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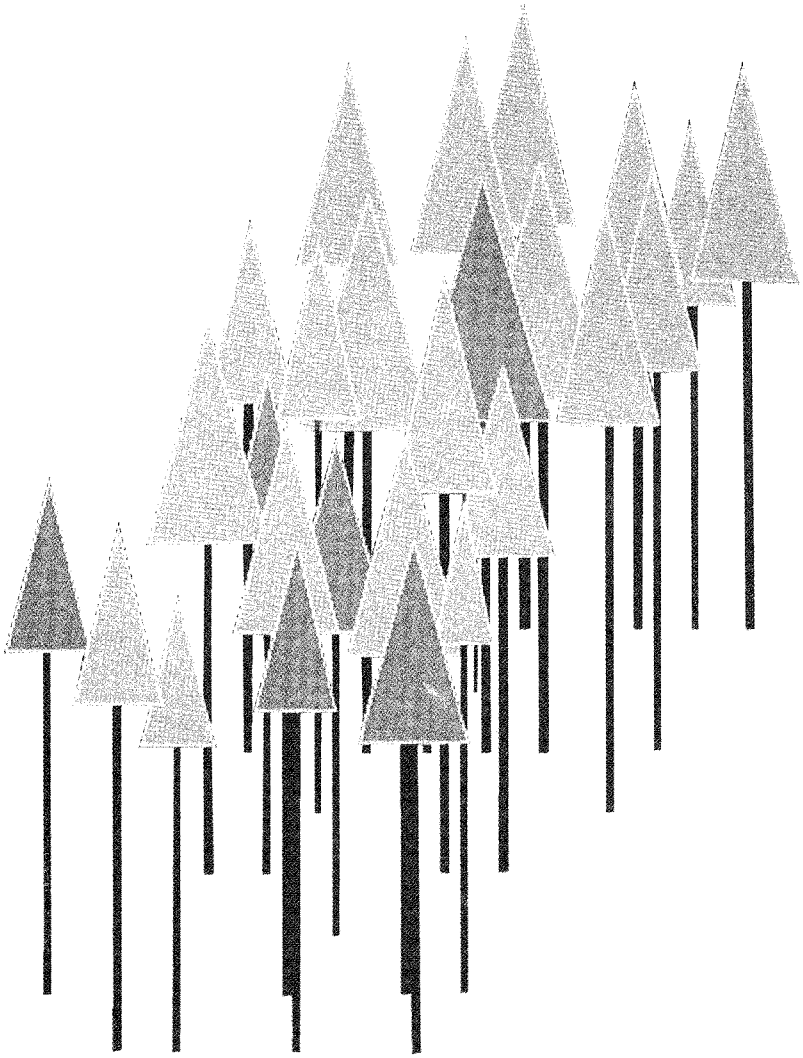
Modelling Stand Response To Silvicultural Practices



Proceedings of the

IUFRO S4.01 Conference

Blacksburg, Virginia
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PREFACE

Scientists have developed a wide array of silvicultural practices for achieving different forest management objectives. When deciding which practices to apply, managers must estimate the likely response of forest stands to each cultural treatment and to combinations of treatments. To provide maximum information and flexibility, models of response to silvicultural practices are needed. The purpose of this conference, sponsored by IUFRO Subject Group S4.01, was to discuss philosophy and approaches to modelling stand response to silvicultural practices such as genetic selection, control of competing vegetation, application of fertilizers, and thinning. The conference was held at the Center for Continuing Education on the Virginia Polytechnic Institute and State University Campus in Blacksburg, Virginia, U.S.A., September 27-October 1, 1993.

This proceedings volume was compiled from full papers or abstracts of the oral presentations plus abstracts of the poster presentations. It should be noted that the authors submitted camera-ready copy of their manuscripts and that they are solely responsible for the contents. No attempt was made to obtain review or to edit (other than minor format changes) the material submitted. The contributions are divided into two sections ("Papers" and "Posters") and arranged in alphabetical order within each section according to the surname of the first-listed author.

We appreciate the authors' contributions to this volume, and we trust that these proceedings will prove helpful to advancing the science of modelling stand response to silvicultural practices.

Harold E. Burkhart
Timothy G. Gregoire
James L. Smith
August, 1993

MODELING GROWTH OF LOBLOLLY PINE STANDS FOLLOWING MIDROTATION NITROGEN AND PHOSPHORUS FERTILIZATION

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ABSTRACT

Established stand fertilization represents a largely unrealized opportunity to increase the productivity, value, and health of millions of hectares of loblolly pine plantations in the southeastern United States. Although strong responses have been clearly demonstrated, a lack of confidence in identifying responsive stands and prescribing the appropriate elements and rates remain obstacles to widespread use of fertilizers. To address these issues, forest industry members of the North Carolina State Forest Nutrition Cooperative (NCSFNC) initiated a regionwide study to assess the response of midrotation loblolly pine plantations to a factorial combination of nitrogen (0, 112, 224, 336 kg/ha) and/or phosphorus (0, 28, 56 kg/ha). A total of 42 installations were established in site-prepared plantations across the Southeast with the twelve treatment matrix being replicated two or four times at each site.

A number of different approaches have been used to model fertilizer response. The most simple and commonly used method has been to relate response (the difference between growth on treated and control plots) to site, soil, stand, and foliar characteristics; however, this method provides response predictions for only one treatment. A more complex approach is to incorporate fertilizer element and/or rate effects into a growth model that is developed using data from nonfertilized and fertilized plots. We chose this latter approach to take advantage of data from all twelve treatments and to provide a unified N x P response surface. Models were developed to predict four-year stand growth as a function three components: 1) stand and site factors that affect growth, 2) N and P rate factors that characterize an average treatment response surface, and 3) interaction effects between the first two sets of factors (i.e., factors that define site-specific response).

Models based on soil or foliar data were remarkably similar in structure. The foliar model accounted for 67% of the variation in four-year growth and included five site variables: site index, latitude, drainage class, foliar N, and foliar P. Site index, latitude, and drainage class affected the base growth model but did not interact with either N or P rate. The N x P response surface was described by curvilinear N and P rate terms and their interaction. Foliar N and P interacted with both N and P rate and with each other. Measures of stand density did not affect growth or response in these fully stocked stands. Sensitivity analyses indicated that fertilizer response will be greatest following additions of N+P on most site types. Foliar P and the foliar N/P ratio were critical determinants of response magnitude and provide for the identification of optimum N and P rates on a site specific basis. Incorporation of fertilizer treatment effects into existing growth and yield models will need to account for the site specific magnitude and duration of response and the interactive effects of N and P additions.

ROLE OF LONG TERM SPACING * THINNING EXPERIMENTS IN THE PLANNING AND REFINEMENT OF PLANTATION YIELD MODELS

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A long term spacing X thinning experiment at Merryville, Louisiana, is used to illustrate volume/diameter tradeoffs, mortality curves, maximum stocking relationships, crown dynamics, and total yield production, for both thinned and unthinned loblolly pine (*Pinus taeda* L.). The 38-year-old experiment includes both a wide range in the initial "square" planting spacings, from 1.8 m X 1.8 m to 3.7 m X 3.7 m, and a wide range in subsequent thinning levels, from residual basal area of 13.8 m^2/ha to 27.6 m^2/ha, to unthinned. The role of long term experimental sample plots is discussed in terms of the development and/or refinement of plantation yield tables.

A GROWTH MODEL WITH A SILVICULTURAL APPROACH FOR FORESTERS

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Abstract:

Norway Spruce is now the most common conifer species and economical the most important tree species in Denmark. It is normally easy and cheap to use for reforestation and plantations. The wood industry and wood market have developed a strong preference toward it. Norway Spruce was introduced throughout the country on sites normally covered by hardwood (Oak, Beech). Norway Spruce stands (as we grow them) have proved to be unstable. They are deteriorating - especially in the western part of the country, where the largest areas with spruce are situated.

The problem
Forest administrations have lost control of whole forests and plantations. Parts of the stands have to be clear-cut every year and reforested at an in optimal age - mostly from the west. Norway Spruce is often planted again thus introducing the problem again.

The objectives
The objective with this study is 1) to find ways radically to change existing plantations toward forests with a higher level of stability and an increasing value for the public and an eventual investor. The turnover period should be no more than 20 years - 2) to analyze the financial possibilities and constraints of the change by using simulators and planning tools - and 3) to introduce planning and simulation tools to forest managers, so they can handle the above problems better.

The models
The used logging simulator uses taper curves and diameter distributions in connection with user-driven bucking instructions and price information to calculate assortments and net values for a certain stand.
The model used for stand modeling is a *Stand Model*. Many scientists are working with tree-based models, which theoretically of course is correct. In Denmark, however, almost all the growth and production research is designed to describe the development of stands. Data from these experiments are used to test the model.
The planning system used by our local managers can specify all kinds of actions, output and resources related to stands or operations. You may link stand treatment to specific years to get a silvicultural balanced short-term plan.

Results
The financial effect of the following 'treatments' were analyzed:

- Traditional Norway Spruce as monocultures (Optimal cycles). Clear-cut systems.

- Norway Spruce that begins to die at the age of about 60 years. Reforestation on clearcuts with Norway Spruce.
- Introducing new and more stable generations under the shelter (canopy) of Norway spruce at max. height 15 m.

Cash flow analysis shows that a declining spruce stand is very inferior compared to an optimal - but unrealistic - growth. It also shows that after a period of 20 years introducing a new generation under a shelter of an unmature, but risky spruce stand has the same accumulated cash flow than optimal growth.

A management plan for a plantation of 270 ha - consisting mostly of Norway spruce stands - with the objective to create a more stable ecosystem was produced. The financial result of the conversion period of 20 years was in average positive.

I expect, however, that the main problem in this project will be of a physiological nature. We have spent much time teaching foresters to treat and thin the stands up to a stand height of 15 m. After that the risk of wind damage increases. Now we are saying that just after finishing the thinning operations they should start to introduce the next generation. That will be difficult to accept, but the main argument is that in many areas in Denmark Norway Spruce should not be considered as the main tree species but as an intermediate one.

By giving the local management the opportunity to deliver most of the information and carry out the calculations themselves on their computer we have found, that they take part in the discussions with openness and visions, instead of the conservatism and stubbornness you often find among foresters.

MODELLING AUSTRIAN BLACK PINE RESPONSE TO SILVICULTURAL PRACTICES IN THE SOUTH EAST OF FRANCE

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ABSTRACT

The Stand Management System (Arney, 1985) is adapted to Austrian black pine in the South East of France. The main equations of this individual-tree, distance-independent growth model are fitted using data from increment cores and height measurements on felled trees in temporary plots. First validation tests are performed using data from stands measured for growth periods with or without thinning. Further validation tests will be performed to confirm the good results already obtained. The data base will be extended towards younger stands.

INTRODUCTION

Austrian black pine (*Pinus nigra* Arnold ssp. *nigricans* Host.) covers hundreds of thousand hectares in central and southern Europe either in its natural range (Austria, Italy, Yugoslavia, Albania, northern Greece, Romania, Bulgaria) (Debazac 1971) or in its introduction area (France 174 000 ha, Belgium, the Netherlands, Hungary ...).

It has been introduced in France at the end of the 19th century, mainly in the southern Alps, in order to fight against soil erosion induced by deforestation and overgrazing. Black pine stands now cover more than 93 000 ha (mainly state-owned) in this region and the oldest stands are around 120 years old.
This species demonstrated a good adaptation to the climate (mixed Mediterranean and mountainous influences) and to the soil and topographic conditions (calcareous or calcareous marl, elevation between 500 m and 1200 m, steep slopes). Natural regeneration is quite easily obtained and is often used to renew stands.

In addition, this species proved interesting for wood production. Mean annual increment at age 100 is between 3 and 9 m^3/ha·yr which is quite good under these soil and climatic conditions.
Generally speaking, wood production in the Mediterranean region is poor, both in volume and in quality. In spite of the relatively small area occupied, Austrian black pine is one of the main species in this region as far as timber harvest is concerned. Stem form is usually straight and mechanical properties of its wood are similar to those of some other pine species grown in France (CTBA 1990).

In the early 1970's, yield tables were built for Austrian black pine in the South East of France (Ottorini and Toth 1975, Toth and Turrel 1983) but they mainly reflect minimal silvicultural practices because wood production was only belatedly added to the soil protection goal.

Silvicultural practices greatly changed during the last fifteen years and now consist in line thinnings (often combined with selective thinning) and in selective thinnings with various intensities. A few young stands are pruned.
During the same period, initial spacing commonly used for plantations dramatically increased (about 3 x 3 m nowadays). When the stand originates from natural regeneration (obtained by shelterwood system), a precommercial thinning is performed initially to reduce stocking level (Dreyfus 1988).

At present, many functions are assigned jointly to Austrian black pine stands : soil protection (still necessary), wood production, wood and grass production (silvopastoral activities) ... and many constraints, often conflicting, must be taken into account in silvicultural practices : prevent brush understorey development to limit fire risk (Dreyfus 1990), avoid clearcutting on wide areas for landscape safety, but perform heavy enough thinnings to interest wood buyers.

In that context, the state forest service has no efficient tool for decision making. The current yield tables do not permit to forecast the growth of stands with so different objectives among the ones listed above. For this reason why we projected to replace these tables by a growth model supposed to be more flexible and to give more detailed informations.

After investigation of the modelling strategies used in France (Douglas fir, maritime pine ...) and abroad, we fixed our choice on an individual-tree, distance-independent growth model.
As the economic weight of Austrian black pine at the national level in France is rather moderate, it was decided to try to adapt an existing model rather than to build an entirely new one. This could also be less time-consuming.

After several contacts with J.D. ARNEY, his Stand Projection System (Arney, 1985) was finally chosen for this attempt. SPS has already been adapted for a wide span of North American species and for several regions. Moreover, all growth coefficients by species and region reside in a library file which is external to the model and can be expanded to other species without modifying SPS itself. An other interesting feature of SPS (and of some other growth models) is the stratification of model functions into potential and modifier effects (Arney, 1985). Last of all, it seemed that the data required for adapting SPS to a new species could be obtained for Austrian black pine.

However, long-term permanent field trials in Austrian black pine are lacking in France and our task largely lied in finding alternative data sources.
This paper deals with the current results of this adaptation and with its first validation tests.

MATERIALS AND METHODS

Data

The data required for fitting an individual-tree growth model are individual tree increments (diameter and height) and stand characteristics (top height, stand density or diameter distribution, number of dead trees ...). Unfortunately, individual data from tagged numbered trees in permanent plots has been systematically collected for Austrian black pine in France only for a few years.

Therefore, the data used in this study came mainly from a sample of 111 plots established between 1968 and 1973 all over the range of Austrian black pine in the South East of France when the yield tables were built. Most of these plots are in rather old stands because the main afforestation effort happened during the late 19th century and the beginning of the 20th :

	Mean	SD	Minimum	Maximum
Age (years)	64	22	32	104
Site index (height at 50 bh-age in m)	15.3	2.9	9	21
Stem number (/ha)	1623	765	206	3435
Basal area (m^2/ha)	43.8	13.1	13.7	72.9

These plots are not experimental plots and are operationally treated. Each plot is located in a different stand.
Measurements mainly consisted in a complete inventory in girth classes and in the height measurement of 20-25 trees aimed at building a height over diameter equation. Some of these temporary plots have been remeasured twice or three times.

Individual height increments were obtained from 4 trees felled in each plot (2 dominant, 1 intermediate and 1 suppressed) at the time when the plot was established. A stem analysis had been performed on each dominant tree in order to develop the site index curves used in the yield tables. Visible annual height increments had also been measured in the upper part of all four felled trees.
A sample of these increments was selected for this study and stand density at the beginning of the growth periods has been estimated (Dentand 1990).

At the beginning of this study in 1989, a sample of plots was selected according to site index and age. These plots were remeasured for stand characteristics with complete inventory and height measurements. Five trees equally spaced through the range of diameter were bored at breast height (four cores per tree). Bark thickness at breast height was also measured. Increments were read on the cores. The assumption was made that the [diameter over bark/diameter under bark] ratio at the beginning of the increment period was the same as at the end of this period. Initial stand density was obtained from previous measurement(s) of the plot. Half of the growth periods began just after thinning, and half did not include any thinning.

Plot size ranges from 0.14 to 0.66 ha. All data are from plantations, almost pure stands (more than 95% of basal area in black pine). Other limitations for inclusion in the analyses concerned top height increment over the growth period (at least 1.5 m), length of growth periods (at least 4 years), annual top height increment (at least 0.10 m per year). Plots where mortality was largely induced by severe damages (windfalls, decay following snowbreaks) were rejected.

Model Fitting and Validation

Fitting of SPS equations for Austrian black pine was performed using nonlinear regression package in SAS ® software (release 6.07). Weighting in nonlinear regression was used (*i*) for height increment analyses in order to compensate oversampling of dominant trees, (*ii*) for diameter increment analyses because of unequal samples over growth conditions.

The SPS version used for this study was version 2.1.
The coefficients obtained from the analyses were introduced in the SPS library file under a new heading for Austrian black pine in the South East of France.

Only 6 completely independent plots were available for the validation tests and we resolved to use also 19 initial sample plots where increments were obtained for fitting the equations. The use of these 19 plots was admitted considering that (*i*) growth periods used for validation coincide only partially with individual increment periods used for fitting, (*ii*) increments used for fitting the equations come from few trees (4 trees for height increment, 5 trees for diameter increment) and not from all trees in the plot, (*iii*) each of these trees was chosen at random in its size class (rejecting damaged trees) and not as the mean tree of the class.
There were no significant difference between the results of validation tests obtained for these plots and those obtained for the 6 independent plots.

