experiments which were planted throughout the forestry regions of South Africa. The most important modification is the very high planting density of 6726 trees per ha in Plot 1. The Langepan experiment is a randomized complete block design with three blocks and twenty treatments. Twelve of these are unthinned spacing treatments, representing the so-called basic series. The remaining eight treatments were subjected to different types of thinnings and are known as the *thinning* series. Additional detail is given by Bredenkamp et al. (2000). Currently only one of the original three blocks remains. Four plots of the *basic* series, which are still intact, were selected for the present study. Each plot covers an area of 0.04047 ha and is surrounded by a buffer strip (30m around each measurement plot) which is subject to the same treatment as the plot.

The complete dataset used in this study is presented in Table 1. For analysis standardised data per ha were used. The number of surviving trees per ha are displayed in Figure 1.

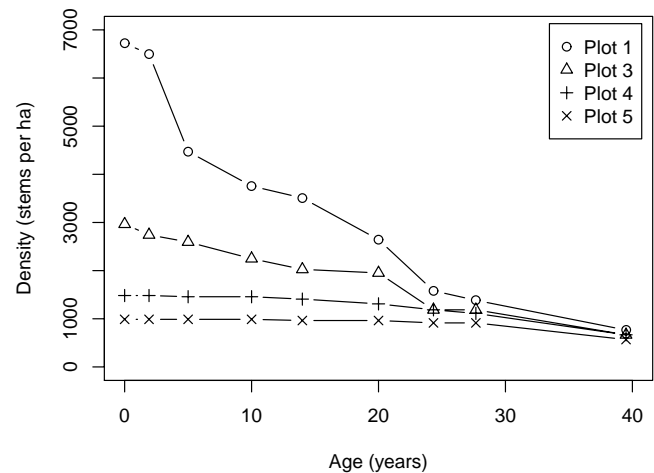


Figure 1: Observed density (stems per ha) as a function of age.

2.2 Modelling Approach One of the traditional methods used in the analysis of forest growth and tree survival is based on the state-space approach described by García (1994), where the system is characterized by a set of state variables which are assumed to be known at a given initial stage; transition functions are used to project all or some of the state variables to future stages. In selecting the state variables, the principle of parsimony must be taken into account. This means that the model should be the simplest one among alternative models which are consistent with the dynamics of the biological system (Milsom, 1966; Vanclay, 1995; Gadow, 1996; Burkhart, 2003).

In forests which are thinned ahead of natural mortality, dominant height and stand basal area (G_i) may be sufficient for estimating the system state at a given age (Pienaar and Turnbull, 1973; Decourt, 1974; García, 1988). In unthinned forests, especially those which are planted at high densities, it has been found to be necessary to include tree mortality, maximum density or the number of surviving trees (N_i) per unit area (Amateis et al., 1995; Álvarez-González et al., 1999; García, 2003; Diéguez-Aranda et al., 2006; Castedo-Dorado et al., 2007).

The *Langepan* trial is an unthinned spacing experiment which includes very high planting densities. Thus, tree mortality is a very important component of the biological system. In contrast, height growth is regarded as density independent. The emphasis of the study is density-dependent dynamics of growth and mortality. Thus, height growth is not considered in the analysis

Table 1: The observations. Age (A_i) refers to years after planting, N_i the number of surviving trees, and G_i the basal area (m^2) in the 0.04047 ha plots.

Index	Age	Plot 1		Plot 3		Plot 4		Plot 5	
i	A_i	G_i	N_i	G_i	N_i	G_i	N_i	G_i	N_i
0	0.00	0.00	272	0.00	120	0.00	60	0.00	40
1	1.92	0.52	263	0.33	111	0.22	60	0.12	40
2	5.00	1.62	181	1.43	105	1.32	59	5.00	40
3	10.00	2.29	152	2.06	91	2.07	59	10.00	40
4	14.00	2.68	142	2.39	82	2.43	57	14.00	39
5	20.00	2.94	107	2.86	79	2.85	53	20.00	39
6	24.33	2.87	64	2.74	48	3.00	48	24.33	37
7	27.67	2.82	56	2.92	48	3.07	45	27.67	37
8	39.50	2.80	31	2.93	27	2.95	27	39.50	23

of our data.

