

Modelling individual tree growth from data with highly irregular measurement intervals

Thomas Nord-Larsen*

Royal Veterinary and Agricultural University, Forest & Landscape
Hørsholm Kongevj 11, DK-2970 Hørsholm, Denmark

1 Introduction

The majority of applications of growth models for predicting forest growth in forest management and research are based on yield tables for even-aged monocultures (Holten-Andersen, 1989). However, due to the rigid structure of the yield tables, the validity of the application is limited if the silvicultural practise differs from that of the yield table. Since changed price structures, differing goals of the forest owners, calamities during the lifespan of the stand etc. frequently alters the applied silvicultural practise, the need for a more flexible tool for predicting tree and forest growth is evident.

The shortcomings of the yield tables has become increasingly clear as the political awareness of the need for sustainable forest management has created a demand for uneven-aged management of mixed forests. The aggregation made by using a yield table for planning or research purposes may be valid in monospecific, even-aged management because the even-aged monocultures are relatively homogeneous. However, as the stands become increasingly diverse, the spatial and temporal heterogeneity increases and at some point existing growth models are no longer applicable because they do not include the effects of spatial and

*e-mail: tnl@kvl.dk, phone: (+45) 45178343

temporal distribution of individual trees.

The effect of the spatial arrangement of the individual trees on tree growth was first recognized by the Danish forester C.D.F. Reventlow in 1816. It is however just recently that it has become possible to explicitly model the complex competitive interactions among individual trees (Opie, 1968; Tomé and Burkhart, 1989; Biging and Dobbertin, 1992; Pukkala, 1989; Pretzsch, 1997). Most of these studies have found that although spatial measures of competition provided useful insight to the effects of competition, they only provided little improvement in predicting individual tree growth compared to a mean field model.

The hypothesis tested in this study is that the spatial arrangement of individual trees influences individual tree growth, and that the effect can be quantified in a mathematical model.

2 Materials

The data for spatially explicit modelling growth of European beech in Denmark originate from 16 permanent thinning experiments and 20 plots of the Danish Forest and Landscape Research Institute. Plot sizes vary between 0.10 and 2.2 ha with an average of 0.55 ha. The experiments are located in the eastern parts of Denmark where the growth conditions are more suitable for growing beech than the sandy soils in western Denmark. The data were collected during the period from 1903 to 2004 and includes a total number of 305 measurement occasions.

The individual trees are positioned (x,y) on every plot (see example in Appendix (Figure 3)). Measurements of diameter are obtained by averaging two perpendicular calliper readings taken at breast height (1.3m) for each tree. Observations also include records on whether the tree is alive or dead at the time of measurement. Individual height of live trees was measured using a hypsometer and felled trees were measured on the ground using a tape measure. The data include 25,617 individual diameter measurements and 5,886 height mea-

surements.

3 Methods

The hypothesis tested is that individual tree growth, here diameter increment (Δd_i), may be described as a function of tree size (d_i) and some measure of competition modelled as a spatially explicit competition index (CI_i). A large variety of mathematical models have been used to describe individual tree increment. Despite this seeming variety, many of the models may be reduced to entail only two opposing factors: the biological potential for unlimited multiplicative growth and a reduction due to aging and environmental constraints (Zeide, 1993). Hence individual tree growth may be described as an initial multiplicative expansion that is increasingly damped as the tree grows larger. This growth pattern was modelled by a function with a multiplicative term and an exponential dampening:

$$\Delta d_i = \alpha d_i^\beta e^{-\gamma d_i} \quad (1)$$

The resulting growth curve has a sigmoidal form but no asymptote.