In a few cases, two or three successive growth periods were used for the same plot. In such a case, the initial conditions for each period were featured by the observed stand table rather than by the stand table simulated by SPS for the previous period.

Among these plots, 8 have been thinned between the two measurements.

For each plot, the entire stand table (height and trees per hectare for each diameter class) was the input for SPS. When the plot had been thinned during the period studied, thinning conditions were specified as follows : age of the stand at the time of thinning, number of remaining trees per hectare, thinning method (dbh ratio of cut trees over original stand, or cutting from below with a dbh limit). Other criteria available in SPS for thinning specification (Arney 1989) were not used in these tests.

FITTING SPS TO AUSTRIAN BLACK PINE

Four in the five basic equations of SPS were fitted to Austrian black pine. They are :
- top height increment equation,
- tree height increment,
- tree diameter increment,
- mortality.

A diameter-total height volume table exists for Austrian black pine in France, but it is not yet converted into taper equations (the tree volume equation is the fifth basic equation used in SPS). As volume is simply computed using the other stand characteristics output by the model, validation tests were made only for these stand characteristics.

Several other SPS coefficients of lesser importance were fitted to Austrian black pine (number of years to reach breast height, minimum and maximum observed diameter/top height ratio ...).

The stand density measure used in SPS is Crown Competition Factor (Krajicek *et al.* 1961). In order to permit computation of CCF, a [maximum crown width - breast height stem diameter] equation was developed for Austrian black pine using data from eighty open-grown trees (height between 2 and 20 m, dbh 2-64 cm). Although a linear relation was statistically equivalent (same residual mean square) for this data set, the relation was fitted in the exponential form used in SPS.

Top Height Model

The relation between top height (average height of the 100 largest diameter trees per hectare), total age and site index (defined as the top height reached at total age 50 years) had been developed for Austrian black pine when the yield tables were built. This relation plays a fundamental part in most of the growth models as the top height increment indicates a potential growth. The older the stand and the lower the site index, the weaker the potential growth obtainable in a given period of time.

As SPS uses breast height age, the relation and the site index definition were converted in accordance.

SPS uses the standardized site index curves technique (Zeide 1978) : top height is expressed as a percentage of top height at breast height age 50 years and an index value assigned from 1 to 18.
It has also been observed that the top height of a stand often increases in a way which is not completely consistent with the site index curves. The standardized site index curves technique provides a means to take such a local condition into account.

The Austrian black pine site index curves were standardized and the corresponding growth type values were included in the SPS library file.

Height Increment Model

This model provides the relative height growth (height growth/top height increment) as a function of relative tree size (defined as tree height/top height), crown competition factor and top height growth. This relative tree size concept provides a means to compare status of trees from different stands (Arney, 1985).

SPS can use two forms for this relation. The form that appeared to be suitable to black pine is :

$$dH/dH0 = (H/H0)^{b1} [1 - (CCF/600)^{b2}]$$

dH = tree height increment for period
dH0 = top height increment for period
H = initial (*i.e.* at beginning of period) tree height
H0 = initial top height
CCF = Crown Competition Factor at beginning of period
b1, b2 = regression coefficients for the species.

Characteristics of the 112 increments from 28 plots that were used in analyses sum up as follows :

	Mean	SD	Minimum	Maximum
Years (in period)	10.6	2.5	4	15
dH/dH0	0.92	0.21	0.14	1.86
dH (m/year)	0.23	0.09	0.02	0.59
dH0 (m/year)	0.25	0.09	0.11	0.54
H/H0	0.89	0.12	0.49	1.20
H (m)	12.4	3.4	4.3	20.8
H0 (m)	14.1	3.4	5.8	21.8
CCF	250	63	106	469

The values of the parameters were :

	value	standard error	correlation with b1	correlation with b2
b1	0.596	0.13	1	0.18
b2	7.99	3.27	0.18	1

Residual mean square was 0.05 m/m.

Residuals displayed by initial tree size (figure 1a), stand density, top height showed very little bias.

The form of the equation (figure 1b) shows how potential growth is dampened by stand density and individual tree size.

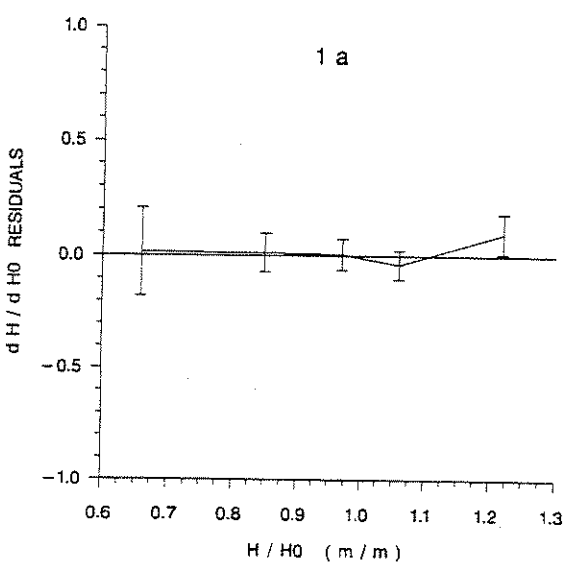

FIG. 1a : Distribution of residuals of the height increment equation. Plotted values are means ± 2 SE. One unit on vertical axis is equal to dH/dH0 mean in the data set.

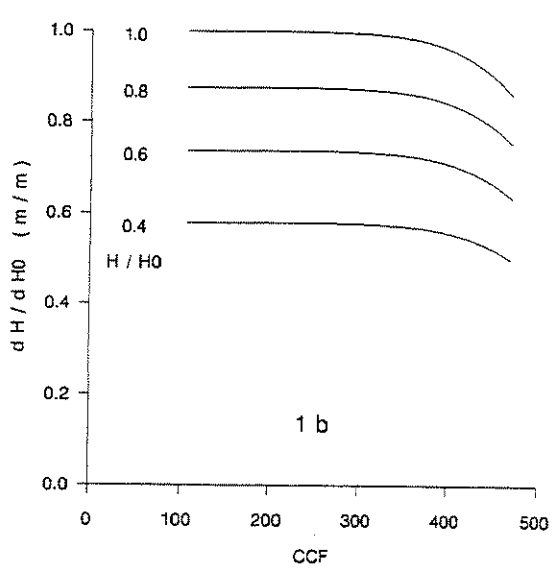

FIG. 1b : Predicted relative height growth as a function of relative tree size and stand density.

Diameter Increment Model

This model provides the relative diameter (at breast height) growth as a function of relative tree size (defined as diameter at breast height/top height), crown competition factor and top height growth :

$$dD/dH0 = b1\ (CCF/100)^{b2}\ [1 - \exp(D/H0)^{b3}]^{b4}$$

dD = tree diameter increment for period
D = initial (*i.e.* at beginning of period) tree breast height diameter
b1, b2, b3, b4 = regression coefficients for the species.

Characteristics of the 159 increments from 26 plots that were used in analyses sum up as follows :

	Mean	SD	Minimum	Maximum
Years (in period)	11.5	3.5	5	20
dD/dH0 (mm/m)	11.8	5.5	1.1	30.5
dD (mm/year)	2.5	1.2	0.4	7.0
dH0 (m/year)	0.23	0.07	0.13	0.41
D/H0 (mm/m)	13.4	3.7	3.3	22.5
D (mm)	202	68	36	430
H0 (m)	15.4	4.2	7.6	25.0
CCF	264	78	108	495

For this analysis, the technique used is similar to the one used by Arney (1986) for western hemlock.
The 159 individual observations were distributed in 23 cells defined by 100 units of CCF classes and 2.5 mm/m diameter/top height classes. These cells define a growth surface across stand density and relative tree size. Residuals were computed using individual observations.

As b3 and b4 were found to be highly correlated (r^2=0.98), b4 was redefined as a function of b3.

The final values of the parameters were :

	value	standard error	correlation with b1	b2	b3
b1	21.5	3.12	1	-0.86	-0.45
b2	-0.405	0.14	-0.86	1	0.06
b3	-0.253	0.02	-0.45	0.06	1

Value of b4 was 5.42.

Residual mean square was 6.7 mm/m.

Residuals displayed by initial tree size (figure 2a), stand density, top height showed very little bias.

The form of the equation (figure 2b) shows how potential growth is dampened by stand density and individual tree size.

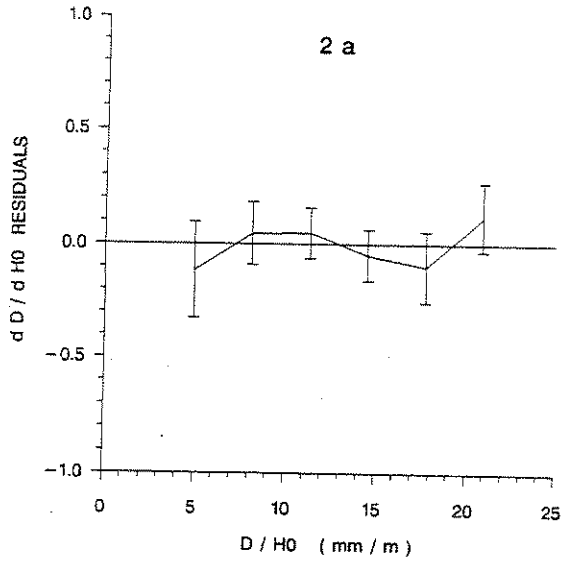

FIG. 2a : Distribution of residuals of the diameter increment equation. Plotted values are means ± 2 SE. One unit on vertical axis is equal to dD/dH0 mean in the data set.

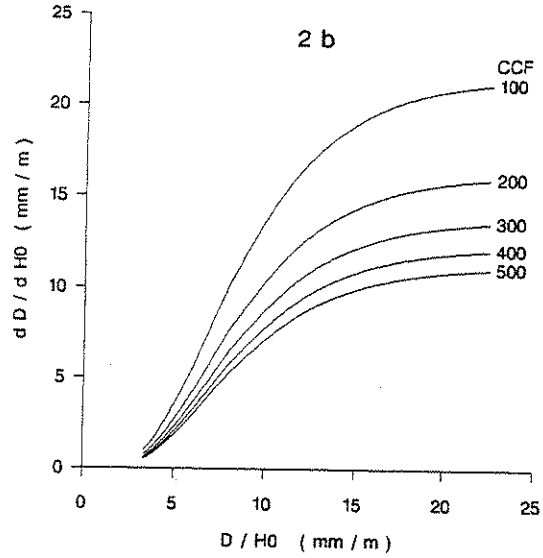

FIG. 2b : Predicted relative diameter growth as a function of relative tree size and stand density.

Mortality

At the present stage, too few data are available to entirely refit the SPS mortality model for Austrian black pine. For two coefficients, first-approximation estimates provided in the SPS library file were used for this species too.
The mortality model used in SPS is based on a limiting CCF value in an approach similar to (but less strict than) the maximum density concept (Drew and Flewelling 1977, Arney 1986). Based on the data available, this CCF value was estimated to 400 for Austrian black pine.

VALIDATION TESTS

The main validation results were obtained by comparing top height, stem number, mean diameter and basal area at the end of each growth period with the values predicted by SPS. Plot measurements were available both for the beginning and for the end of each growth period.

Top Height

Top height simulation appeared to be unbiased (at the probability level 1%, with 32 observations). There were no noticeable differences in results between growth periods with or without thinning.

Observed and simulated values are plotted in figure 3a and are summarized as follows :

	Mean	SD	Minimum	Maximum
Initial top height (m)	15.2	4.7	7.4	24.6
Top height increment observed (m)	1.9	1.0	0.4	4.2
Residual (simulated-observed) on final top height (m)	0.01	0.3	-0.6	0.5

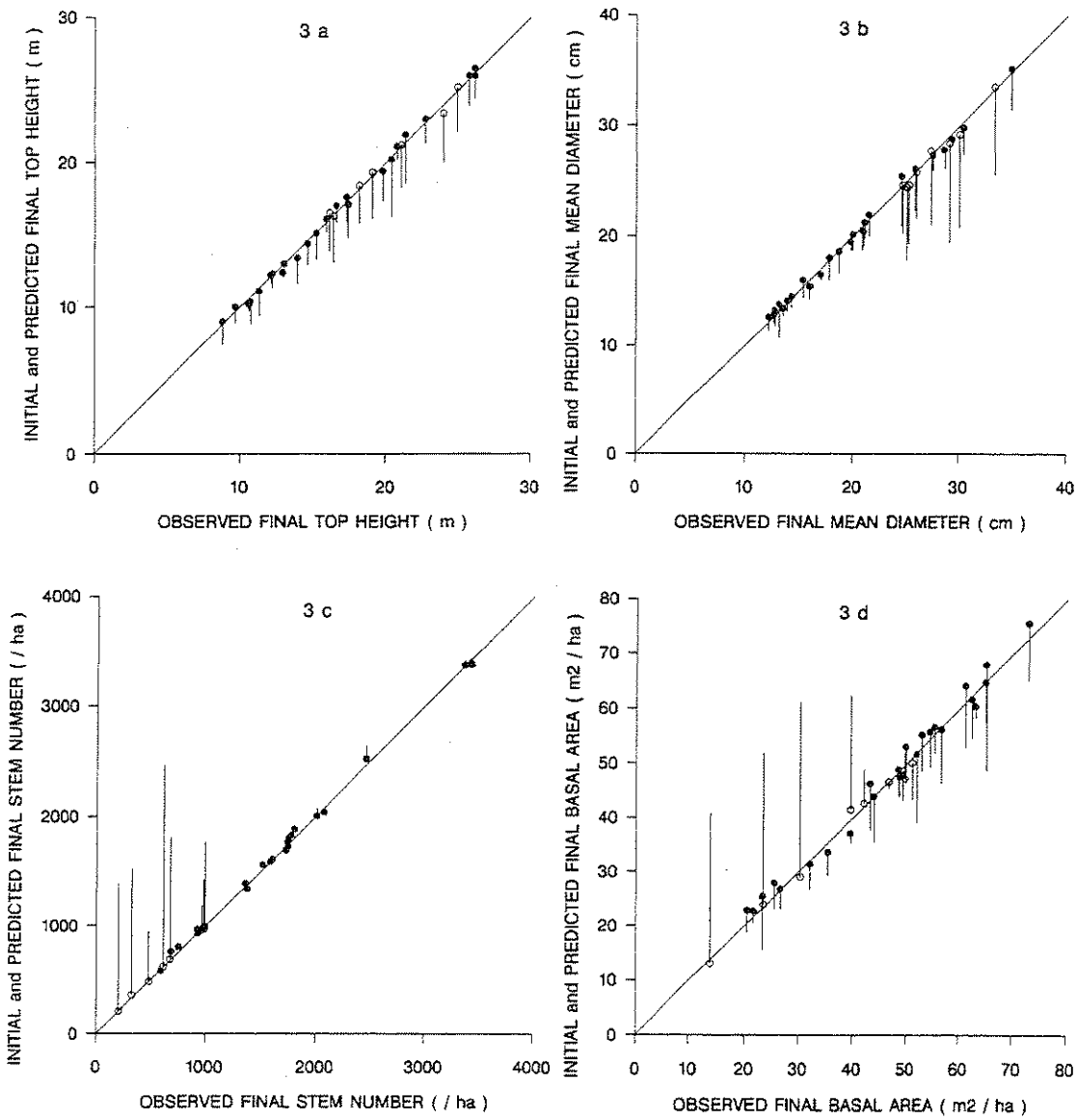

FIG. 3 : For each growth period, a straight line joins initial value to final predicted value (dot for period without thinning, circle for period including a thinning). A diagonal line represents predicted values that would be equal to observed values. The closer the dot (or circle) to this line, the better the prediction.

Mean Diameter

In SPS, the growth of each diameter class is estimated using the diameter increment model. These increments are accumulated in the respective diameter class and provide

the new distribution at the end of the period, which is then corrected by applying the mortality model. Finally, the new mean diameter can be computed.

When a stand is selectively thinned, mean diameter increases progressively by the growth of remaining trees (like without thinning) but is also immediately raised because cut trees are usually smaller on average than remaining trees.

Values are plotted in figure 3b and can be summarized as follows :

	Mean	SD	Minimum	Maximum
Growth periods without thinning				
Initial mean diameter (cm)	18.4	5.8	10.7	31.4
Mean diameter increment observed (cm)	1.7	0.9	0.5	3.6
Residual (simulated-observed) on final mean diameter (cm)	0.02	0.46	-0.8	0.9
Growth periods including a thinning				
Initial mean diameter (cm)	20.7	2.3	17.8	25.6
Mean diameter increment observed (cm)	6.8	2.0	4.3	9.7
Residual (simulated-observed) on final mean diameter (cm)	-0.28	0.46	-0.8	0.4

For growth periods without thinning, the mean diameter estimate showed very little bias (not different to zero at the 15% probability level, with 25 observations).
For growth periods including a thinning, the bias was higher : mean diameter was slightly underestimated.

Stem Number

The evolution of the total stem number depends on ingrowth, mortality and thinnings. In this validation data set, stem number decrease was very low, except when plot was thinned (most thinnings are very heavy). In fact, faster natural decrease due to various kinds of damages has been noticed in several plots but these plots where rejected because only competition-induced mortality can be simulated by a growth model like SPS.