As a first approach for estimating basal area we use the linear form of two models that had been applied in the past, designated here as the “Schumacher” and “Rodríguez-Soalleiro” models. Both models use age and initial basal area as explanatory variables. However, in an unthinned spacing experiment, especially one with high planting densities, basal area growth is strongly affected by tree mortality. We therefore introduce an alternative modeling approach which takes account of the number of surviving trees as an additional explanatory variable. The initial age and basal area are assumed to be known, but the number of trees that survive to a given age is a random variable whose distribution can be modelled, which we do using a binomial distribution. Although the initial number of live trees (N_0) is known, the probability that a given tree will survive to the given age has to be estimated. We do this by assuming that the lifetime of the trees follows a Weibull distribution. The parameters of the Weibull distribution, which depend on N_0 , can be estimated (for each N_0 separately) using the method of maximum likelihood. In that way the second parameter of the binomial distribution (‘the probability of success’) becomes available. In turn this allows us to explicitly take into account the variability in the basal area that is attributable to the uncertainty regarding the number of trees that will survive. This source of variation is ignored if one simply uses the *expected number* of trees that will survive in the model for basal area. The latter approach provides a model for the distribution of the basal area under the condition that (precisely) the expected number of trees survive. Our approach provides a model that takes account of all possible survival outcomes (except the case in which no trees survive); in other words it provides a model for the unconditional distribution of basal area.

2.2.1 Models for area growth Traditionally, basal area at time point i (G_i) is estimated as a function of age at time point $i - 1$ (A_{i-1}), the basal area at time point $i - 1$ (G_{i-1}), and one or two other covariates. We denote this as the “initial approach”. The approach proposed here, which we will refer to as the “alternative approach”, is to allow the distribution of basal area to depend on the number of surviving trees at time point i . This number is of course unknown in advance but, as was indicated above, its distribution can be estimated. For the estimation of basal area interval data of successive measurements are used, starting from the age at planting.

Initial approach: Models that do not take account of survival

A straight-forward model to estimate basal area is an age-related model, which was first proposed by Schumacher (1939):

$$\log(G_i) - \log(G_{i-1}) \frac{A_{i-1}}{A_i} = \alpha_1 \left(1 - \frac{A_{i-1}}{A_i} \right) \quad (1)$$

One further model was proposed by Rodríguez-Soalleiro et al. (1995):

$$\log \left(\frac{G_i - G_{i-1}}{A_i - A_{i-1}} \right) = \alpha_0 + \alpha_1 \log(G_{i-1}) + \alpha_2 \log(A_{i-1}) \quad (2)$$

Alternative approach: Models that involve the number of surviving trees

We begin by noting (see Figure 2) that there is an approximately linear relationship between G_{i-1}/N_{i-1} and G_i/N_i , $i = 1, 2, \dots, 8$. From this starting point, and after taking logs, we add two further covariates, namely the age difference, $(A_i - A_{i-1})$, and the square of the

age, A_i^2 . The latter was included following an analysis of the residuals of the model without this term. The resulting model is

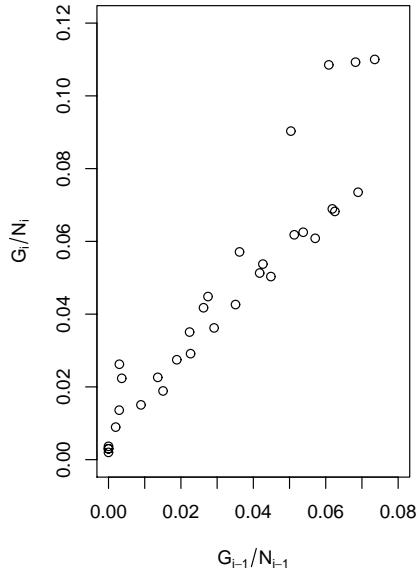


Figure 2: Relationship between the ratios G_{i-1}/N_{i-1} and G_i/N_i .