Competition indices

The effect of competition on individual tree growth may be modelled in a variety of ways. In so-called mean field models competition received by the individual tree is described by stand level measures of density regardless of the distance between individual trees. Examples of such measures of competition are basal area, G ($m^2 ha^{-1}$) and basal area of trees larger than the subject tree, G_L ($m^2 ha^{-1}$):

$$G = \sum_{j=1}^n \frac{\pi d_j^2}{4} \quad (2)$$

$$G_{L,i} = \sum_{\substack{j \neq i \\ d_i < d_j}} \frac{\pi d_j^2}{4} \quad (3)$$

In heterogeneous stands such measures of competition tend to break down as the stand level density does not describe the local level of competition. Intuitively, spatially explicit measures of competition would perform better in this case. A large number of different spatially explicit competition indices have been developed for application in tree growth models. Among the different indices those developed by Hegyi (1974) (H), Martin and Ek (1984) (ME), Bella (1971) (B), and Schneider et al. (2005) (L) were chosen for this study:

$$CI_H = \sum_{i \neq j} e_i \frac{d_j}{d_i(Dist_{ij} + 1)} \quad (4)$$

$$CI_{ME} = \sum_{i \neq j} e_i \frac{d_j}{d_i} \exp\left(\frac{-16Dist_{ij}}{d_i + d_j}\right) \quad (5)$$

$$CI_B = \sum_{i \neq j} e_i \frac{O_{ij}d_j}{Z_i d_i} \quad (6)$$

$$CI_L = \sum_{i \neq j} e_i \frac{O_{ij}}{2} (1 + \tanh(\rho(r_j - r_i))) \quad (7)$$

where $Dist_{ij}$ is the distance between the competitor and the subject tree, Z_i is the influence zone (crown surface area) of the subject tree, O_{ij} is the overlap of influence zones of i and j , and ρ is an indicator of competition asymmetry.

Estimation

The hypothesis tested is that individual tree growth, expressed as current annual diameter increment, is dependent on initial tree size and the amount of competition. Further, it is hypothesized that the spatial competition indices more appropriately express competition and hence results in better estimates of individual tree growth. The data has a simple three-layer hierarchical structure with individual measurements on individual trees nested within different forest stands. Hence the estimation problem may be formulated as:

$$\Delta d_{ijk} = \beta_1 d_i^{\beta_2} e^{\beta_3 d_i} e^{\beta_4 CI_i} e^{u_{plot(i)} + v_{tree(i)} + \varepsilon_i} \quad (8)$$

where $u_{plot} \sim N(0, \sigma_p^2)$, $v_{tree} \sim N(0, \sigma_t^2)$, $\varepsilon_i \sim N(0, \sigma^2)$, $\beta_1 - \beta_4$ are parameters to be estimated and CI_i is some measure of competition for the individual

tree. For the estimation procedure, the structure of repeated measurements on the individual tree was ignored as the increments in different periods are not believed to be correlated. The model was analysed using a nonlinear mixed effects model in winBUGS. However, the MCMC algorithm had a rather large burn-in period (>50,000 iterations) and poor mixing properties suggesting large correlation between individual parameters. To minimize this problem the model was reparameterized as:

$$\begin{aligned}\Delta d_{ijk} &= \beta_0 \left(\frac{d_i}{\tilde{D}}\right)^{\beta_2} e^{\beta_3 d_i} e^{\beta_4 CI_i} e^{u_{plot(i)} + v_{tree(i)} + \varepsilon_i}, \\ \beta_0 &= \left(\beta_1 \tilde{D}^{\beta_2}\right), \\ \tilde{D} &= \left(\prod_{i=1}^n d_i\right)^{\frac{1}{n}}\end{aligned}\tag{9}$$

Although this model had improved properties convergence was slow due to the large number of random parameters. Thus, the method was not feasible to analyze the problem at hand given the available time for this course. Consequently, the problem was analyzed in MLwin after having linearized equation (8) and adding the competition term:

$$\log(\Delta d_i) = \beta_1 + \beta_2 \log(d_i) + \beta_3 d_i + \beta_4 CI_i + u_j + v_k + \varepsilon_i\tag{10}$$

As some of the observed increments are negative due to measurement error, the log-transformation creates missing values for a number of observations. In those cases, increment was set to a small value (0.01 mm). The linearized model was estimated was using a burn-in period of 10,000 iterations and a monitoring period of 50.000 iterations.