Values are plotted in figure 3c and can be summarized as follows :

	Mean	SD	Minimum	Maximum
Growth periods without thinning				
Initial stem number (/ha)	1738	800	597	3434
Stem number decrease observed (/ha)	46	42	166	0
Residual (simulated-observed) on final stem number (/ha)	11	38	-54	80
Growth periods including a thinning				
Initial stem number (/ha)	1564	462	947	2469
Stem number decrease observed (/ha)	906	536	1854	217
Residual (simulated-observed) on final stem number (/ha)	4	11	-10	27

In both situation a small bias is observed : stem number is slightly overestimated.

Basal Area

Total basal area can be computed as the sum of the basal area of each diameter class but can also be obtained using mean diameter and total stem number. Therefore, results for basal area are influenced by those obtained for mean diameter and stem number.

Values are plotted in figure 3d and can be summarized as follows :

	Mean	SD	Minimum	Maximum
Growth periods without thinning				
Initial basal area (m^2/ha)	40.6	13.7	15.5	65.0
Basal area increment observed (m^2/ha)	6.1	3.4	1.1	16.3
Residual (simulated-observed) on final basal area(m^2/ha)	0.7	1.8	-2.6	3.1
Growth periods including a thinning				
Initial basal area (m^2/ha)	50.7	7.9	40.8	62.4
Basal area variation observed (m^2/ha)	-13.7	15.3	-30.9	7.7
Residual (simulated-observed) on final basal area (m^2/ha)	-0.3	1.3	-2.5	1.9

A small bias was observed in both situations (with or without thinning).

DISCUSSION OF RESULTS

The fitting of SPS increment equations to Austrian black pine is rather satisfying as shown by the residual mean squares obtained, especially considering that the data available are somewhat few and that they do not originate from a permanent experimental network with tagged numbered trees.
Some attempts to slightly modify the form of the equations have been performed in a preliminary study (Dentand 1990) but improvement was not important and this direction was not followed up.

Refinement of the fitting should be provided by extension of the data base especially towards mortality data and, above all, towards increment data from young stands. Data from plots in stands younger than 40 years are almost completely lacking in the current data base.

Validation tests presented above are the first performed for adaptation of SPS to Austrian black pine. Validation will be carried on with new completely independent stand data. Results obtained for now are considered as promising. Although statistically significant, biases observed are small in amount.

Considering growth periods without thinning :
- mean diameter predicted are good (virtually unbiased),
- the slight overestimate of stem number is probably related to the only partial fitting of mortality model,
- and errors on basal area prediction arise mainly from those on stem number.

Considering growth periods including a thinning, the stress must be put on the fact that 5 of the 8 plots with thinning included in the growth period were subjected to a cutting aimed at inducing or preparing natural regeneration (most stands in this study were rather old). In such a case, the cutting is much heavier than a stand improvement thinning and growth prediction might be more imprecise.

In addition, the thinning characteristics were known but not the complete stand table just after thinning (stem number for each diameter class). Therefore, the growth periods used were beginning several years before the thinning (8 years before, on average) and were ending at least 5 years after the thinning (10 years after, on average). The prediction concerned growth before and after thinning together. The mean total length of these growth periods is 18 years versus 9 years for growth periods without thinning.

Last of all, these thinnings were operationally designed and could not be exactly specified using thinning specification criteria such as diameter limit for cutting from below or [dbh cut/dbh before] ratio.

In spite of all this and of the weak number of observations, the results of the tests with growth periods including a thinning are rather good. Certainly, further validation with more observations is necessary in order to confirm these first results.
Better results could probably be achieved with a growth period beginning immediately after thinning and with the complete table (stem number for each diameter class) of the remaining stand used as a starting point.

Concerning the stem number, the amount of the bias revealed by the validation test is very small compared with the average stem number reduction during the period. One reason for this is that approximatively 90% on average of the disappeared stems were removed by the thinning, this thinning being specified by residual stem number (with a diameter limit in addition). After thinning, mortality is low as the weakest trees are usually removed.
Generally speaking, when stands are under normal thinning regimes with lower stocking levels than in unthinned stands, mortality should be lower and therefore the mortality prediction should be better in absolute value.

Whether the growth period included a thinning or not, the top height predicted was correct. However, for several plots the prediction was not good unless a particular growth type number was specified in input. Taking local conditions into account via the growth types technique proved useful in this study. This suggests for practical use of the model that dominant trees (at least two) should be felled in the stand in order to count total age, and measure current height and the height 20 or 30 years ago. These data give a way to evaluate growth type number when no information on past top height is available.

Finally, it should be noticed that the rather good results in these validation tests are obtained for short growth periods (from 4 to 21 years, 11 years on average). Prediction in a subsequent period might diverge from real growth if the values predicted for the first period were taken as the new starting point.

CONCLUSION

This first attempt to fit SPS to Austrian black pine is globally positive. In spite of difficulties lying in the amount and nature of data available, it has been shown that adaptation of an existing model is possible under certain circumstances.
A favourable circumstance is probably the stratification of model functions into potential and modifier effects. We suppose that such a model is more qualified for taking into account the behaviour of various tree species, for example their specific ability to undergo competition.

Certainly the model adapted here cannot be operational for forest management as it stands. Further improvements have to be undertaken and the adaptation has to be worked towards an end : reduce the growth step of the model to a level more suitable to Austrian black pine vigour, convert the existing volume table into taper equations ...

The most important improvement will be the extension of the range of model validity towards younger stands, currently lacking in the fitting data base. As a large percentage of older black pine stands have been renewed, young stands now cover wide areas. At the same time, silvicultural practices become more and more varied. And the young stage is the time of maximal impact of silvicultural operations on the future growth of the stand.

This extension of the model range has already been prepared by starting the establishment of a new permanent experimental network. In each location of this network, three to five treatments are compared on research trial basis with individual measurement of each tree. The experimental treatments are very diverse (including a control and a very heavy thinning) in order to avoid the problem met with the yield tables when silvicutural practices are changed.

The more the forest service will be interested in this growth model the faster this network will be developed.

The first adaptation presented here will help convince forest managers. Such a decision tool will allow adjusting treatment regimes to the goals stated by the management plans. The model will provide the wanted informations about stem distribution in size classes and then in potential product types, both for cuttings and main stand.

As product quality is as important as product size, we started studying the influence of growth conditions, including pruning, on branching (and then on knots). This kind of informations could be added to current output of the model.

Other secondary prediction models could be added after the growth model. As fire risk is at a high level in the South East of France, the possibility of predicting brush development from predicted stand characteristics (stand closure, mean crown ratio ...) should be investigated.

At last, it should be kept in mind that whatever the quality of a forest stand growth model will be, the growth forecast will never be perfect because of the influence of climate on tree growth and on mortality, even when only competition induced mortality is considered.

But the interest in a growth model is not reduced for that : anyhow this tool can be used at least to elaborate treatment regimes and range and landscape management strategies in accordance with the various goals assigned to forest stands.
This would be particularly useful for Austrian black pine in French conditions because of the lack of traditional silvicultural knowledge appropriate for present and future situations.

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Beyond Covariance Analysis: Modeling the Effect of Thinning on Individual Tree Diameter Growth

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An increase in individual tree diameter growth typically follows thinning. Experimental units for thinning studies are often a fixed-area plot. In classical covariance analysis the average diameter would be used as a covariate to predict average diameter growth. As a minor expansion, the covariate does not necessarily need to enter the equation as a linear function. Using plot averages may obscure differences in post-thinning growth. However, while modeling growth of individual trees rather than plot averages overcomes some of these problems, other problems arise--observations are not independent and ability to define a thinning response as a single number is lost. Real and contrived data sets are used to describe problems and opportunities in analysis of thinning experiments. The objectives of the analysis define the best method.

GENETIC DIFFERENCES IN BASAL AREA CARRYING CAPACITY: EVIDENCE FROM A CLOSE-SPACING STUDY

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ABSTRACT

Five years of data from a close-spacing study of five open-pollinated loblolly pine families indicated that stand basal area (assessed at 1 feet or .3 meters above groundline) converges toward an asymptote whose level differs by family. For a given dominant height, better families tended to have higher basal areas and higher numbers of trees. The close-spacing plots exhibited many of the same stand development trends over a short time interval as conventional stands do over longer periods, allowing tests of treatment response sooner than is possible with conventional field studies. The study included five open-pollinated families, representing a broad range of known height performance, and utilized a square planting spacing of 1.5 feet (0.5 m) to accelerate competitive interactions and self-thinning. Relationships involving stand basal area, percent survival, mean diameter, dominant height, and age were examined, and curves of basal area and survival over dominant height were modeled by nonlinear least squares. Results suggest that growth and yield models cannot necessarily be adjusted to account for genetic improvement simply by adjusting the height - age relationship. Validation of this result, and of the general approach of using close spacings to accelerate stand dynamics, must await longer-term data from companion plots of more conventional spacings.

INTRODUCTION

The forest products industry of the southeastern U.S. has made a substantial investment in tree improvement programs for loblolly pine. Today these range from traditional tree breeding with deployment of selected open-pollinated families, to exploration of clonal forestry opportunities and biotechnology research. All such ventures are costly, but the potential payoffs are thought to be high. Unfortunately, assessing the magnitude of that potential is difficult, even when we restrict the question to gains in total wood fiber production. Most data from genetic trials are designed to rank family differences, achieving efficiency through the use of single-tree plots or row plots. Such trials have been highly successful for their intended purpose, but are not designed to quantify yield response. The large plot sizes and long duration required for appropriate assessment of yield response make such studies difficult. Hence, decisions to invest in tree improvement programs and research are made with little observed data on the productivity gains (volume per unit area) we can expect from genetic improvement.

In spite of the scarcity of yield-response data, growth and yield modelers have, of necessity, addressed the question of genetic gain. A readily observable outcome of genetic improvement is increased tree height over that of unimproved trees at a given age. Estimates of such a height gain are readily available from any remeasured genetic trial, including single-tree or row-plot tests, and can be applied to the height-age or site index curves which drive many growth and yield models. Using such a height adjustment to account for genetic improvement is a common convention, and has been suggested by a number of loblolly pine modelers (e.g. Buford and Burkhart 1987, Sprinz et al. 1989).

A height-based approach is appealing, particularly because the height-age relationship is often a fundamental component of growth and yield models. For example, Harrison and Daniels (1988) described a system of equations for modeling loblolly pine growth and yield in which stand basal area and number of trees per unit area are predicted from dominant height, which removes some variation due to site quality, and allows any particular height-age or site index model to be inserted to drive the basal area and survival predictions. Stand volumes are then derived from relationships of basal area, dominant height, and mean size. Changes in the height-age pattern are thus propagated through the entire system, implying corresponding changes in volume per acre. We can be fairly comfortable with estimating the stand volume response to height-age differences when those height differences arise from differing soils and climate (embodied in the useful but imperfect concept of *site index*). But when height differences arise from intensive management such as genetic improvement, we are left with more uncertainty as to the nature of the volume response.

Stands of differing site quality tend to support different levels of basal area carrying capacity (Strub and Bredenkamp 1985, Harrison and Daniels 1988). Do height gains from genetic improvement imply similar gain in carrying capacity, or is the basal area asymptote fixed by soils and climate, and simply approached faster by superior genotypes? This question has yet to be answered with certainty.

Buford and Burkhart (1987) and Buford (1989) reported genetic differences due to geographic seed source in tree and stand volume for fully-stocked self-thinning loblolly pine. These analyses used perhaps the only available long-term study for assessing genetic effects on loblolly pine yield, the Southwide Pine Seed Source Study (Wells and Wakely 1966). Buford and Burkhart (1987) reported no genetic effects on volume when dominant height and number of trees are correctly specified. Buford (1989) invoked the framework of the -3/2 power rule to depict volume gain when height and survival are not specified. Because volume is something of a "composite" measure of stand development incorporating both height and stand density, these results are difficult to apply in model systems that rely on component equations for more fundamental attributes of stand dynamics (i.e. height, basal area, survival). Also, the genetic variation represented by that 40-year old study may be different from the variation represented by today's tree improvement programs and open-pollinated family deployment. We have moved from exploiting differences between seed sources to exploiting differences

within a seed source. The genetic differences in which we're most interested represent a moving target, and this will always be so when we rely on long-term field studies to test the yield performance of rapidly changing populations.

An approach with some promise for addressing this "moving target problem" is to accelerate the development of stand dynamics (i.e. "compress time") in field studies by utilizing a close spacing. Franklin (1983) used this approach in a genetic gain test, with square spacings as close as 1 foot (.3 m), but results are somewhat confounded by overly small plot sizes and inadequate buffer between treatments. Burkhart and Amateis (1987) established a "miniature spacing study" (without additional treatments) to compare the behavior of closely-spaced seedling stands (spacings on the order of inches) over short time intervals to that of a conventional spacing study over longer time intervals. Westvaco Corporation established a genetic gain test in 1988 using three square spacing treatments ranging from a near-conventional spacing of 6 feet (2 m) to a close spacing of 1.5 feet (.5 m). At age 5, plots of the latter spacing exhibit substantial competition and self-thinning.

This paper will present general results from the close-spacing plots of the Westvaco study. A comparison of close-spacing stand development patterns with those expected for a conventional stand will be presented, followed by a model-based analysis of genetic gain in basal area growth, survival, and mean diameter. The validity of using such close spacings to compress time in genetic trials has yet to be determined, and will require comparison of these results with results of similar analyses on data from the study's wider spacings at corresponding states of competition.

METHODS

Data

Westvaco's Loblolly Pine Genetics X Spacing Study was established in two adjacent old fields in the 1987-88 dormant season. The study objective was to test our ability to identify and describe genetic effects on growth and yield traits of loblolly pine by using close spacings to accelerate stand development. The study site is a Goldsboro soil, a moderately well-drained loamy sand. Five open-pollinated families were used in the genetic treatments, representing height performance levels (Hatcher *et al.* 1981) ranging from 31 to 77. For the first three years of the study, competing vegetation was controlled with herbicides as necessary to provide a weed-free environment. First-year mortality was replaced with seedlings of appropriate families planted in buffer areas. Seedlings were hand-planted in 100-tree plots representing a given genetic treatment, with a 64-tree interior measurement plot (hence two border rows lie between adjacent measurement plots). Buffers of 30 feet or more were provided between adjacent spacing treatments.

A number of spacing and genetic treatments were included in the experimental design, to test hypotheses regarding genetic differences in stand development between families, between single-family plots and mixture plots, and between close and conventional spacings. For this paper, only the five single-family-plot treatments of the closest spacing (1.5 ft, .5 m) were utilized. This portion of the study includes six plots of each family, or 30 plots in all.

The close-spacing plots have been remeasured annually for five years. Survival and total height were recorded each year. Diameter at breast height (dbh) was recorded each year for trees at least 4.5 feet (1.3 m) tall. One replication of each close-spacing plot was destructively sampled at ages 2 and 4 for biomass, stem taper, and crown attributes. Hence all six replications for each family are available at ages 1 and 2; five are available at ages 3 and 4, and four remain at age 5. The total number of observations across families and time is 130.

For this analysis, individual-tree data on survival, height, and diameter were summarized to compute percent survival, dominant height, relative spacing, and stand basal area for each close-spacing plot. Dominant height was computed as the mean height of all trees with diameter larger than the quadratic mean diameter. (At age one, dominant height was set equal to mean height of all trees.) Relative spacing was computed as the ratio of average inter-tree distance (assuming square spacing) to dominant height. In addition, diameter at one foot (.3 m) above groundline (d_1) was estimated for each tree at each year based on taper data from destructive samples, and a non-destructive subsample of one replication at age five. (Estimates for d_1 at age one were extrapolated from a model developed from small trees at age two.) The d_1 estimates were constrained such that d_1 is always greater than or equal to dbh, and the annual growth in d_1 is non-negative. These data were also summarized to values of "stand basal area" and a corresponding "dominant height" based on trees larger than the quadratic mean d_1 was also computed.

Graphical Analysis

General time trends for survival, relative spacing, stand basal area, dominant height, and mean diameter (summarized across families) were plotted and compared to expected time trends from a conventional-spacing loblolly pine model (Harrison and Daniels 1988). The model projections were for a stand with site index 80 feet (24 m), base age 25, a square spacing of six feet (2 m) between trees, and perfect survival at crown closure. These inputs were selected to simulate the expected behavior of the widest-spacing companion plots in the study, which are not yet old enough to provide an empirical comparison. The "basal area crash" phenomenon which this model provides was removed to simplify these comparisons, as neither these close spacing plots nor those examined from other close-spacing studies exhibit a basal area "crash" in spite of their high densities.

These stand-development comparisons were used to subjectively assess the degree to which close-spacing plots mimic the behavior of conventional spacings, but on different scales. As part of this assessment, stand

basal area (assessed at breast height) in the close-spacing data was found to be unsuitable as a measure of stem and stand development analogous to conventional measures of stand basal area. Radial growth at breast height over the first five years of a close-spacing plot is at first nonexistent, and later occurs within or just below the crown where radial growth can be substantial even under intense competition. Assessing basal area at 1 foot (.3 m) above groundline (via estimates of d_1) provides a measure of stem and stand development for short-term close-spacing plots that is more analogous to dbh in long-term conventional spacings, in which breast height is usually well below the base of the live crown.