$$\log(G_i) = \alpha_0 + \alpha_1 \log(N_i) + \alpha_2 \log\left(\frac{G_{i-1}}{N_{i-1}}\right) + \alpha_3(A_i - A_{i-1}) + \alpha_4(A_i)^2 \quad (3)$$

A further refinement of the model would be to include the ratio of the heights at ages A_{i-1} and A_i as an additional covariate. Since the heights are not available, we used a proxy for them, based on a logistic function approximation, to obtain:

$$\log(G_i) = \alpha_0 + \alpha_1 \log(N_i) + \alpha_2 \log\left(\frac{G_{i-1}}{N_{i-1}}\right) + \alpha_3(A_i - A_{i-1}) + \alpha_4(Age_i)^2 + \alpha_5 \log\left(\frac{1 - \exp(k A_i)}{1 - \exp(k A_{i-1})}\right) \quad (4)$$

Finally, we also considered a simplified version of the above model having no time-lagged covariates, i.e. that describes $\log(G_i)$ as a function of only N_i and A_i . Apart from being much simpler, this has the (minor) advantage that it overcomes the problem of dealing with undefined

logarithms¹.

$$\log(G_i) = \alpha_0 + \alpha_1 \log(N_i) + \alpha_2 \log(1 - \exp(k A_i)) + \alpha_3(A_i) + \alpha_4(A_i)^2 \quad (5)$$

We emphasise that, although Models (3)-(5) are conditional on the values of N_i , and although the observed N_i were used to estimate the parameters of these conditional models, we will go on to develop unconditional versions of the models that do not depend on knowing N_i , the number of trees that will survive to age A_i . However, the implementation of the unconditional versions requires an estimate of the parameters of the distribution of N_i , and we now outline how this can be obtained.

2.2.2 Probability distribution for the number of surviving trees Ideally, in order to estimate lifetime distribution of trees planted at a given density, one would like to know the exact age of each tree when it dies. Such information can be used to select a suitable distributional form. However, the data available to us are severely interval-censored. In Plot 1, for example, we only know that 9 trees died in the interval 0 to 1.92 years after planting, 82 died in the interval 1.92 to 5 years after planting, and so on. Secondly, the experiment covers a time-span that is evidently shorter than the maximum lifetime of the trees — many trees were still alive when the last observations were made 39.50 years after planting. These deficiencies in the observations force us to make assumptions regarding the form of the model that describes the lifetime distribution. We selected the Weibull distribution because it is widely used to describe lifetimes, and also because it has only 2 parameters. The cumulative distribution function of the lifetime of the trees is assumed to have the form ($t \geq 0; \gamma, \beta > 0$)

$$P(\text{lifetime} \leq t) = F(t; \gamma, \beta) = 1 - \exp\left(-\frac{t}{\beta}\right)^\gamma \quad (6)$$

The parameters describe the shape (γ) and scale (β) of the distribution. It is assumed that the parameters, and hence the lifetime distribution, depend on the planting density, i.e. on N_0 , and so the parameters are estimated separately for each plot. The parameters are estimated using the maximum-likelihood method which can accommodate interval-censored data.

Let $N_{i,k}$, $i = 0, 1 \dots, 8$; $k = 1, 3, 4, 5$, be the number of surviving trees aged A_i in Plot k (see Table 1), and let $D_{i,k} = N_{i,k} - N_{i-1,k}$, $i = 1, 2 \dots, 8$. Then $D_{i,k}$ is the number of trees in Plot k that died between A_{i-1} and

¹To avoid taking logs of zero in Models (1)-(4) the zero value of G_0 at planting age is replaced by a value slightly above zero.