4 Results

Estimation og non-linear model in winBUGS

Parameters of Equation (9) was estimated for a mean-field model where the competition term was expressed as $exp(\beta_4 G + \beta_5 G_L)$. The estimation was car-

Table 1: Statistics of the bayesian estimation procedure of a nonlinear, mean field model after a burn-in of 20,000 iterations and a monitoring period of 30,000 iterations.

node	mean	sd	MC error	2.5%	median	97.5%
β_0	17.72	1.641	0.1233	14.64	17.53	20.96
β_1	0.01296	0.001862	1.245E-4	0.009652	0.01285	0.0171
β_2	1.277	0.0283	0.001962	1.223	1.276	1.332
β_3	-0.003298	8.284E-5	6.049E-6	-0.003452	-0.003293	-0.003141
β_4	-0.009934	7.902E-4	4.939E-5	-0.01156	-0.009937	-0.008397
β_5	-0.02133	7.05E-4	3.147E-5	-0.02266	-0.02134	-0.01991
tau	0.3091	0.003228	3.062E-5	0.3029	0.3091	0.3155
tau.u2	28.49	1.473	0.04725	25.7	28.45	31.47
tau.u3	16.55	6.558	0.1918	6.251	15.67	31.67

ried out in winBUGS with a burn-in of 20,000 iterations and a monitoring period of 30,000 iterations (Table 1).

The iterations took about 7.5 hrs, but it was evident from the trajectories of the various parameters that the estimation had not yet converged (Figure 1). An obvious solution to this problem was to do more iterations, which was not possible for this course. The effect of the reparameterisation is evident from plots of β_1 vs. β_2 compared to plots of β_0 vs. β_2 .

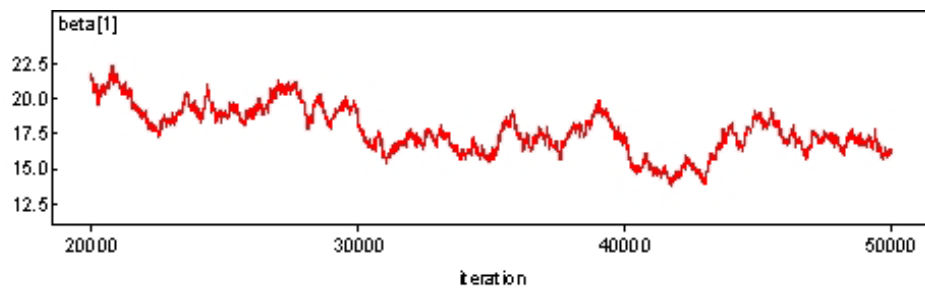


Figure 1: Trajectory of parameter β_1 .

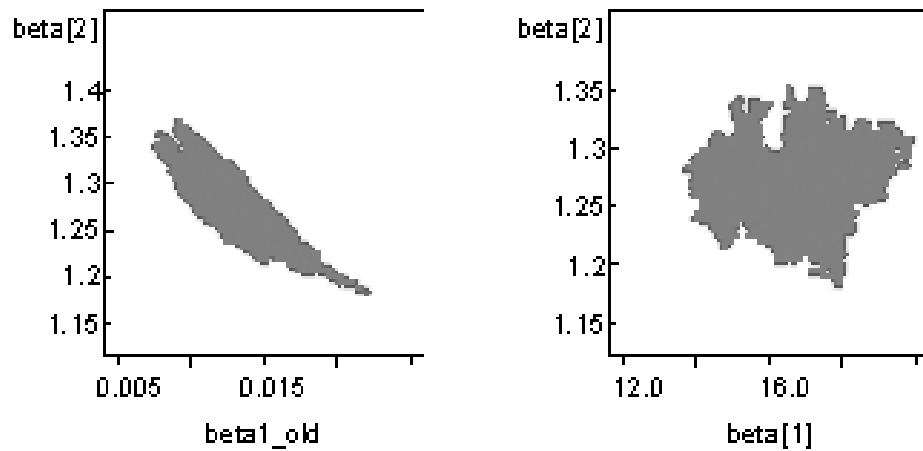


Figure 2: The correlation between β_1 and β_2 before and after reparameterisation.