Family-specific development curves for dominant height over age, and for basal area, survival, and mean d_1 over dominant height were plotted to gain insight into how growth and yield traits were affected by genetic differences, and to suggest model forms for testing hypotheses about those differences via regression.

Statistical Analysis

To test for genetic differences in stand development curves, mathematical models were fit to the data using linear or non-linear least squares (PROC REG, PROC MODEL; SAS Institute 1988, 1990). A "full model" was fit with family-specific parameters, then a "reduced model" was fit with parameters of interest held constant across families. The F-statistic for comparing full and reduced models was formed as follows:

$$F = \frac{(SSE_r - SSE_f) \;/\; (df_r - df_f)}{SSE_f \;/\; df_f}$$

Where $SSE_{r,f}$ = sum of squared error and $df_{r,f}$ = error degrees of freedom (for reduced and full models, respectively).

For large values of the F-statistic, the null hypothesis that there were no genetic differences in model parameters of interest was rejected.

RESULTS AND DISCUSSION

Overall Stand Development

The concept behind a close-spacing study such as this one is that experimental plots at close spacings should behave just like conventional stands, but in miniature and much faster. Hence results from the experimental plots could be examined on different spatial and temporal scales. A miniature spatial scale is necessary because competition and self-thinning occurs when trees are much smaller than in conventional stands at a similar developmental state. A compressed time scale is necessary because competition and self-thinning are achieved much sooner.

The true extent to which such scaling can be applied will be unknown until companion plots at wider spacings reach similar developmental states. Such an empirical validation is also important for verifying any apparent genetic effects on stand development, regardless of scale. In the meantime, it is instructive to compare the overall behavior of the close-spacing plots to the expected behavior of a conventional model (Harrison and Daniels 1988) to assess the "realism" of stand dynamics at close spacings.

Some measures of stand development are dimensionless, so that examining them in a close-spacing context requires no particular spatial scaling. The trend of percent survival over time, for instance, is a useful measure of the degree to which competition and self-thinning has reduced stand density. Percent survival (number of trees surviving as a percentage of the number planted) is particularly appealing for comparing close-spacing plots with a conventional stand because it is computed from count data, rather than measurements along spatial dimensions.

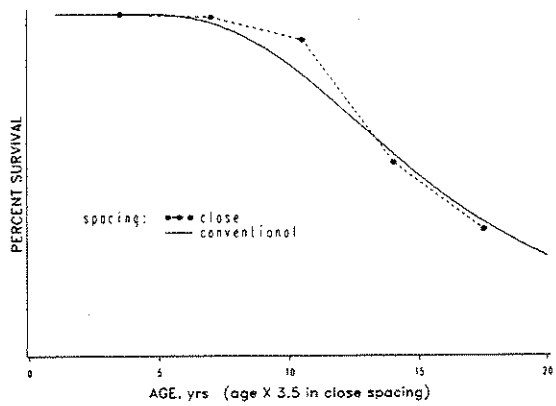

Figure 1. Percent survival over scaled time for close spacing, compared to model predictions for conventional spacing.

Figure 1 depicts percent survival, averaged across all families, over time for the close-spacing plots compared to that for the conventional model. The time axis was multiplied by 3.5 for the close-spacing data, in order to achieve the close correspondence between the curves. In both curves, percent survival is 100% until the trees grow large enough to experience inter-tree competition and the onset of self-thinning. Mortality then proceeds as the most disadvantaged trees lose the competition for resources. The chosen scaling factor implies that this process occurs about three-and-a-half times faster in the close-spacing plots than the conventional model would imply.

The same temporal scaling factor of 3.5 was applied in graphical comparisons of two other dimensionless measures of stand development, averaged across families (Figures 2 and 3). Relative spacing is the ratio of inter-tree distance to tree height, and stand basal area can be expressed as the ratio of total stem cross-sectional area to ground area. While each of these measures are dimensionless (the distance and area terms cancel), their computation does involve comparing spatial measurements (height and inter-tree distance, stem area and ground area).

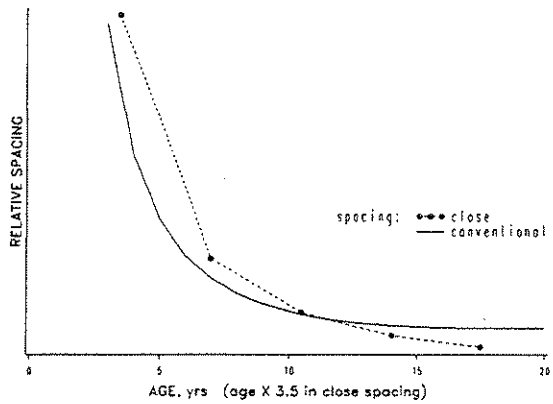

Figure 2. Relative spacing over scaled time for close spacing, compared to model predictions for conventional spacing.

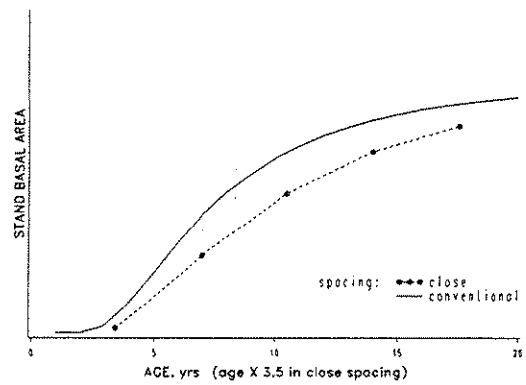

Figure 3. Stand basal area over scaled time for close spacing, compared to model predictions for conventional spacing.

In Figure 2, the shape of the relative spacing curves are similar, but not as closely matched as the percent survival curves. Both appear to be approaching some minimum value, or size-density limit, but the limit approached by the close spacing is clearly lower than that of the conventional model. In Figure 3, both curves imply that the rate of basal area accumulation moderates over time (due, presumably, to competition and mortality) and approaches an asymptote. But in this case, basal area per unit ground area is consistently less than the conventional model would indicate.

Figures 1-3 suggest that in these close spacings, stand development is proceeding in a fashion similar to that of a conventional stand, but the relative spacing and stand basal area comparisons (Figures 2 and 3) indicate that relationships of tree dimensions (height or stem area) to growing space (inter-tree distance or ground area) might not be the same as expected in a conventional stand. This conclusion is subjective however, since a different choice of temporal scaling factor would improve the correspondence between the curves in Figures 2 and 3, while worsening that of Figure 1.

Comparing absolute measures of stand development (e.g. dominant height, mean diameter) in close-spacing and conventional stands is more problematic, as a spatial scaling factor must be introduced. In this case, a scaling factor of 4 is implied because we have fixed the initial spacings being studied at a ratio of 4:1 (6 ft vs. 1.5 ft, 2 m vs. .5 m). Figures 5 and 6 illustrate such a comparison for time trends of dominant height (Figure 5) and diameter (Figure 6), averaged across families. For consistency, the same temporal scaling factor of 3.5 is retained, while height and diameter values are multiplied by 4.

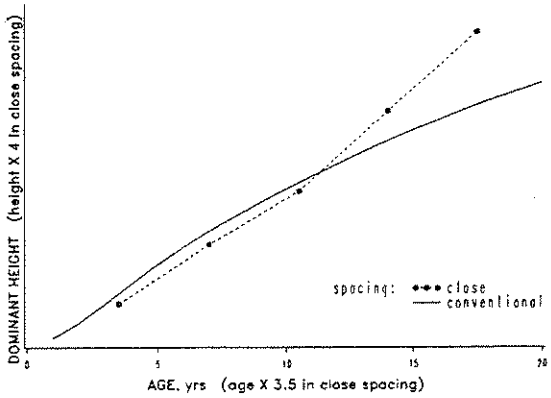

Figure 4. Scaled dominant height over scaled time for close spacing, compared to model predictions for conventional spacing.

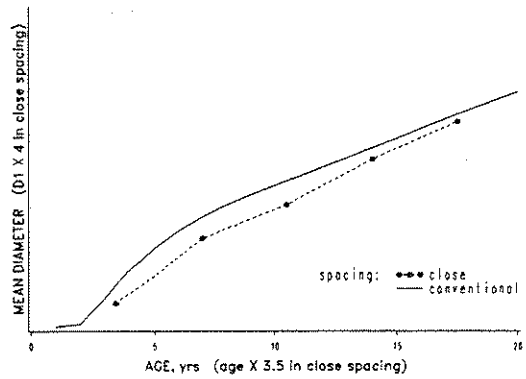

Figure 5. Scaled mean diameter over scaled time for close spacing, compared to model predictions for conventional spacing.

As one might expect, the scaled height curve does not have the same shape as a long-term height curve. Height growth for the close-spacing plots has not declined, and departures from linearity are related more to annual weather than to stand dynamics. The scaled diameter curve has a more appropriate shape, but its level is somewhat lower than diameter growth from the conventional model (reflecting the stand basal area difference observed in Figure 3). Again, different choices for scaling factors would change these comparisons. The scaling factors used in this exercise were chosen simply to be consistent with the time scale of the percent survival comparison (Figure 1) and the spatial scale implied by comparing spacings of 1.5 feet (.5 m) and 6 feet (2 m).

While interpreting the absolute value of stand attributes from close spacing plots is probably unwise, the general shapes of many stand development curves appear to be plausible and interpretable. It seems reasonable to assume that the biological processes and interactions that give rise to such curve shapes in both close-spacing plots and conventional stands are essentially the same, regardless of the initial spacing and time scale.

Based on that assumption, any genetic differences in stand development exhibited by the close-spacing plots may be treated as preliminary evidence for such differences in conventional stands. To examine such differences, analyses were performed as if the plots had been planted at conventional spacings and monitored over a longer period of time. However, since we are most interested in genetic effects on the parameters and forms of stand development curves, rather than their absolute numerical implications, no particular scaling is employed.

Genetic Differences

For this paper, the five families will be labeled simply as Families 1 through 5 in order of decreasing height performance (as previously

assessed in progeny tests). As shown in Figure 6, the development of dominant height over time for these data is relatively consistent with the families' known height performance. The difference between the three best families and the two worst families is still diverging.

A useful stand modeling convention is to exploit established height-age patterns to better describe other development curves, such as survival or basal area. Using dominant height as "time" when modeling such development curves removes a source of variation previously identified in the height-age curves. Applying that convention here, we find that using dominant height as "time" does not remove variation due to genetics from either the basal area curves (Figure 7) or the survival curves (Figure 8). The genetic differences appearing here are similar in ranking to the differences in height, but the correspondence is not exact. Apparent genetic differences in the mean diameter curves (Figure 9) are less consistent with the other rankings. Figures 7-9 plot only mean values across all replications; determining the actual significance of any apparent differences requires a statistical test, and cannot be discerned from the figures.

Figure 7 does suggest, however, that the basal area curves are asymptotic with apparent differences occurring primarily in the asymptote of the curves, or basal area carrying capacity. To test for such differences, the Chapman-Richards growth function (Pienaar and Turnbull 1973), a flexible 3-parameter sigmoid curve, was specified as a model for the family of basal area curves:

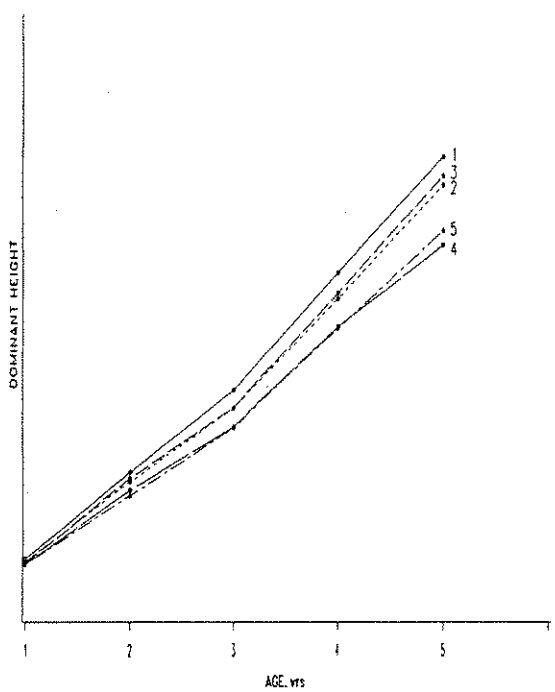

Figure 6. Dominant height for open-pollinated families 1-5 at close spacing.

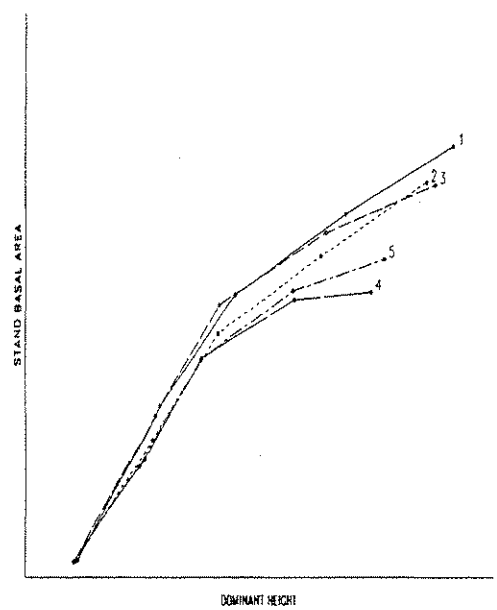

Figure 7. Stand basal area (at one foot) over dominant height for open-pollinated families 1-5 planted at close spacing.

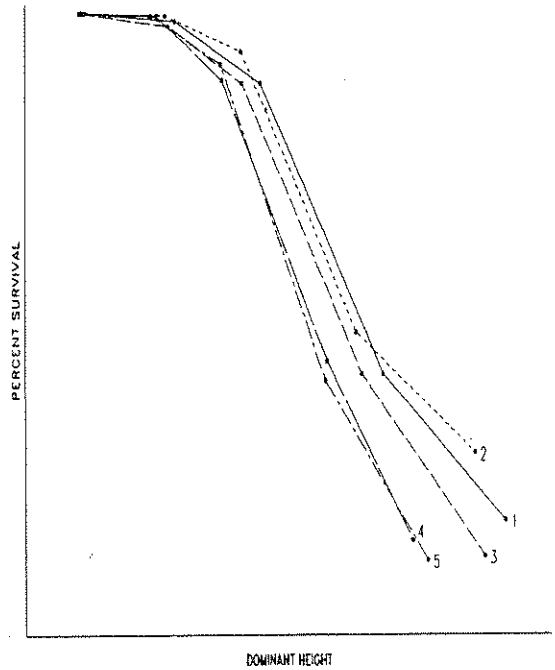

Figure 8. Percent survival over dominant height for open-pollinated families 1-5 planted at close spacing.

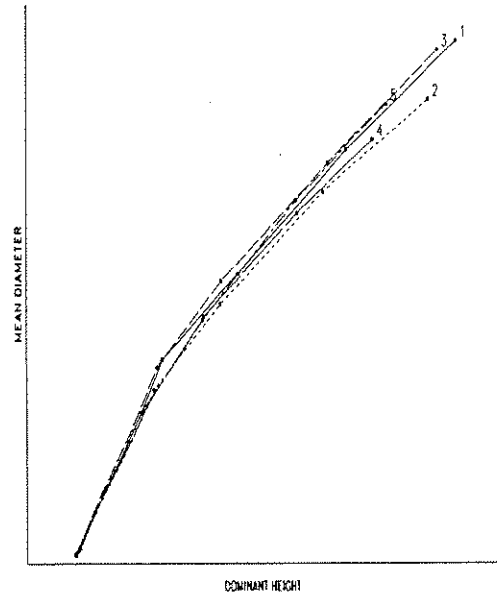

Figure 9. Quadratic mean diameter (at one foot) over dominant height for open-pollinated families 1-5 planted at close spacing.

$$B = a\ (1-e^{-b(H\ -\ 1)})^{c} \qquad (1)$$

where

B = basal area per acre (at one foot above groundline)

H = dominant height

a,b,c = parameters to be estimated for each family with nonlinear (ordinary least squares) regression.

Equation 1 is conditioned so that B is zero when H=1, and B tends toward an asymptote (carrying capacity, parameter a) as H gets large. Parameters b and c determine the rate and shape of the approach to carrying capacity. Equation 1 was fit to all 26 observations of basal area and height for each of the five families. The resulting set of five equations with 15 unique parameter values constitutes the full model for basal area growth. A reduced model was then specified in which parameter a, which defines the asymptote, was held constant across all families. In each case, the nonlinear regression produced excellent fits to the data, with no bias or extraneous correlation in residuals. Plotted curves of the full model are almost indistinguishable from Figure 7. The F-test for full vs. reduced models indicated that we could reject the null hypothesis that the asymptotes are equal (Table 1).

Table 1. Full-versus-reduced model F-tests for genetic differences in basal area carrying capacity, survival over height, and mean diameter over height.

TEST	Full Model SSE	Full Model df	Reduced Model SSE	Reduced Model df	F-statistic	p-value
BA Carrying Capacity	22192	115	27122	119	6.39	.0001
Survival over Height	.2799	120	.4979	128	11.7	<.0001
Diameter over Height	.1639	60	.2669	68	4.71	.0001

A similar test was carried out for the survival curves. An analogous sigmoid model was specified:

$$S = 1 - (1-e^{-b\,H})^{c} \qquad (2)$$

where

S = survival proportion (number of trees surviving as a fraction of establishment density).