A_i years after planting. The likelihood function for the two parameters of the Weibull distribution for Plot k , namely γ_k and β_k , is given by (see, e.g., Cox and Oakes, 1984):

$$\begin{aligned}
 L(\gamma_k, \beta_k \mid A_1, \dots, A_8, D_{1,k}, \dots, D_{9,k}) = & \\
 & F(A_1; \gamma_k, \beta_k)^{D_{1,k}} \\
 & \cdot [F(A_2; \gamma_k, \beta_k) - F(A_1; \gamma_k, \beta_k)]^{D_{2,k}} \\
 & \cdot [F(A_3; \gamma_k, \beta_k) - F(A_2; \gamma_k, \beta_k)]^{D_{3,k}} \\
 & \dots \cdot [F(A_8; \gamma_k, \beta_k) - F(A_7; \gamma_k, \beta_k)]^{D_{8,k}} \\
 & \cdot [1 - F(A_8; \gamma_k, \beta_k)]^{N_{8,k}} \quad (7)
 \end{aligned}$$

Note that the last term takes care of the number of trees that are still alive when the last observation was made. There are no explicit expressions for the maximum likelihood estimators; the likelihood has to be maximized using numerical maximization software, such as the function ‘nlm’ or ‘optim’ in the statistical package **R** (Ihaka and Gentleman, 1996).

The parameter estimates, $\hat{\gamma}_k$ and $\hat{\beta}_k$, $k = 1, 3, 4, 5$, are displayed in Figure 3, plotted against the corresponding planting densities (in stems per ha). Also shown are exponential functions that were fitted to these points. This relationship is potentially useful in that it allows one, by means of interpolation, to estimate the parameters of the lifetime distribution for planting densities that are different from those that were investigated in the experiment. In a second estimation pass we therefore estimated these two exponential functions directly from the original data by maximizing a single combined likelihood function. Since the resulting curves did not change much, we will not give details of the second, and more complicated, computation here.

Having estimated the survival distribution as a function of N_0 we are now in a position to estimate the distribution of the number of trees that survive any given age t . Given that there are N_0 trees initially, the number of trees that survive to age t can be regarded as a binomial experiment with N_0 trials. Each trial results in one of two mutually exclusive outcomes, survival and death. The Weibull distribution is used to estimate the binomial parameter, namely the probability that a tree survives longer than t time units, say p_t (also called the ‘probability of success’). The number of surviving trees t time units after planting is binomially distributed random variable with parameters N_0 and $p_t = 1 - F(t; \gamma, \beta)$ where γ and β can be estimated the exponential function displayed in Figure 3 from the known value N_0 . The probability that precisely n of the N_0 trees survive longer than t time units is given by

$$\binom{N_0}{n} p_t^n (1 - p_t)^{N_0 - n}, \quad n = 0, 1, \dots, N_0. \quad (8)$$

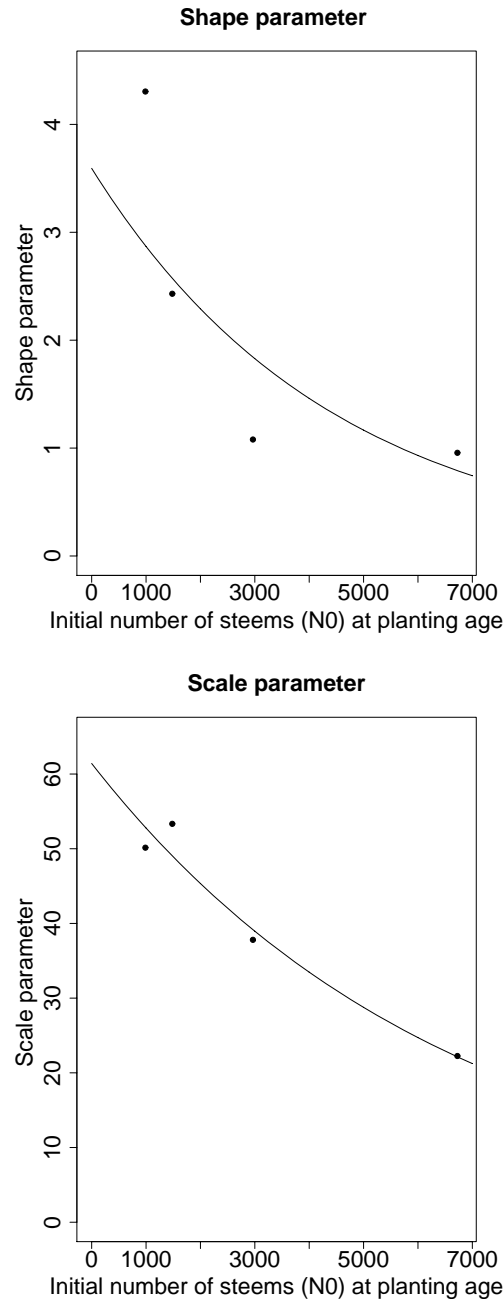


Figure 3: Weibull shape and scale parameters estimated from the number of trees per ha planted.