Estimation of linearized model in MLwin

The parameters of Equation (10) was estimated for a NULL model where no competition effect was included in the model, for a mean-field model (as described above) and for various competition indices (Table 2). Estimation was carried in MLwin with a burn-in of 10,000 iterations and a monitoring period of 50,000 iteration, which exceeded the required number of iterations (Raftery-Lewis) by a factor of 8-10. An example of the trajectories is seen in Appendix (Figure 4).

Compared to the non-linear estimation in winBUGS the different models had excellent mixing properties. Kernel-densities of the individual parameters were close to normally distributed. Analyses of residuals at the lowest level showed that the residuals were not normally distributed. This is to be expected because zero and negative growth were given a low value. Residuals at higher levels were also not normally distributed. However, the non-normality of residuals was not evaluated to influence parameter-estimates given the size of the data.

Table 2: Statistics of the bayesian estimation procedure after a burn-in of 10,000 iterations and a monitoring period of 50,000 iterations for different competition indices (Equation (10)). Variance of the parameter estimates are given in *italics*.

Model	β_1	β_2	β_3	β_4	β_5	σ^2	$\sigma_{v(tree)}^2$	$\sigma_{u(plot)}^2$	DIC
Null	-12.618	2.772	-0.007	-	-	1.038	0.414	0.591	62869.13
	<i>0.418</i>	<i>0.079</i>	<i>0.000</i>	-	-	<i>0.012</i>	<i>0.019</i>	<i>0.248</i>	
Mean field	-10.124	2.592	-0.007	-0.016	-0.055	0.982	0.372	0.295	61656.23
	<i>0.384</i>	<i>0.076</i>	<i>0.000</i>	<i>0.002</i>	<i>0.002</i>	<i>0.011</i>	<i>0.016</i>	<i>0.128</i>	
CI_H	-10.837	2.483	-0.006	-0.236	-	1.031	0.421	0.471	62745.01
	<i>0.442</i>	<i>0.084</i>	<i>0.000</i>	<i>0.024</i>	-	<i>0.011</i>	<i>0.019</i>	<i>0.196</i>	
CI_{ME}	-11.583	2.701	-0.007	-0.368	-	1.015	0.428	0.454	62437.49
	<i>0.397</i>	<i>0.077</i>	<i>0.000</i>	<i>0.020</i>	-	<i>0.011</i>	<i>0.019</i>	<i>0.190</i>	
CI_B	-14.734	3.291	-0.007	-0.143	-	1.015	0.369	0.553	62327.37
	<i>0.384</i>	<i>0.079</i>	<i>0.000</i>	<i>0.005</i>	-	<i>0.011</i>	<i>0.016</i>	<i>0.230</i>	
CI_{RL0}	-14.646	3.255	-0.007	-0.295	-	1.019	0.401	0.602	62470.45
	<i>0.398</i>	<i>0.078</i>	<i>0.000</i>	<i>0.014</i>	-	<i>0.011</i>	<i>0.017</i>	<i>0.250</i>	
CI_{RL1}	-14.619	3.255	-0.008	-0.165	-	1.020	0.381	0.563	62441.52
	<i>0.392</i>	<i>0.077</i>	<i>0.000</i>	<i>0.007</i>	-	<i>0.011</i>	<i>0.017</i>	<i>0.234</i>	
CI_{RL2}	-14.603	3.251	-0.008	-0.163	-	1.020	0.381	0.563	62444.47
	<i>0.392</i>	<i>0.077</i>	<i>0.000</i>	<i>0.007</i>	-	<i>0.011</i>	<i>0.017</i>	<i>0.234</i>	

Discussion

The parameteres estimated for each of the different equations (Table 1 and 2) confirmed the prior notion of initial multiplicative growth followed by exponential dampning. Further the signs of the parameter estimates confirmed that competition had a negative effect upon individual tree growth. Finally, the DIC statistic confirmed that models that included some measure of competition performed better than the model without some measure of the effect of competition.