H = dominant height

b,c = parameters to be estimated for each family with nonlinear (ordinary least squares) regression.

Equation 2 is conditioned so that S is 1.0 when H=0, and S tends toward zero as H gets large. Parameters b and c determine the rate and shape of decay in the survival curve. No lower asymptote on S was deemed necessary because we would expect such a number to be very close to zero as a fraction of this establishment density (19360 trees/ac, 47838 trees/ha). As before, the full model was fit with different parameter values for each family. In this case, the reduced model was specified by holding both the b and c parameters constant, as it is difficult to make a clear distinction between their roles in defining the shape of the curve. As before, the nonlinear regression produced excellent fits for both full and reduced models, with the plotted curves from the full model appearing almost indistinguishable from Figure 8. The F-test (Table 1) indicated that we could reject the null hypothesis that the survival curves are equal.

Because the relationship of mean diameter (Figure 9) to dominant height is conveniently linear for ages 3-5, only these years were used in testing genetic effects on this relationship. A simple linear regression of mean diameter as a function of dominant height was fit with family-specific coefficients (full model) and fixed coefficients (reduced model). Once again, the F-test indicated that we could reject the null hypothesis that the diameter-height lines were equal.

Table 1 presents the error sums of squares, degrees of freedom, F-statistics and p-values for all three tests. These tests suggest that basal area carrying capacity can be significantly altered by genetic improvement, and that genetic differences also appear in survival and mean diameter for a given dominant height. Figures 7-9 suggest that the carrying capacity differences are probably more closely related to differences in survival than differences in mean diameter, given the divergence in survival (Figure 8) between the three better families and the two poorer families.

The genetic differences in carrying capacity and survival reported here represent possible mechanisms (in addition to adjustments in the height - age curve) for incorporating genetic improvement effects in growth and yield models. While these differences are distinct from height gains noted by previous researchers, they may still be explainable by changes in "site index" (i.e. projected height of a particular family at an arbitrary base age) depending on the structure of the growth and yield model applied. For instance, in the model of Harrison and Daniels (1988), site index determines the level of carrying capacity, even though dominant height is already in the model as the "time" variable. The carrying capacity estimates derived from this study are indeed related to observed height at age 5 (analogous to site index) though the correspondence is not perfect (Figure 10). Similarly, site index may function in survival models to allow higher sites to maintain a higher number of trees at a given dominant height (Assman 1970, Buford 1979). Such a relationship would also be generally consistent with these data. Those wishing to use reported genetic differences in height, basal area, survival, or volume to adjust an existing growth and yield model should have a clear understanding of all the relationships and assumptions inherent in that model.

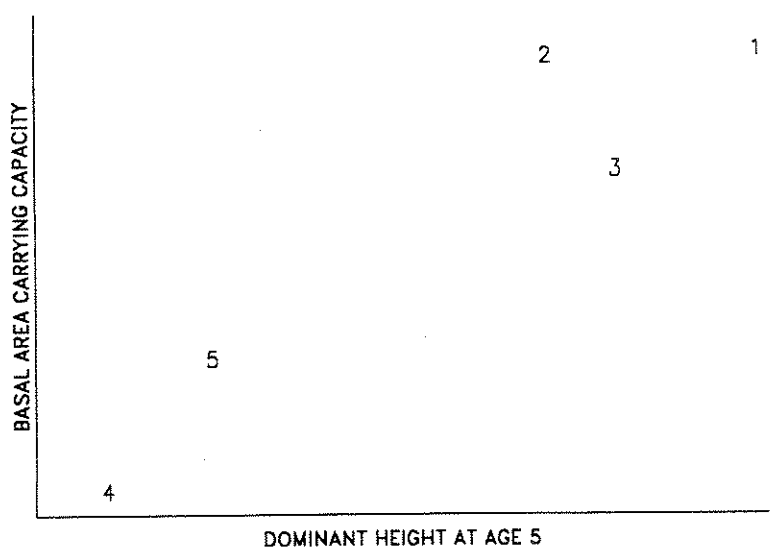

Figure 10. Relationship of basal area carrying capacity (parameter *a* in equation 1) to dominant height at age 5, for open-pollinated families 1-5 planted at close spacing.

CONCLUSION

Experimental plots at close spacings appear to exhibit many of the same stand development trends over a short time interval as conventional stands do over longer periods. This similarity provides an opportunity for relatively quick tests of differences in stand development due to silvicultural treatments, tests that require only a fraction of the time required by conventional long-term growth and yield studies of treatment response. However, the validity of close-spacing results must await comparisons with companion treatments at conventional spacings.

The close-spacing results reported here indicate that genetic improvement not only alters the height - age curve, but also affects basal area carrying capacity. Higher basal area levels at a given dominant height tend to be associated with higher numbers of trees.

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HEIGHT AND DIAMETER INCREMENT RELATIONSHIPS FOR EUROPEAN MIXED SPECIES STANDS

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ABSTRACT

Monserud's (1975) model for simulating Wisconsin hardwood stand dynamics was modified by using 22 permanent plots of mixed Norway spruce (*Picea abies* L. Karst) - Scots pine (*Pinus sylvestris* L.) stands and 5 plots of mixed Common beech (*Fagus silvatica* L.) - Norway spruce stands. The data consisted of trees' coordinates and the diameters at breast height, total heights and the heights to the base to the live crown of each measurement.

The potential height development was calculated with existing site index functions. A correction factor for each tree species, observation period and plot was developed in order to eliminate possible shortcomings in the potential height estimation. Because no adequate data for open-grown trees were available, which were assumed to exhibit the potential diameter development, Sterba's (1975) extension of the competition density rule of Kira et al. (1953) was applied.

Several of Monserud's proposed parameters were not significant with regard to nonlinear regression runs. The height increment models for all tree species contained the crown ratio exhibiting the past growing conditions and the competition factor (Ek and Monserud 1974) after crown release. The diameter increment models generally showed the same results. Only for Common beech the crown ratio did not affect the model. Including a release parameter increased the accuracy of the beech diameter model significantly.

Finally the influences of the significant parameters and the relative increment ratios are shown for each tree species and mixed stand type. Result of the study is that at any given competition in the mixed beech/spruce stands the more tolerant Common beech exhibited higher increment rates. In the spruce/pine stands Scots pine showed the smaller increment reductions with regard to the potential increment.

INTRODUCTION

Traditionally the European Forest system is strongly related to the idea of "ideal forests" or "normal forests" which means even-aged pure stands at different stand ages. Based on this approach yield tables were developed for simulating even-aged "reference stands" by tree species and site properties to predict the stand growth (Weise 1880, Schwappach 1890, Assmann and Franz 1963, Kennel 1965, Marschall 1975).

The increased interest in uneven aged mixed tree stands, resulting from great damages in even-aged pure stands, the improved knowledge of thinning experiments and the move in growth and yield research to a more complex view including environmental impacts on the forest, made the shortcomings of existing yield tables more and more evident.

In the sixties in North America the first single tree simulators for pure stands were developed (Newnham 1964, Mitchell 1967, Bella 1970, Arney 1972, etc.). Ek and Monserud (1974) and Monserud (1975) extended the idea by developing a single tree simulator for uneven-aged mixed tree stands. This approach offers the opportunity of the demanded flexibility in modern growth and yield research. In Europe the first steps in single tree oriented growth models were taken by Filla (1981), Sterba (1982), both based on Monserud's (1975) approach and by Pretzsch (1992).

The objective of the paper is to present the first results of an ongoing research program concerning growth simulations of European mixed species tree stands. Monserud's (1975) simulator FOREST was adapted to simulate height and diameter increment relationships for mixed Norway spruce (*Picea abies* L. Karst) - Scots pine (*Pinus sylvestris* L.) and Common beech (*Fagus silvatica* L.) - Norway spruce stands in central Europe.

DATA

Norway Spruce - Scots Pine Data

In 1977 22 permanent plots with different ages and site indices were established in mixed Norway spruce - Scots pine (spruce/pine) stands. The plots are located in the northern part of the Bohemian Massif near the border between Austria and the Tschech Republic. Remeasurements were done within a five year cycle.

For each tree coordinates, height, diameter at breast height and height to the base of the live crown were measured. With the dominant height and the mean age of the dominant trees by tree species and plot, the site index at plot establishment was calculated using Marschall's (1975) yield tables for Norway spruce and Scots pine.

In order to study increment reactions at different density levels, the plots were treated twice by selecting a number of trees at different stand levels and different levels of crown release according to the suggestions of Johann (1982).

Common Beech - Norway Spruce Data

Data for simulating mixed Common beech - Norway spruce (beech/spruce) stands came from 5 permanent plots located in the Bavarian Forest in Germany established in 1954 by Assmann and Magin (Pretzsch 1992). The four remeasurements were done in 1959, 1969, 1982 and finally 1987. Before and after plot establishment several thinning treatments took place which provided different stand densities.

Again for each tree the belonging coordinates, heights, diameters at breast height and heights to the base of the live crown were documented. At plot establishment the site indices by tree species and plot were determined by using Kennel's (1972) yield table for Common beech and Assmann and Franz's (1963) for Norway spruce.

MODEL DEVELOPMENT

The Ek - Monserud Model

The distance dependent single tree growth model of Ek and Monserud (1974) and Monserud (1975) is based on the assumption that the current annual height or diameter increment (i_{obs}) depends on the potential increment (i_{pot}) for a given tree reduced by a function of the crown ratio (CR) as the allometric multiplier representing the past growing conditions and the overstocking multiplier (OVS) for the current competition situation.

$$i_{obs} = i_{pot} \cdot CR^{b_6} \cdot OVS \tag{1}$$

The overstocking multiplier depends on the adjusted competition index (CIA) and represents the competition situation after crown release resulting either from thinning treatments or natural mortality;

$$OVS = (1 - e^{\frac{-1}{b_4 \cdot CIA}})^{b_5} \tag{2}$$

with

$$CIA = 1 + 0.1 \cdot CI \cdot (1 - b_1^{h+1}) \cdot (1 + b_2 \cdot \Delta CI)^{-b_3} \tag{3}$$

For determining the current competition (CI), Ek and Monserud (1974) weighted the influence area overlap for a given tree according to Bella (1971) by the ratio of crown radius times height for the subject and competitor trees.

This index is adjusted by the shade tolerance of different tree species depending on the tree's height (h) and the change in competition (ΔCI) by crown release.

For predicting height increment a SHIFT parameter is included in the model in order to account to the fact that young stands grow occasionally independent from stand density and that the maximum height growth may occur in a forest grown rather than open grown condition.

$$SHIFT = 1 - [b_7 \cdot (1 - b_8^{h+1})]^{CIA} \tag{4}$$

In summary, Monserud's competition model requires 8 parameters for the height and 6 parameters for the diameter increment model.

The Height Increment Model

In order to eliminate correlations between the observed height increment (ih_{obs}) and potential height increment (ih_{pot}) within an observation period the model we used has the form:

$$\frac{ih_{obs}}{ih_{pot}} = OVS \cdot CR^{b_6} \cdot SHIFT \tag{5}$$

In the model are included the overstocking multiplier (OVS) as defined in equation (2), the crown ratio (CR) and the SHIFT parameter. The potential height increment was predicted for each tree by estimating the calculatory age in dependence of the tree's height and the plot's site index.

Adding the length of growing period and reinserting in the site index function provides the future height of a tree. Consequently the difference of the two heights results in the potential periodical height increment of any tree.

Because site index curves represent only the average height increment of dominant trees for a given region, a correction factor (q) was developed as the ratio between observed height increment (ih_{obs}) of dominant trees versus computed height increment from site index functions (ih_{SI}).

$$q = \frac{ih_{obs}}{ih_{SI}} \tag{6}$$

The idea was to use existing site index functions for predicting plot, periodic and tree species related potential height increments after eliminating possible shortcomings with the correction factor.

Furthermore the correction factor (q) also accounts for environmental influences resulting from acid rain or air pollution on height increment.

Once the q values are determined from stem analyses or the data to be simulated, it can be tested, if significant relationships between the correction factor and some stand data exist.

For the spruce/pine stands stem analyses from 51 dominant Norway spruce trees and 50 dominant Sots pine trees were available. For the beech/spruce stands the correction factor was calculated from the data themselves by using only dominant trees where all 5 height measurements were available. In summary 40 dominant Common beech and 39 Norway spruce trees were used. Additionally the data consisted of different sites and ages to cover the variety of possible influences to the q value.

After calculating the correction factor for each selected tree and growing period the following linear model was applied to the data;

$$q = a_0 + a_1 \cdot A + a_2 \cdot h + a_3 \cdot SI + a_4 \cdot (A \cdot SI) + a_5 \cdot (A \cdot h) + a_6 \cdot (SI \cdot h) \quad (7)$$

where q — the correction factor per tree and period
A — tree age at the beginning of each growing period
h — tree height at the beginning of each growing period
SI — site index
a_0-a_6 — parameters to be estimated

Table 1 shows the results by tree species and stand mixture.

Table 1. Coefficients from the linear regression runs using equation (7) for determining relationships between the correction factor (q) and some stand data. The parameters in the models are significant at a 5 % probability level.

Stand-type	Species	Coefficients						
		a_0	a_1	a_2	a_3	a_4	a_5	a_6
Spruce / Pine	Norway spruce	2.701	0.0128	-	0.149	-	-	0.0076
	Scots pine	3.155	-	0.217	-	-0.0058	0.0025	0.0120
Beech / Spruce	Common beech	-0.547	0.0247	-	-	-	-	-
	Norway spruce	0.5395	0.0107	-	-	-	-	-

With the results shown in Table 1 for each tree species, stand and observation period a correction factor was computed and multiplied by the periodic height increment of the selected site index function.

Diameter Increment Model

Again only the ratio between observed diameter increment (id_{obs}) and the potential diameter increment (id_{pot}) was calculated by using Monserud's (1975) approach including the crown ratio (CR) and the overstocking multiplier (OVS);

$$\frac{id_{obs}}{id_{pot}} = CR^{b_6} \cdot OVS \qquad (8)$$

Because no adequate data from open-grown trees were available, which were assumed to show the potential diameter development, Sterba's (1975) extension of the competition density rule of Kira et al. (1953) was used for determining the theoretical development of an open-grown tree by stand mixture and tree species. After setting the stem number to zero the theoretical development of an open-grown tree can be calculated.

The height of the tree at the beginning of a growing period gives the belonging open-grown diameter at breast height. By inserting the potential height increment predicted from the tree's site index function and adjusted by the belonging correction factor, the diameter at breast height at the end of the growing period can be calculated. Consequently the potential diameter increment to be used in the model is the difference of the two diameters.

RESULTS

The Height Increment Model

After fitting the whole data set by tree species and stand mixture to the height increment model several of Monserud's (1975) estimated 8 parameters were not significant in the nonlinear regression analyses. The main driver of the model was the crown ratio and the competition factor after crown release without any adjustments. The release parameter (ΔCI), which accounts for diverse species specific responses to sudden release was removed, because either the parameter was not significant or its influence on the multiplier was unimportant. Therefore the height increment model for the simulated tree species consisted only of two parameters;

$$\frac{ih_{obs}}{ih_{pot}} = CR^{b_6} \cdot (1 - e^{\frac{-b_4}{CIA}})$$

where: ih_{obs} observed height increment
ih_{pot} potential height increment
CR crown ratio
CIA competition index after crown release

The coefficients of this equation were estimated by nonlinear regression analyses and are shown in Table 2.

Table 2: Results from the nonlinear regression runs for the height increment relationships for the Norway spruce - Scots pine stands (spruce/pine) and the Common beech - Norway spruce stands (beech/spruce).

Stand type	Species	b_6	b_4	R	n
Spruce/Pine	Norway spruce	0.6579	-2.815	0.507	1800
	Scots pine	0.1373	-15.109	0.173	221
Beech/Spruce	Common beech	0.1275	-4.810	0.393	489
	Norway spruce	0.6579	-2.815	0.456	193

b_4,b_6 parameters to be estimated
R multiple coefficient of correlation
n number of used cases

In order to test the impact of the two parameters on the height increment model, the theoretical development of different competition situations was calculated using equation (9) with the belonging parameters.

Figure 1 shows the relationship between the crown and height increment ratio as it may result from the past competition situation for each tree species in mixed spruce/pine and beech/spruce stands. The allometric multiplier CR^{b6} (see equation 9) describes the effect of the crown ratio on the height increment without any current competition.

For testing the development between the height increment ratio and competition after crown release the crown ratio was assumed to be one. This means that an open-grown tree with a crown length equal to the tree's height will be more and more overlapped by its neighbors determined by an increasing competition index. Figure 2 gives the results by tree species for the spruce/pine and beech/spruce stands.