Thus (and, for simplicity, dropping the subscript k) $N_i, i = 1, 2, \dots, 8$ is binomially distributed with first parameter (the number of trials) equal to N_0 and second parameter (the probability of success) is given by $1 - F(A_i; \gamma, \beta)$.

We note that the conditional distribution of N_i , given N_{i-1} , is also binomial, but the number of tri-

als is N_{i-1} , and the probability of success is given by $1 - F(A_i; \gamma, \beta)/(1 - F(A_{i-1}; \gamma, \beta))$. This probability is computed using a left-truncated Weibull distribution so as to take account of the fact that the N_{i-1} trees have already survived A_{i-1} time units after planting.

2.2.3 Unconditional distribution stand basal area Models (3)-(5), which are based on the ‘alternative approach’, contain the covariate N_i , the concurrent number of surviving trees. These models only describe the *conditional* distribution of $\log(G_i)$ for given values of N_i . We will assume that these conditional distributions are normal and have a constant variance. The *unconditional* distribution of $\log(G_i)$ is then a *mixture distribution*; its density is a weighted sum of conditional (normal) densities taken over all possible values of N_i . The weights are given by the binomial probabilities $P(N_i = n)$. Thus the density of $\log(G_i)$, which is not itself normal, is given by:

$$\sum_{n=0}^{N_0} P(N_i = n) \cdot \phi(E(\log(G_i)|N_i = n, N_{i-1}, G_{i-1}, A_{i-1}, A_i), \sigma^2),$$

where $\phi(\mu, \sigma^2)$ represents the density of a normal distribution with mean μ and variance σ^2 . Although the range of N_i extends from 0 to N_0 , we will omit the term with $n=0$ in the above sum in order to avoid taking the log of zero when computing the unconditional distributions. This is reasonable if A_i is not ‘too large’ or, more precisely, if A_i is such that the probability that *all* N_0 trees will die within A_i years after planting is small enough to be negligible.

The main motivation for considering Models (3)-(5) is to take account of tree survival in the modeling of basal area, because, as is illustrated in Figure 1, the rate of survival in unthinned forests can vary enormously as a function of planting density. One can take survival into account by including N_i as a covariate in the model for basal area. However, having done this, one must then also account for the variability in the distribution of basal area that is attributable to uncertainties regarding how many trees will survive. This can be done by computing the unconditional distribution of the (log) basal area. We note that this is not the same as simply replacing the term N_i in the conditional distribution of $\log(G_i)$ by $E(N_i)$, because the distribution of $\log(G_i)$ is different to that of $\log(G_i|N_i = E(N_i))$. The latter is a normal distribution, whereas the former is a mixture of normals. The mixture distribution has following moments (Frühwirth-Schnatter, 2006):

Expectation:

$$E(\log(G_i)) = \mu \approx \sum_{n=1}^{N_0} P(N_i = j)\mu_n \quad (9)$$

Variance:

$$E(\log(G_i) - \mu)^2 \approx \sum_{n=1}^{N_0} P(N_i = n)(\mu_n^2 + \sigma_n^2) - \mu^2 \quad (10)$$

where μ_n denotes the mean, and σ_n^2 the variance, of the conditional distribution of $\log(G_i|N_i = n)$. We assume that all the conditional variances are equal. The above moments are approximations because we have omitted the summand for $n = 0$.