The performance of different competition indices was evaluated from the DIC statistic of the different models (Table 2). Judging from the results, the use of spatially explicit indices of competition does not result in markable (if any) improvements in the models ability to predict individual tree growth. This is in concordance with findings of most studies on spatially explicit individual tree growth models(e.g. Biging and Dobbertin, 1992). This finding may in part be caused by the fact that the beech stands included in this study are quite homogeneous and hence that the spatial effects are difficult to estimate. Another reason is that the competition indices chosen for this study are very simple and are generally viewed as inferior to other, more complex indices such as Area Potentially Available (APA) (Tomé and Burkhart, 1989). Finally, the processes of the temporal variation of competition among trees are not well understood. Several studies have indicated that availability of nutrients and water essentially influences competition asymmetry and hence the competition experienced by the individual tree (Wichmann, 2002). These findings may indicate that a relatively simple spatial competition index that does not include the effect of climatic variation does not adequately express the competition experienced by the individual tree. Hence, such index may not predict individual tree increment any better than a simple non-spatial measure of competition.

References

- Bella, I. E. (1971). A new competition model for individual trees. *Forest Science*, 17:364–372.
- Biging, G. S. and Dobbertin, M. (1992). A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *Forest Science*, 38(3):695–720.
- Hegy, F. (1974). A simulation model for managing Jack pine stands. In Fries, J., editor, *Growth models for tree and stand simulation*, pages 74–90. Royal College of Forestry, Stockholm, Sweden.
- Holten-Andersen, P. (1989). Danish yield tables in the past century. *The Danish Forest Experiment Station*, 42(2):71–145.
- Martin, G. L. and Ek, A. R. (1984). A comparison of competition measures and growth models for predicting plantation red pine diameter and height growth. *Forest Science*, 30(3):731–743.
- Opie, J. E. (1968). Predictability of individual tree growth using various definitions of competing basal area. *Forest Science*, 14(3):314–323.
- Pretzsch, H. (1997). Analysis and modeling of spatial stand structures. methodological considerations based on mixed beech-larch stands in Lower Saxony. *Forest Ecology and Management*, 97:237–253.
- Pukkala, T. (1989). Predicting diameter growth in even-aged Scots pine stands with a spatial and non-spatial model. *Silva Fennica*, 23:101–106.
- Reventlow, C. D. F. (1816). Formentlige resultater af en deel fortsatte undersøgelser angaaende indflydelsen af træernes gjensidige afstand på deres mere eller mindre fordelagtige vegetation. *Det Kongelige Danske Videnskabskabernes Selskabs skrifter for aar 1809, 1810, 1811 og 1812*. 3. Række, 6. Bind, II. Hæfte.

- Schneider, M. K., Law, R., and Illian, J. B. (2005). Dynamics of neighbourhood-dependent plant growth: quantitative estimation of spatial interactions in *Arabidopsis thaliana*. *Unpublished*.
- Tomé, M. and Burkhart, H. E. (1989). Distance-dependent competition measures for predicting growth of individual trees. *Forest Science*, 35(3):816–831.
- Wichmann, L. (2002). *Modelling the effects of competition between individual trees in forest stands*. PhD thesis, Royal Veterinary and Agricultural University.
- Zeide, B. (1993). Analysis of growth equations. *Forest Science*, 39(3):594–616.