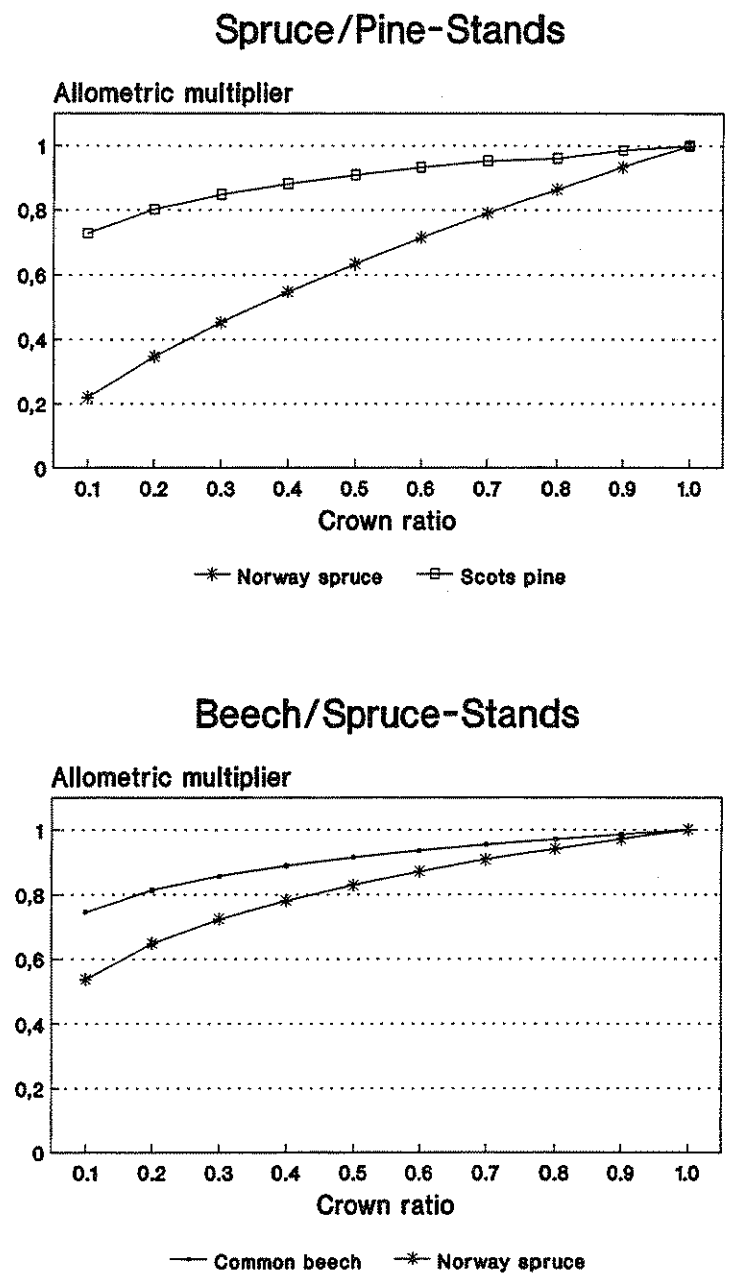
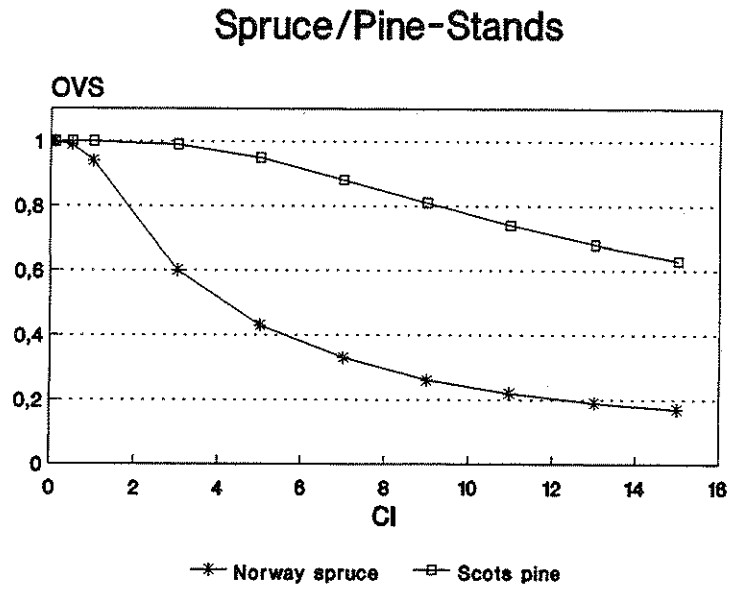


Figure 1. Allometric multiplier CR^{b6} for the height increment at a given crown ratio estimated with the parameter b_6 of equation (9) by stand type and species.



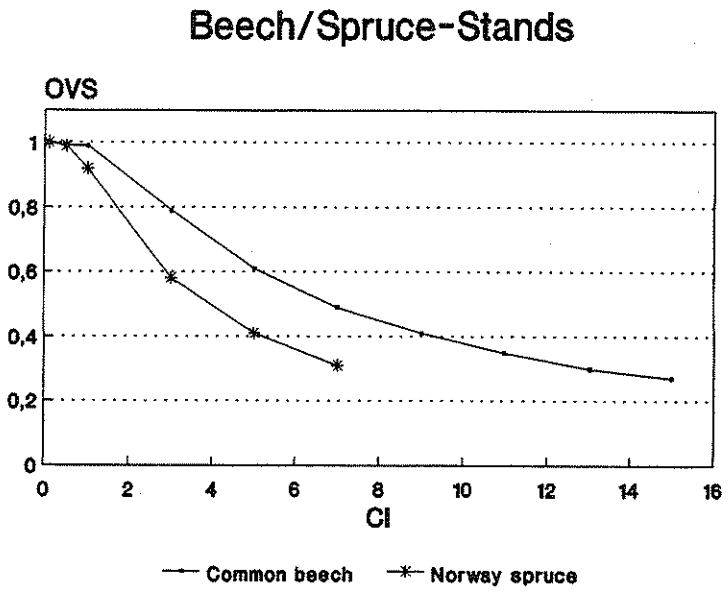


Figure 2. Overstocking multiplier (OVS) for the height increment depending on the competition index after crown release (CI) by stand type and tree species.

The Diameter Increment Model

Again the nonlinear regression runs showed that several of the 6 parameters in the diameter increment model (Monserud 1975) were not significant. For Norway spruce and Scots pine only effects of the crown ratio and the competition factor after crown release were significant. For Common beech the crown ratio did not affect the results but including the release parameter the accuracy of the predicted diameter increment ratio did improve significantly. Depending on the tree species the final form of the model was;

$$\frac{id_{obs}}{id_{pot}} = CR^{b_6} \cdot (1 - e^{\frac{-b_4}{CIA \cdot (1 + b_2 \cdot \Delta CI)}}) \qquad \textbf{(10)}$$

where id_{obs} observed diameter increment
id_{pot} potential diameter increment
CR crown ratio
CIA competition index after crown release
ΔCI crown release

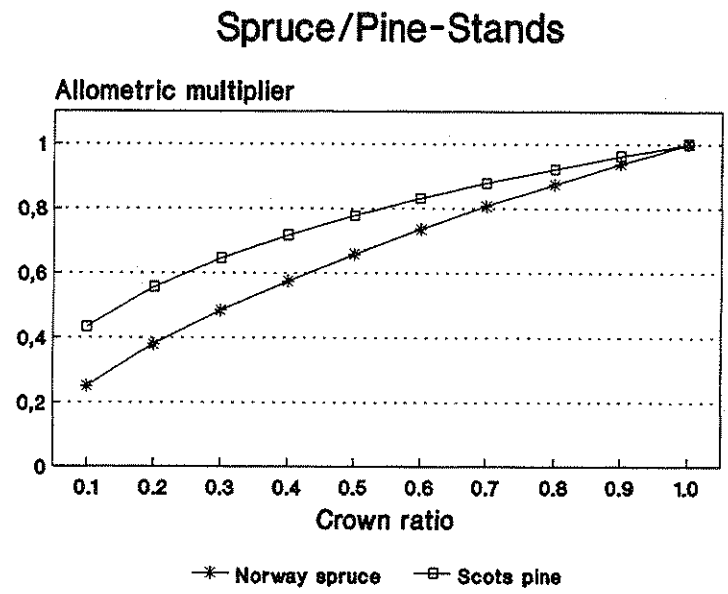
The parameters of equation (10) were estimated by nonlinear regression and are shown in Table 3.

Table 3: Results of the diameter increment relationships for Norway spruce - Scots pine (spruce/pine) and Common beech - Norway spruce (beech/spruce) stands. Parameters included in the model are significant at a 5 % probability level.

Stand type	Species	b_6	b_4	b_2	R	n
Spruce/Pine	Norway spruce	0.6026	-0.7100	-	0.577	1800
	Scots pine	0.3632	-4.6503	-	0.342	221
Beech/Spruce	Common beech	-	-1.3897	-0.2034	0.698	489
	Norway spruce	0.5870	-1.4127	-	0.653	193

b_6,b_4,b_2 parameters to be estimated
R coefficient of correlation
n number of cases o be used

Similar to the height increment relationship we wanted to investigate the theoretical impact of the used parameters within each model. Figure 3 gives us the influence of the allometric multiplier CR^{b6} to the diameter increment without any current competition. For Common beech the crown ratio is a constant because no relationships could be detected.



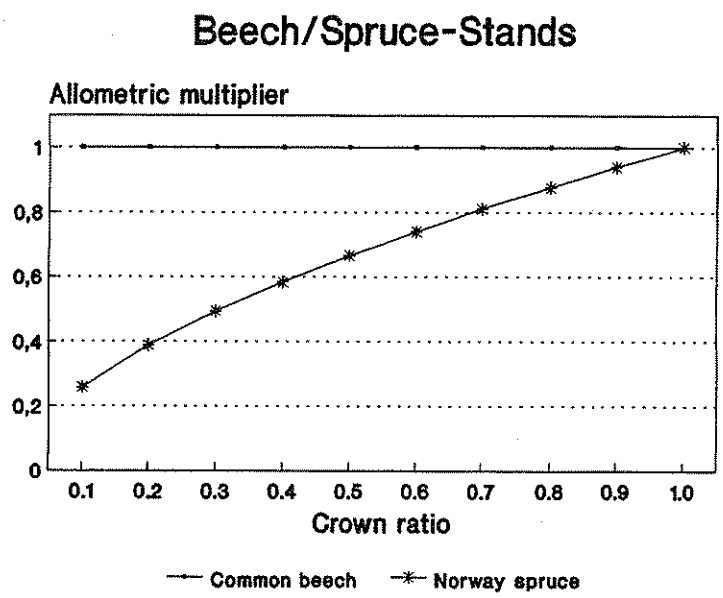


Figure 3. Allometric multiplier CR^{b6} for the diameter increment at a given crown ratio estimated with the parameter b_6 of equation (10) by stand type and species.

Figure 4 describes the overstocking multiplier by the relationship between competition index after crown release and the diameter increment ratio. An increase in overlapping

of an open-grown tree is shown. For Common beech additionally the significant influence of crown release was assumed to be zero.

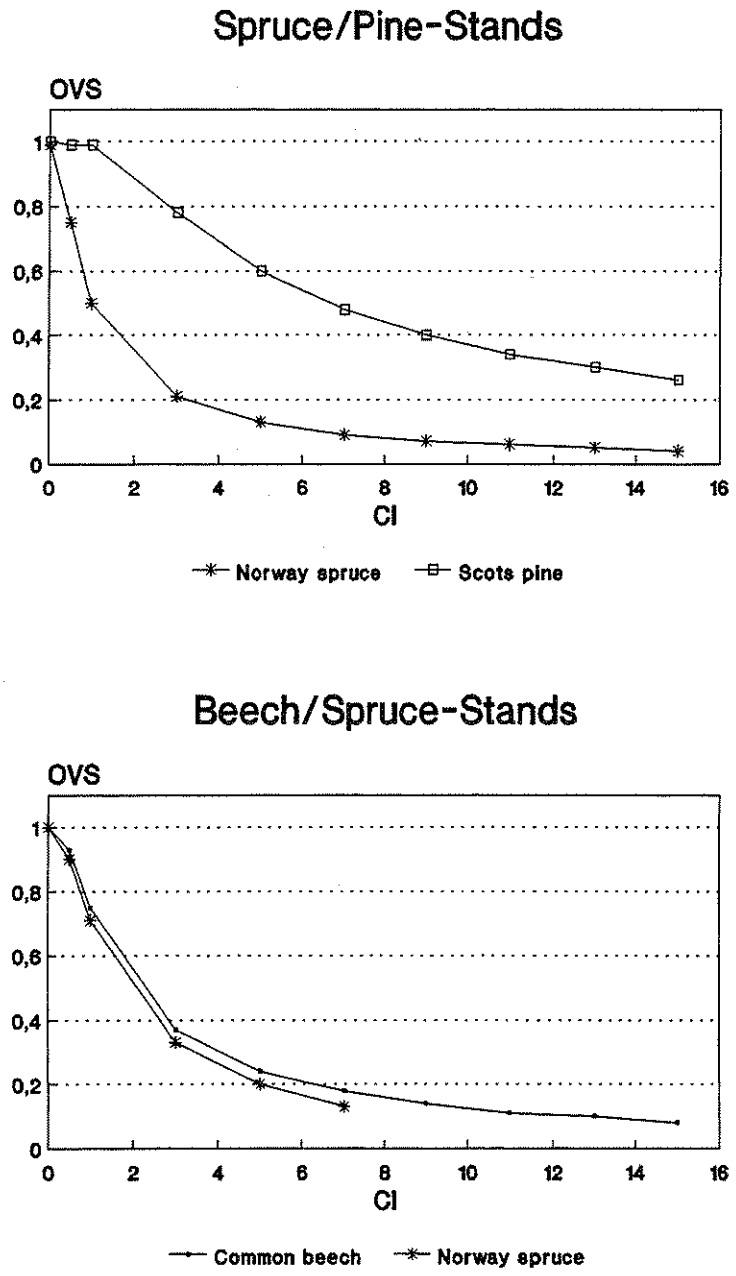


Figure 4. Overstocking multiplier (OVS) for the diameter increment depending on the competition index after crown release (CI) by stand type and tree species.

Considering the results of the Common beech - diameter increment relationship, the significant impact of the crown release parameter (b_2) leads to an acceleration of the diameter increment because the parameter was negative.

In order to get the effect of acceleration to the diameter increment ratio four different cases with an competition index (CI) of 1, 2, 3 and 4 before crown release and increasing rates of crown release were simulated. The results are shown in Figure 5. The percentage of acceleration represents the increased increment ratio for a released tree versus a tree which already had the same growing condition in the past.

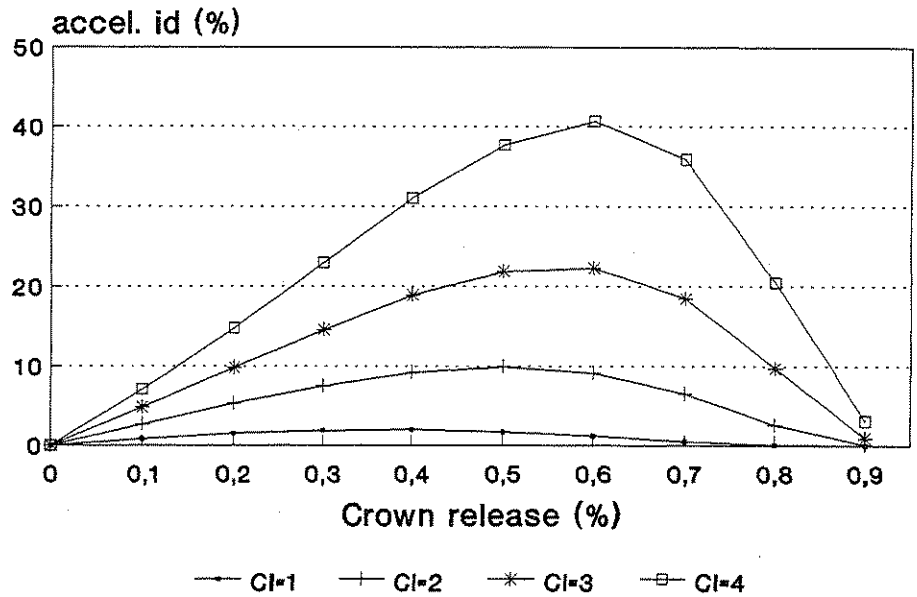


Figure 5. Percentage of acceleration in the diameter increment ratio (accel.id) caused by crown release (ΔCI) at four different competition indices before crown release. The rates in the diameter acceleration represent the influence of crown release versus a tree which already had these growing conditions in the past.

DISCUSSION AND CONCLUSION

Several of Monserud's (1975) 8 parameters in the height- and 6 parameters in the diameter increment model could be omitted. Possible reasons are the used bounds and the heuristic functions for determining the trees' height and diameter development versus our model. For each tree we used in the regression analyses the coordinates and the diameter at breast height, total height and the crown length from repeated field measurements were available.

In the model the increment ratios with regard to the potential increment were used. This results in lower multiple coefficients of correlation but on the other hand trivial relationships between potential and observed increments were excluded from the results.

The main driver in the height as well as in the diameter increment model were the crown ratio, representing the past growing conditions and the competition index (Ek and Monserud 1974) after crown release. Only the diameter increment model for Common beech showed a different behavior. The crown ratio for beech trees did not improve the model but the release parameter, which accounts for the species specific responses to sudden release, was significant.

Considering the results of Figure 1, 2, 3, and 4, in the beech/spruce stands Common beech as the more tolerant tree species exhibits the higher height and diameter increment versus Norway spruce. In the mixed spruce/pine stands Scots pine displays through all simulated relationships smaller increment reductions with regard to the potential increments. This was not expected because it is generally assumed that Scots pine is the more light demanding species. A possible reason might be the reported species specific light rates for initialize growth. According to Mitscherlich (1981), Scots pine needs at least 12 hours with light per day versus 16 hours for Norway spruce.