2.2.4 Model evaluation criteria Three different model selection criteria were applied for comparing the models that describe the log of stand basal area growth. The Bayesian Information Criterion: $BIC = -2\log(L(\hat{\theta})) + \log(n)d$, where $\log(L(\hat{\theta}))$ represents the estimated maximum log-likelihood of the model, n the sample size and d the number of estimated parameters. This affords a balance between the quality of the fit, which is measured by the log-likelihood term, and complexity, as measured by the ‘penalty term’ $\log(n)d$. The model with the smallest BIC is judged best. Akaike’s Information Criterion, $AIC = -2\log(L(\hat{\theta})) + 2d$, has a similar structure but uses a different penalty term. Except for very small samples the BIC applies a more severe penalty for complexity than does the AIC. For a discussion of these criteria see, e.g., Zucchini (2000). We also report values of the residual standard error: $RSE = \sqrt{\hat{\sigma}^2}$, where $\hat{\sigma}^2 = \frac{\sum_i (Y_i - \hat{Y}_i)^2}{\text{degrees of freedom}}$ is the estimated residual variance. In terms of this criterion the model for which RSE is the minimum should be selected (Maddala and Lahiri, 2009).

3 RESULTS

In this section we present the parameter estimates and the results for the models for tree survival and basal area growth that were outlined in the previous section.

3.1 Tree Survival The parameters of the exponential relationship between the Weibull parameters and the number of planted trees per ha are estimated using the maximum likelihood method. The maximization is done using a stochastic global optimization method implemented in the statistical software R (for details see Belisle (1992)). The interval data of successive measurements, all starting from the age at planting, were used,

which gives a total of 32 data points. The estimated exponential function of the shape parameter, γ , and the scale parameter, β , of the Weibull distribution are given by the following functions of N_0 (measured in units of stems per ha):

$$\gamma = 3.5927 \exp(-0.000225 N_0) \tag{11}$$

$$\beta = 61.4138 \exp(-0.000152 N_0) \tag{12}$$

These relationships make it possible to estimate the parameters of the Weibull distribution function for arbitrary planting density in the range 0 to 7000 stems per ha (see Figure 3). The estimated Weibull parameters for each plot of the dataset are shown in Table 2. The Weibull distribution functions for Plots 1,3,4,5 are displayed in Figure 4. It can be seen that the probability that a tree dying in the very dense Plot 1, is initially much greater than in the other, less dense, plots. As expected, the probability of tree survival increases with decreasing number of trees per unit area. Although the distribution functions in Figure 4 are displayed for the age range 0 to 120 years, it has to be kept in mind that the observation interval covered less 40 years. Consequently, the available data do not provide information about the lifetime distribution of trees that are older than 40 years; the extrapolations beyond that age are based on the assumption that the Weibull model continues to hold beyond 40 years. Since this assumption cannot be checked with the available data, the said extrapolations obviously need to be regarded as hopeful approximations.

Table 2: Weibull Parameter estimated for each plot from equations (11) and (12).

	Plot 1	Plot 3	Plot 4	Plot 5
Shape	0.79	1.84	2.57	2.88
Scale	22.14	39.17	49.04	52.87

3.2 Basal area growth The parameters of all models were estimated using linear least squares techniques available in the software environment R. For model estimation successive interval data, all starting from the age at planting, were used.

Table 3 gives the parameters estimates, standard errors, the values of the selection criteria for Models (1) and (2). Table 4 gives a summary of the results Models (3) to (5), all of which use the number of surviving trees as covariate.

The results clearly indicate that the models which use the number of surviving trees as covariate, i.e. Models (3)-(5), lead to much better fits than do those that

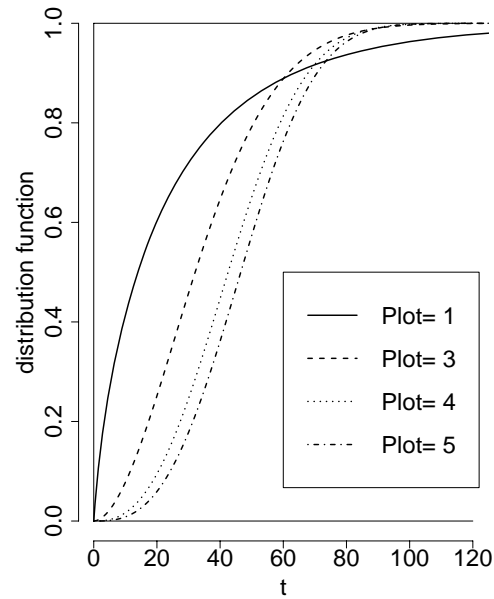


Figure 4: Graph of the cumulative Weibull distribution functions for different initial stem numbers at planting.

do not, namely Models (1) and (2). All three model selection criteria, given in Tables 3 and 5, are substantially lower for the models in the first group. Within the group (3)-(5), Model (3) is judged worst by all three criteria. The RSE of Model (4) and (5) are very similar and Model(5) has the lowest AIC and BIC values. Since Model (5) is also the simplest of the three it is the model used in the following section.