Appendix

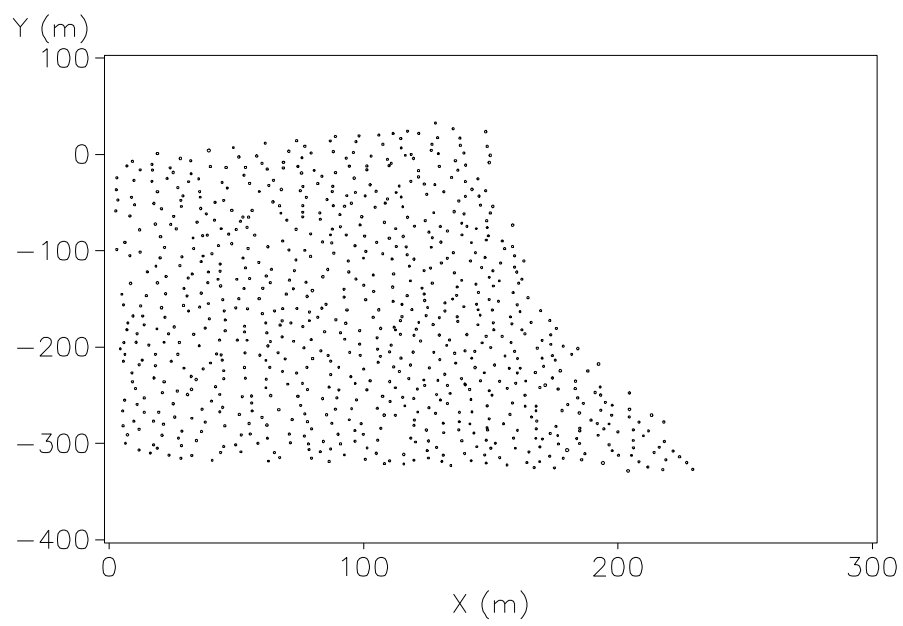


Figure 3: Position of individual trees at experiment DO. Width of circles represent the actual diameter of the individual tree.

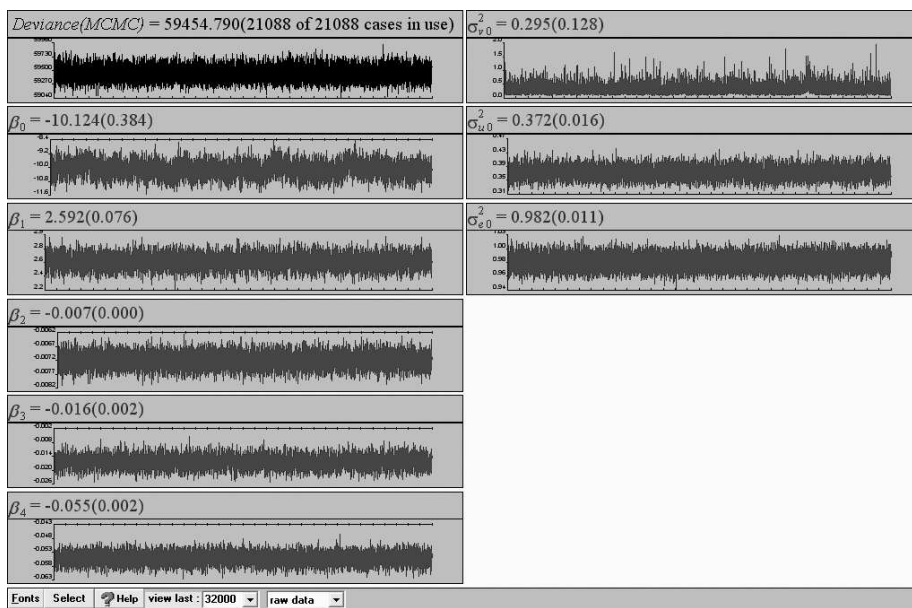


Figure 4: Trajectory of the individual parameters of the mean-field model. Estimation was carried out in MLwin with a burn-in period of 10.000 iterations and a monitoring period of 50.000 iterations.