Crown release for Common beech is more effective if the tree 's competition index before crown release is higher (see Figure 5). The proportion of increment acceleration determined between the ratio of crown release versus a tree, which already had these growing conditions in the past, reaches a maximum. In summary it can be concluded that trees with higher competition indices before crown release provide a higher percentage of acceleration. After reaching a certain point, the impact of acceleration decreases quickly.

Finally it can be seen (Table 2) that Norway spruce exhibits in both mixed stand types a very similar behavior in the height increment due to almost no differences in the predicted parameters. In the diameter increment model (Table 3) the influence of the crown ratio is also nearly the same. Only the competition index - diameter increment ratios differed slightly between the two stand types. This may account for different competition situations resulting from the influence of the second tree species.

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WATER AND NUTRIENT REGIMES AND THINNING RESPONSE IN SCOTS PINE STANDS ON DRAINED PEATLAND

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ABSTRACT

The relationships between thinning intensity and the groundwater table level, as well as between thinning intensity and the nutrient status of Scots pine (*Pinus sylvestris*) stands were investigated on drained minerotrophic peatlands in northern Finland. In the experiments, 0 - 50 % of the initial stand basal area was thinned from below. The groundwater table level was monitored during the growing seasons following thinning. The foliar nutrient concentration of trees representing different canopy layers was determined 3 and 4 years after thinning. Thinning intensity influenced only weakly on the groundwater table level. The nutrient status, as defined by the trees' foliar nutrient concentrations, seemed to improve after thinning in some experiments. This indicated that nutrient characteristics could be used as explanatory variables as such or as additional variables in a model describing the post-thinning growth of trees.

INTRODUCTION

In order to increase the timber production of peatlands and paludified forests, an area of 5.96 mill. ha has been drained by the year 1990 in Finland (Aarne 1992). The initial area of virgin peatlands was approx. 10 mill. ha. In other countries, the importance of peatlands in timber production is much less. Most of the drainage work in Finland was carried out during the 1960's and 1970's. The maximum annually drained area was almost 300 000 ha in 1969 (Aarne 1992). The areas drained during the most extensive drainage period are now at about the stage of first commercial thinning. Estimates based on the data of the 7th National Forest Inventory (carried out in 1977 - 1984) indicate that more than 50 % of the stands on drained peatlands are young and advanced thinning stands (Paavilainen and Tiihonen 1988).

Drainage lowers the groundwater table level and enhances the biological activity on the site through better aeration of the rooting layer. This in turn speeds up nutrient mineralization (Starr 1982). The naturally poor timber production potential of peatlands can be considerably improved by drainage. Tree growth (Heikurainen and Kuusela 1962; Seppälä 1969; Dang et al. 1989) as well as stand density increase in the long run (Hökkä and Laine 1988). Drained peatland stands differ from upland mineral soil stands at corresponding development stages in terms of the more uneven age, size and spatial distribution of the trees (Hökkä and Laine 1986, Hökkä et al. 1991). Also the nutrient regime and water regime are more labile on peatland sites (Kaunisto and Paavilainen 1988; Laiho and Laine 1992; Päivänen 1980).

The present silvicultural guidelines applied to drained peatland stands follow the site-dependent guidelines drawn up for upland stands although the analogy in ground vegetation does not take into consideration differences in nutrient and water regimes. As to thinnings, the quantity, the structure and the spatial distribution of the yield from drained peatland stands are less favourable than in upland mineral soil stands. The drainage system usually needs repairing after thinning, because the ditches tend to become blocked in thinning. Furthermore, decreasing evapotranspiration and interception easily result in higher peat water contents after thinning. Thus, there are several reasons supporting the expectation that increasing growing space in the case of drained peatlands may not necessarily influence tree growth in the same way that it does in upland mineral soil stands.

The research problem concerning the thinning response in drained peatland stands, the variables with assumed relationships, the material, the methods, and tentative results are presented in this paper. The necessity of parameters describing nutrient and water regimes in a post-thinning growth model will be discussed.

FACTORS AFFECTING THE THINNING RESPONSE

The trees in a dense stand compete for growth resources: radiation, nutrients and water. As the average tree size increases in even-aged stands, severe competition reduces tree numbers through self-thinning (Reineke 1933; Hynynen 1993). Due to the uneven size and spatial distribution of trees in drained peatland stands, self-thinning is probable mainly within groups of trees. Thinning reduces this inter-tree competition. The reallocation of growth resources (radiation, nutrients, water) results in increasing the growth of the remaining trees.

Given the climatic conditions of Finland, the availability of water is not a limiting factor for tree growth on drained peatlands (Päivänen 1973). Therefore, if tree growth increases after thinning, it must be the result of changes in nutrient availability and/or allocation or changes in the distribution of photosynthetically active radiation (PAR), or both. It has been pointed out that in the boreal region there is a positive correlation between the amount of radiation and tree growth (Pohtila 1980). On upland mineral soils, the availability of nitrogen is a limiting factor for tree growth (Tamm 1991). On northern and poor sites the competition between trees can be assumed to be for nutrients. On peatlands suitable for forest drainage, nitrogen may not be the most important nutrient for tree growth. Results from fertilization experiments have indicated significant positive correlations between foliar phosphorus content and tree growth rate (Paarlahti et al. 1971). On the other hand, the amount of potassium in the peat of originally treeless, deep-peated mires is low. On sites of this kind, tree growth has increased following potassium fertilization (e.g. Kaunisto 1992).

In addition, thinning in peatland stands may disturb the water and the nutrient regimes with significant effects on the growth rate of the trees. Decreasing evapotranspiration and interception leads to rises in the groundwater table levels (Heikurainen and Päivänen 1970; Päivänen 1980). This may partly offset the expected positive effects of thinning by weakening the functioning of root systems and by decreasing the growth of fine roots. On the other hand, the heat storage capacity of wet peat is greater than that

of dry peat (see for ex. Hytönen and Silfverberg 1991). Especially in the cold climate of northern Finland, an increase in peat moisture due to thinning, together with the simultaneously increasing heat radiation reaching the ground, can significantly improve the thermal conditions in peat.

The removal of nutrients from the system when trees are cut and hauled away can be expected to diminish the storage of nutrients. On deep-peated peatlands, the amount of potassium in peat is estimated either to decrease (Kaunisto and Paavilainen 1988) or not to change significantly (Laiho and Laine 1992) after drainage. The amount of potassium bound up in the stand increases with increasing passage of time since drainage, and it can constitute a considerable proportion (40 - 50 %) of the total potassium stored in the stand and on the site (Finer 1992, Laiho and Laine 1992). When 20 - 50 % of the stem volume is removed in thinning, the removal of potassium is also significant. On the other hand, the mobilisation of nutrients from logging residues will momentarily improve potassium availability.

A conceptual model for describing the factors influencing the post-thinning growth rate of trees on drained peatlands was constructed (Figure 1). The assumed interrelationships of the growth factors and the variables used to measure the factors are presented. The controlled factor is competition between trees. Factors describing the environmental conditions were included in the model for two reasons. First, based on previous studies, there was reason to expect that, in addition to tree and stand variables, additional variables would be of importance when explaining the thinning response. Secondly, it was intended to study the inter-tree competition on the basis of the relationship between growing space and nutrient status.

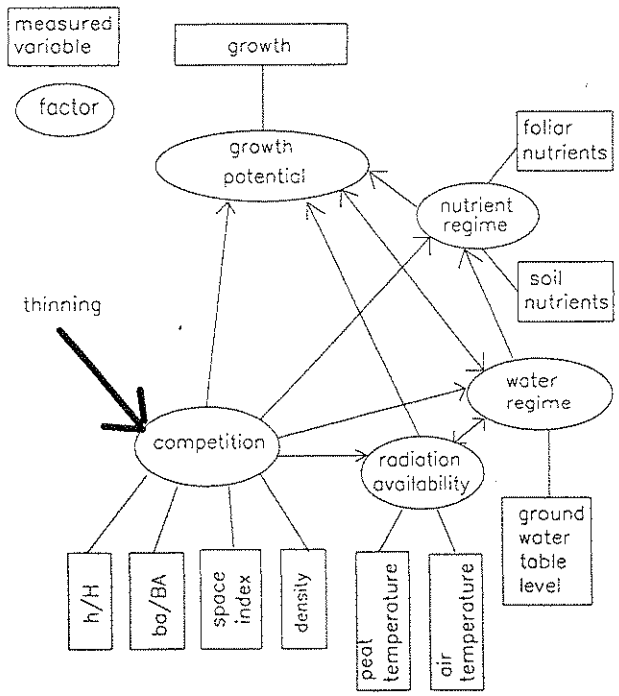

Figure 1. A conceptual model describing the interrelationships between growth factors and tree growth in drained peatland thinning stands.

MATERIAL AND METHODS

Thinning response is studied in field experiments in which changes in tree dimensions are recorded at five years intervals during a period of 15 years after thinning. The experiments were set up in drained peatland stands, which were considered to be in need of thinning according to management practices. The dominant tree species was either Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*). Mixed stands with pubescent birch (*Betula pubescens,* < 30 % of basal area/stem number) were also included. The treatments comprised three different thinning intensities and control. Between 0 - 50 % of the initial basal area (or stem number) was removed by thinning from below. The stem volume in these stands varied between 60 and 220 m^3/ha before thinning. The yield in the thinnings varied between 20 and 120 m^3/ha. The experimental design was based on randomized blocks. In 1985 - 1993, several experiments were established in different parts of northern Finland (Figure 2), where drained peatlands represent a significant proportion of the total forest land area.

In addition, a remedial ditching was carried out to prevent raising of the groundwater table level following thinning. In some of the experiments, remedial ditching was carried out a short time prior to thinning and in some experiments it will be done later.

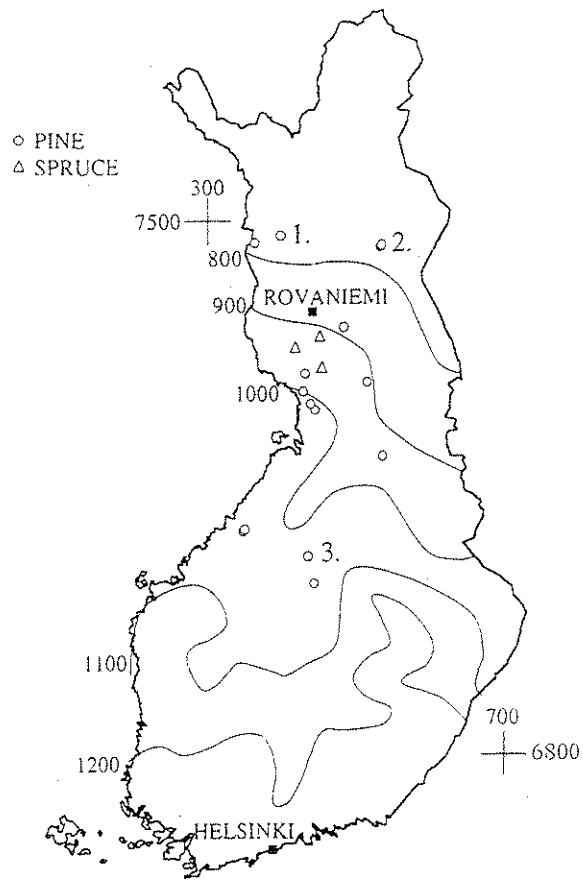

Figure 2. Location of the thinning experiments and the effective temperature sum, dd^{o}C (degree days >5°C) in 1931-61.

The effect of thinning on the nutrient regime and ground water table was studied in three intensive experiments (experiments 1, 2, and 3 in Figure 2). The results of these experiments only are presented and discussed in this paper. An example of the experimental design for an intensive experiment is given in Figure 3.

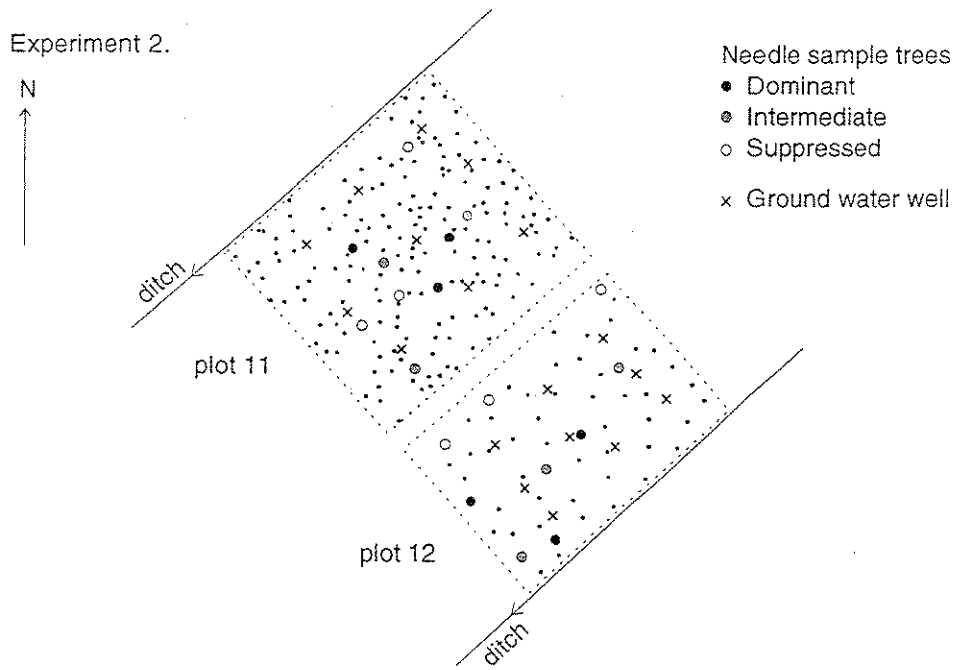

Figure 3. Tree map and and location of groundwater table wells and nutrient sample trees in the control plot (11) and heavily thinned plot (12) in experiment 2.

Experiments 1, 2, and 3 were drained in 1971, 1969 and 1972, respectively. The sites in all these experiments are minerotrophic and the stands are almost pure pine stands fertilized using phosphorus and potassium in 1972 according to normal forestry practice. The stand characteristics represented by the mean values of treatments are presented in Table 1. Experiment 1 lacks the light thinning treatment. In the case of experiments 1 and 2, some trees were cut also from the control plots because of a logging track opened in the middle of the strip.

The possible differences in the nutrient status between the control and two different thinning treatments were studied by defining the foliar nutrient concentrations in individual trees growing in different positions. Nine sample trees (3 dominant, 3 intermediate, and 3 suppressed trees) were subjectively selected on each plot. The needles born in 1991 (three years after thinning in experiment 2 and four years after thinning in experiment 3) were collected from the 4th and 5th branch whorl down from the tree top in March 1992. Total nitrogen, phosphorus, potassium, magnesium, manganese, calcium, zinc, concentrations and the dry weight of the needles were determined.

Table 1. Number (N), basal area (G), and volume (V) of trees comprising the thinning yield and residual stand in experiments 1, 2, and 3 at the time of thinning.

Treat-ment[1)]		N ha^{-1}			G m^2ha^{-1}			V m^3ha^{-1}		
	Stra-tum[3)]	Experiment[2)]								
		1	2	3	1	2	3	1	2	3
0	1	216	321	-	1.43	2.89	-	5.91	15.02	-
0	2	2291	1714	2602	13.85	17.98	20.90	56.66	94.46	115.10
1	1	-	452	1288	-	3.62	5.51	-	18.44	26.48
1	2	-	1318	1305	-	15.05	14.79	-	78.59	81.34
2	1	1008	531	1428	4.99	3.60	7.11	19.65	15.92	33.60
2	2	1287	937	928	10.95	10.10	9.89	49.17	46.85	55.15
3	1	1379	1108	1704	6.26	7.64	9.16	24.49	34.91	44.25
3	2	896	665	727	7.06	8.94	8.31	30.46	47.27	47.35

1) 0 = control
1 = light thinning
2 = normal thinning
3 = heavy thinning

2) see Fig 1.

3) 1 = thinning yield
2 = residual stand

Nine groundwater table wells were set up on every plot in the intensive experiments. The groundwater table level was monitored at 14-day intervals during the latter part of the growing season.

RESULTS

Effect of thinning on the groundwater tabel level

The results on the groundwater table level measurements in experiment 2 (1991 and 1992) and in experiment 3 (1991) are presented in Figure 4. In experiment 2, the distance between the ditches is 50 m and the ditches were cleaned five years prior to the setting up of the experiment. Runoff from the area was rather slow. Drainage has changed the ground vegetation only slightly and the peatland species continue to dominate. Year 1992 was wetter than average and resulted in high groundwater table levels in experiment 2. The difference between the control and heavy thinning seemed to increase when the groundwater table level was high, although the difference was still no more than 10 cm (Figure 4b).