Table 5: Values of the model selection criteria for Models (3) - (5).

Model	RSE	AIC	BIC
(3)	0.180	-12.29	-3.50
(4)	0.164	-17.47	-7.21
(5)	0.165	-17.91	-9.12

3.3 Unconditional distribution $\log(G_i)$ The unconditional distribution of $\log(G_i)$ is the weighted sum over all possible values for N_i of the conditioned distributions of $\log(G_i|N_i = n)$. Figure 5 displays the estimated unconditional distributions for Plots 1,3,4,5 for four different ages, namely 10, 20, 24.33 and 30 years. The horizontal lines depict the observed values, $\log(G_i)$, which we have been modelled as realizations from their respective distribution, all fall well ‘inside’ their distribu-

Table 3: Results for Models (1) and (2): the estimated parameter values and goodness-of-fit statistics.

Model (1), Schumacher (1939)		Model (2), Rodríguez-Soalleiro (1995)	
$\hat{\alpha}_1 = 3.0979$ (Std. Error 0.2417)***		$\hat{\alpha}_0 = -0.7470$ (Std. Error 0.7020)	
		$\hat{\alpha}_1 = 1.1993$ (Std. Error 0.5525)*	
		$\hat{\alpha}_2 = -1.3565$ (Std. Error 0.6001)*	
RSE = 0.6727		RSE = 1.076	
AIC = 68.42	BIC = 71.35	AIC = 82.41	BIC = 88.28
Stat. significant:*** at 0,1% level, ** at 1% level, * at 5% level, · at 10% level			

Table 4: Estimated parameters model (3), model (4) and model (5).

Model	α_0	α_1	α_2	α_3	α_4	α_5
	0.7958	0.4912***	0.1255***	-0.0288	0.0006***	
(3)	(0.5576)	(0.0735)	(0.0.0061)	(0.0208)	(0.0001)	
	0.3697	0.6267***	0.2911***	-0.0207	0.0006***	0.2055*
(4)	(0.5346)	(0.0854)	(0.0650)	(0.0192)	(0.0001)	(0.0804)
	3.1597***	0.3823***	2.0161***	-0.0928***	0.0015**	
(5)	(0.6069)	(0.0667)	(0.1689)	(0.0237)	(0.0004)	

Values of standard errors given in parenthesis.

Stat. significant: *** at 0,1% level, ** at 1% level, * at 5% level, · at 10% level

tion for the respective age; none of the realizations fall in an extreme tail. Note that there are no horizontal lines for the case $A_i = 30$. That is because no observation was made at that age. This illustrates the point that, despite the fact that the number of trees that were alive 30 years after planting is unknown, it is possible nevertheless to estimate the distribution of the log basal area for stands of that age using Model (5). Table 6 presents the expected values and the standard deviations of the fitted unconditional distributions for the ages covered in Figure 5.

We remark on some features of the estimated properties of the unconditional distributions, some of which are given in Table 6.

- The variance remains nearly constant with increasing age. It seems to be independent of the planting density.
- As might be expected, each different planting density leads to a different unconditional distribution for basal area and the differences are substantial in the first few years. Somewhat surprising is that these differences seem to persist. Our estimates indicate that, if convergence to a single distribution occurs, then it takes longer than 40 years before the effects of planting density become small.
- The estimated mean log basal area for Plots 1 and 3, which have the higher planting densities, increases

over the first 20 years and then remains approximately constant, whereas it increased monotonically in Plots 4 and 5. Presumably this is consequence of higher tree mortality, combined with a reduced diameter growth rate in Plots 1 and 3.

4 DISCUSSION

The objective of this study was to analyse the density-dependent tree mortality and stand basal area growth in four unthinned plots planted at different densities on a homogeneous site. The complete dataset is presented, thus allowing researchers to invent and to test alternative approaches for modeling these data. These data clearly show that planting density has an enormous effect on the lifetime distribution of trees. The survival rate of trees in the high-density plots was much lower than in plots with lower density. That being the case it seems necessary to take mortality into account when modeling basal area as a function of planting density. The particular methods used in this study are specific to unthinned plots (Clutter and Jones, 1980; Cieszewski et al., 2000). This study has shown that estimation of the distribution of the log basal area can be considerably improved by including the number of surviving trees as covariate in the model. We have shown how one can circumvent the difficulty that the value of this covariate is not known in advance; one simply regards the unknown number as a random variable whose distribution can be estimated. The approach can then also be used to esti-

Table 6: Expected values and standard deviation (in brackets) of the estimated unconditional distribution of log(Stand Basal Area) for four different ages and four different planting densities. Note that no data were available for age $A_i = 30$.

	Plot 1	Plot 3	Plot4	Plot5
$A_i = 10$	4.28(0.15)	4.14(0.15)	3.90(0.15)	3.75(0.15)
$A_i = 20$	4.44(0.16)	4.37(0.15)	4.17(0.15)	4.03(0.15)
$A_i = 24.33$	4.42(0.16)	4.36(0.15)	4.19(0.15)	4.06(0.15)
$A_i = 30$	4.42(0.16)	4.36(0.16)	4.22(0.16)	4.10(0.16)

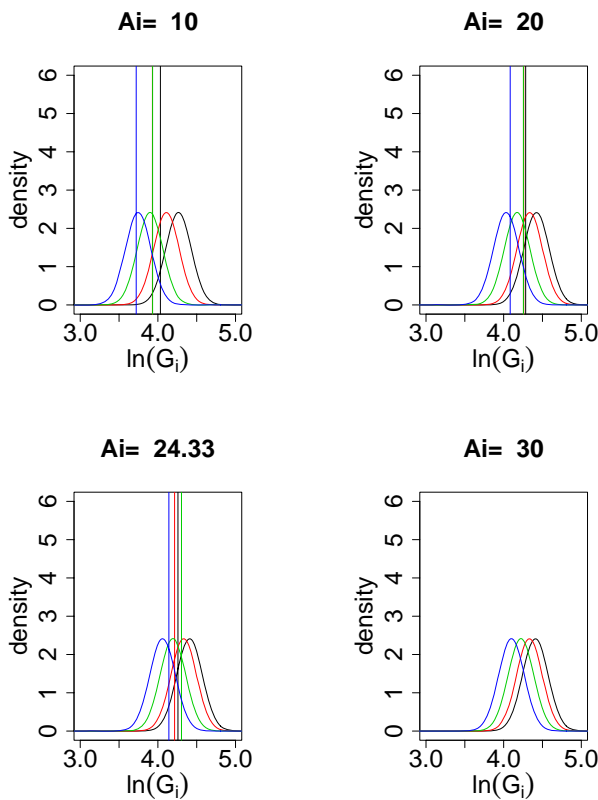


Figure 5: Unconditional distributions Black: Plot 1, red: Plot 3, green: Plot 4, blue: Plot 5 Vertical line: observed values at A_i .

mate the unconditional distribution of the log basal area for any planting density within a specified range.

The Langsaeter hypothesis (Langsaeter, 1944) states that the total volume production in a stand of a given age, composition and site is, for all practical purposes, constant for a wide range of density of stocking. The results of this study do not support this hypothesis (see Gilmore et al., 2005 and Zeide, 2004). The distribution of the future basal area in an unthinned *Eucalyptus*

grandis forest on the Zululand coastal plain is not independent of the planting density, within the (rather wide) range of the experimental densities investigated in this study. The results presented here provide clear evidence that planting density has strong and long-lasting effects on basal area. Our estimates indicate that these effects persist for at least 40 years and that, even after length of time, the rate of convergence is very slow.

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