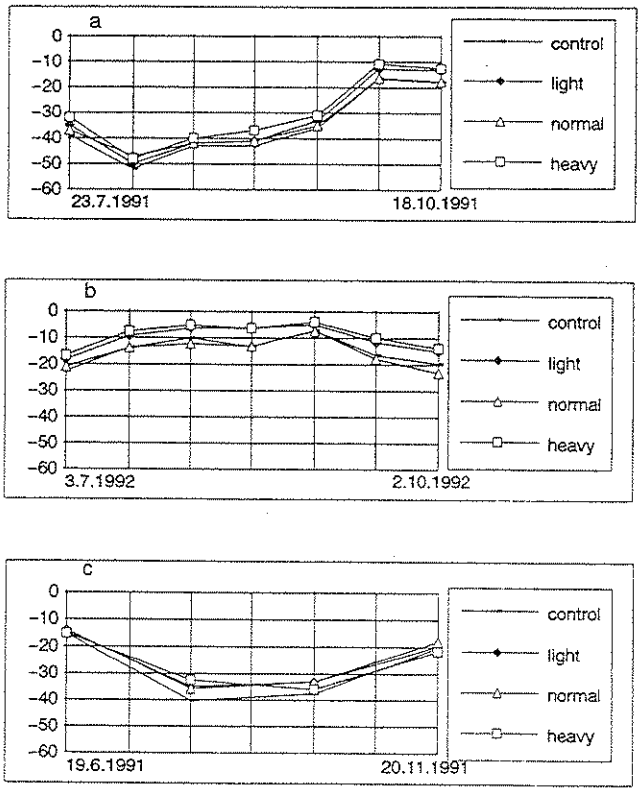

Figure 4(a-c). The groundwater table levels in experiment 2 in 1991 (a) and 1992 (b) and in experiment 3 in 1991 (c). The curves represent mean values in different treatments.

Results presented in Figure 4 c are not altogether comparable with those in Figures 4a and 4b, since the measuring intervals were irregular and the location as well as the amount of groundwater table wells on the plots were different. Drainage was not repaired at the time of the setting up of the experiments, but it was done five years later (in the spring of 1993). The distance between the ditches is 40 m, and drainage has been effective. The differences in groundwater table levels between the control and heavy thinning treatment were not significant.

Effect of thinning on stand nutrient characteristics

Foliar nitrogen, phosphorus and potassium concentrations in the sample trees in experiments 2 and 3 are presented in Figure 5. The experiments differed from each other in terms of the average nutrient status of the trees. In experiment 2, there was a slight deficiency of nitrogen and phosphorus (deficiency limits; N: 1.3 %, P: 1.4 mg/g, K: 3.5 mg/g, according to Paarlahti et al. 1971). In experiment 3, the nutrient status was optimal.

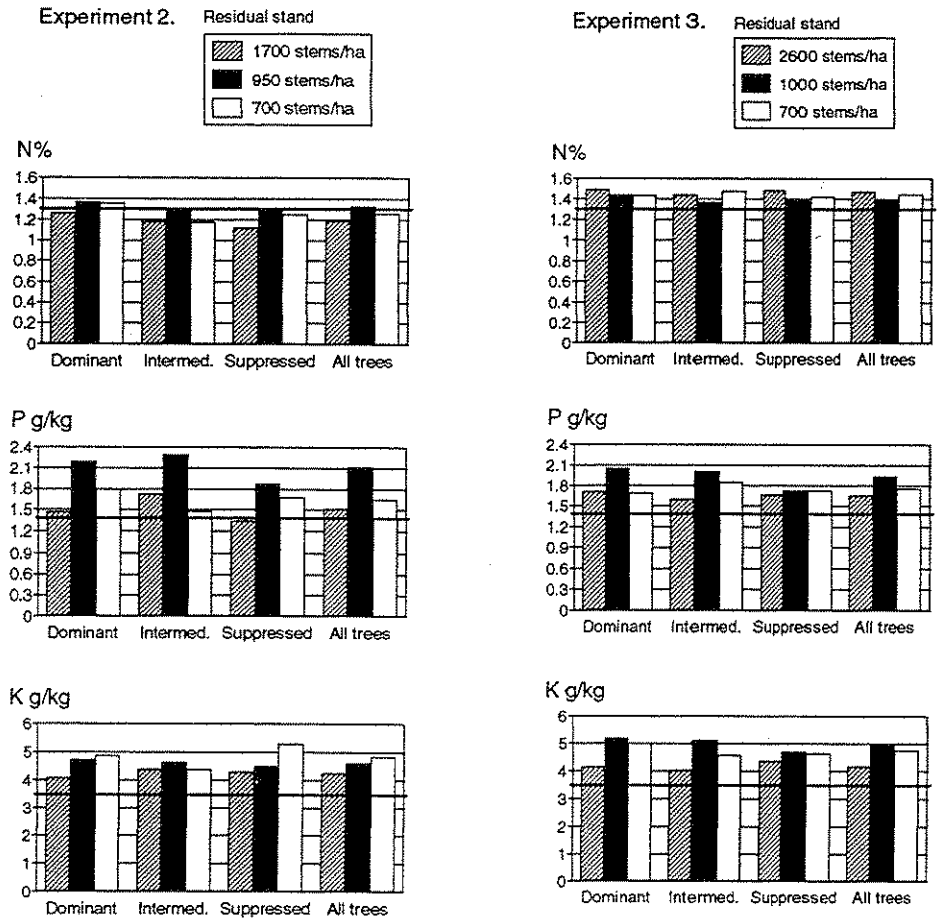

Figure 5. Foliar nitrogen, phosphorus and potassium concentrations of sample trees representing different treatments and different canopy layers in experiments 2 and 3. The deficiency limits are indicated by lines.

Significant differences in the foliar nutrient concentrations were observed after thinning. Trees in all canopy layers responded to thinning. Thinning influenced especially concentrations of phosphorus and potassium. The most distinct differences between the treatments involved experiment 2. The differences between treatments were statistically significant for nitrogen and phosphorus concentrations ($F = 6.86$, $p = 0.0025$, $df = 2$ and $F = 12.63$, $p = 0.000$, $df = 2$, respectively). In experiment 3, the differences were statistically significant for phosphorus and potassium concentrations ($F = 7.03$, $p = 0.0022$, $df = 2$ and $F = 6.77$, $p = 0.0027$, $df = 2$, respectively). No changes indicating impairing nutrient status were observed. Potassium concentrations, both in thinned and control treatments, were clearly above the deficiency limit.

Stand response to thinning

The stand growth data are from the period 1987 - 1992 for experiments 2 and 3. Stand level basal area and volume growth decreased with increasing thinning intensity in both experiments (Table 2).

Table 2. The absolute and relative means of basal area (i_G) and volume (i_V) increment (1987-1992) after different thinning treatments in experiments 1 and 3. Standard deviation in parenthesis.

Experiment	Treatment[1)]	Mean annual increment			
		i_G $m^2ha^{-1}a^{-1}$	i_V $m^3ha^{-1}a^{-1}$	i_G %	i_V %
1	0	0.77 (±0.07)	4.57 (±0.13)	5.74 (±1.38)	8.52 (±2.34)
	2	0.60 (±0.15)	3.81 (±0.18)	5.56 (±1.25)	7.92 (±2.14)
	3	0.47 (±0.04)	2.59 (±0.56)	6.80 (±0.74)	8.46 (±0.47)
3	0	0.90 (±0.11)	6.72 (±0.86)	4.29 (±0.47)	6.18 (±1.36)
	1	0.79 (±0.10)	6.23 (±1.35)	5.41 (±1.07)	7.94 (±2.65)
	2	0.67 (±0.10)	5.31 (±1.64)	6.90 (±1.58)	10.22 (±4.63)
	3	0.63 (±0.10)	4.95 (±0.65)	7.66 (±1.36)	10.74 (±2.83)

1) see Table 1.

In experiment 3, heavy thinning decreased basal area and volume growth by 30 % and 26 %, respectively. In experiment 1, heavy thinning decreased basal area and volume growth by 39 % and 43 %, respectively. In experiment 3, relative basal area and volume growth increased clearly due to thinning and, according to ANOVA, the differences between the treatments were statistically significant (for basal area growth: $F = 7.95$, $p = 0.0164$, $df = 3$ and for volume growth: $F = 5.68$, $p = 0.0346$, $df = 3$). In experiment 1, there was no response to thinning. The lack of thinning response was probably not caused by changes in groundwater table, since there were practically no differences in the groundwater table level between the thinning treatments.

CONCLUSIONS

The correlation between stand density and groundwater table level appeared to be weak. If this proves to be true according to more extensive data, the effect of thinning can be afforded less attention when the essential causalities in the growth model (see Figure 1) are studied. This conclusion was also supported by the positive stand response to thinning in experiment 3, where no remedial ditching was carried out until after the first growth measurement period had passed. Were thinning and remedial

ditching carried out simultaneously, the effects on the groundwater table level should be even less distinct. Differences between different thinning intensities may turn out to be more significant for tree growth, if several wet growing seasons occur in succession. To study this, a more detailed analysis of annual rings and comparison of experiments involving remedial ditching at different points in time will be needed. Because the groundwater table level was not monitored before thinning, the natural differences between the plots could not be analysed in the course of this study. The water conductivity of peat varies according to the composition and degree of humification of the peat and does not necessarily depend on the rate of evapotranspiration. For these reasons the interaction between growth potential and groundwater table level may still be important in the model; this is also suggested by Laine (1986).

In the experiments examined for this paper, thinning did not weaken the nutrient status of trees. On the contrary, the foliar nutrient concentrations for thinned treatments were higher than on the control plots. The probable reasons for this can be in the reduction in nutrient competition or in the input of nutrients mobilised from logging residues. Also, translocation of nutrients to the youngest needles may take place after thinning. The reduction in nutrient competition should result in increasing foliar nurient concentrations most clearly in stands lacking nutrients.

To some extent, foliar nitrogen concentrations can be influenced by a change in light conditions. According to van den Driessche (1974), shaded foliage can be expected to show higher nutrient concentrations than unshaded foliage, since growth is very dependent on light through photosynthesis (see also Helmisaari 1992). On the other hand, it has been observed that foliar nitrogen and phophorus concentrations determined from dominant trees were increased by thinning in a stand of black spruce (Mugasha et al. 1987).

The usefulness of the nutrient characteristics in a growth model is supported by observations of strong correlation between a plant's nitrogen status and its growth rate (Ingestad 1979). The results of this study encourage further studies on predicting growth responses with changes in the nutrient status of the trees. With more data from thinning experiments, a structural equation model combining both conventional tree or stand variables and variables describing the nutrient status of trees will be tested in order to predict the post-thinning growth of trees on drained peatlands.

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MODELLING TREE BASAL AREA GROWTH RESPONSE AFTER NITROGEN FERTILIZATION

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ABSTRACT

Individual-tree simulation models were developed for predicting tree basal area growth response following nitrogen fertilization. The models were based on data from permanent research plots located in middle-aged, managed Scots pine (*Pinus sylvestris* L.) stands in southern Finland. Using data from unfertilized control plots, a reference growth model for basal area growth was developed for calculation of the annual tree basal area growth response. The growth response of a fertilized tree was calculated as the difference between observed growth and predicted reference growth. The temporal distribution of tree basal area growth response was modelled using the Weibull function. The parameters of the Weibull function were expressed as a function of stand characteristics. Relative tree basal area growth response increased with increasing nitrogen doses between 80 - 450 kg N/ha. The growth response also varied according to site index; it reached its maximum level with the site index between 21 - 22 m. The relative response was not affected by neither stand density nor tree size.

INTRODUCTION

In Scots pine stands growing on mineral soil sites in Finland, the lack of available nitrogen is one of the most important factors limiting tree growth. Nitrogen fertilization has been used to increase timber production in commercial forests in Finland since the early 1970s.

In forest management planning, growth simulators are used for predicting the development of forest growth and yield. To forecast growth reliably for fertilized stands, growth simulators should include not only growth models, but also models that predict the growth response after nitrogen fertilization. At stand-level, growth response following nitrogen fertilization has been modelled by Rosvall (1980), Kukkola and Saramäki (1983) and Ballard (1984), among others. At present, growth in most simulators is predicted using individual-tree models. Therefore, growth response should also be modelled at the tree-level. Individual-tree growth models for fertilized stands have earlier been introduced by Burkhart et. al. (1987) and Shafii et. al. (1990), for example.

The aim of this study was to develop a model for predicting tree basal area growth response after nitrogen fertilization. A method was introduced to describe the temporal distribution of the growth response. The models were developed for application in growth simulators used for forest management planning purposes. Therefore, the independent variables of the models were restricted to those measured in practical forest inventories.

MATERIAL

The study material consisted of eight experimental Scots pine stands (*Pinus sylvestris* L.) established at the beginning of the 1970s for growth and yield studies. The experiments were set up in naturally regenerated, middle-aged stands growing on mineral soil sites in southern Finland. The experiments were arranged using factorial design. They consisted of sample plots representing two types of nitrogen fertilizers and three levels of nitrogen doses. There was at least one unfertilized control plot in every experimental stand. The nitrogen fertilizers used were ammonium nitrate with lime (Os) and urea (U). In one of the experiments, ammonium sulphate (As) was used instead of ammonium nitrate with lime. The nitrogen doses varied from 80 to 450 kg N/ha. Fertilizations were carried out in the spring of the same year that the experiments were set up. The number of replications varied between 1 and 10. Sample plot size was 1000 m^2 on average.

Study periods of the experimental stands varied between 10 - 15 years following fertilization. Although the stands were well managed, no thinnings were carried out during the study period, nor during the five-year period prior to the establishment of the experiments.

The sample plots were measured at intervals of five years. Each tree was measured for its breast height diameter over bark. An average of 17 sample trees were selected from each sample plots. Each sample tree was measured for its bark thickness and increment cores were examined to determine the annual radial growths for the preceding 15 years. The study material consisted of 2158 sample trees from 117 sample plots (Table 1). The number of annual radial growth observations was 37 800.

TABLE 1. Information about the experimental stands.

Exp. no.	Site index m	Age a	Stem number no./ha	Basal area m^2/ha	Mean height m	Nitrogen doses kg N/ha	No. of sample plots	Number of sample trees Control	Os	Urea
224	24.1	85	410	19.7	20.0	0- 80-160-240	52	176	353	337
301	24.6	75	520	16.3	18.7	0-150-300-450	21	60	194	186
312	26.9	60	745	25.1	19.5	0-150-300-450	7	26	77	70
315	21.5	80	460	16.9	17.2	0-150-300-450	7	19	56	52
319	20.0	120	290	16.4	21.2	0-150-300-450	7	16	51	49
320	19.6	120	445	17.9	21.4	0-150-300	6	29	38	34
332	22.9	85	410	17.3	19.0	0-150-300-450	7	20	59	62
336	23.1	65	645	18.5	16.5	0-150-300-450	10	36	89	69

On the basis of the measurements, tree diameters (d), basal areas (g) and relative diameters (d_r) at breast height without bark of all trees were calculated for every year of the study period. Relative tree diameter (d_r) was defined as the ratio between tree diameter and the diameter of the thickest tree in the sample plot (d/D_{max}). For sample trees, annual basal area growths (i_g) were calculated from increment core measurements. The largest experiment no. 224 (with an area of 11 ha), was divided into three blocks before analysis. Separate reference growth models were developed for each of the blocks.

The models were tested against independent data collected from six repeatedly-measured experimental Scots pine stands located in southern Finland. Two of the stands were middle-aged, while four of them were considerably younger and denser than those included in the study material. The test material consisted of 74 sample plots with 1104 sample trees and 7969 annual growth observations. Ammonium nitrate with lime (Os) was the only fertilizer used in the sample plots. The nitrogen doses varied between 55 and 750 kg N/ha.

MODEL DEVELOPMENT

Determination of growth response

The aim of the study was to develop a model for predicting annual tree basal area growth after nitrogen fertilization. To calculate the growth response of trees following nitrogen fertilization (ΔI_f), it was necessary first to estimate tree growth as if it had never been fertilized. This "hypothetical" growth was defined as reference growth (I_0).

The information collected from the control plots was used to develop reference growth model that was then applied to predict the annual reference growths of fertilized trees ($\hat{I}_0$). The annual growth response of a fertilized tree was defined as the difference of observed growth (I_f) and the estimated reference growth ($\hat{I}_0$):

$$\Delta\hat{I}_f = I_f - \hat{I}_0. \qquad [1]$$

Reference growth model

Annual basal area growth measurements from sample trees of the unfertilized control plots were used in developing the reference growth model. Model parameters were estimated separately for each control plot. A logarithm of annual tree basal area growth, $ln(i_g)$, was chosen as a dependent variable in the linear regression model [2]. The independent variables in the model were the logarithm of tree diameter without bark, $ln(d)$, describing tree size, and stand basal area without bark (G), describing stand density. Neither site index nor relative tree size was included in the model, because the parameters were estimated separately for each experimental stand. The variation in tree growth between successive years was taken into account by adding fixed annual effects ($v_1, v_2, \ldots, v_n$) into the model [2].

$$\ln\left(\hat{i}_g\right) = a_0 + a_1 \ln(d) + a_2 G + v_1 + v_2 + \ldots + v_{n-1}, \qquad [2]$$

where $\hat{i}_g$ = predicted tree basal area growth, cm^2
d = tree diameter at breast height, cm
G = stand basal area, m^2
$v_1, v_2, \ldots, v_{n-1}$ = fixed annual effects
n = number of years in study period
a_0, a_1, a_2 = parameters

A logarithm of tree diameter ($ln(d)$) and stand basal area (G) proved to be significant independent variables in the model, execpt in experiments 224 and 301, where $ln(d)$ was the only significant explanatory variable (Table 2).

TABLE 2. Annual tree basal area growth models for unfertilized sample plots (= reference growth models). Dependent variable $\ln(i_g)$.

Variable	Experiment									
	224(1)	224(2)	224(3)	301	312	315	319	320	332	336
	Coefficients									
Constant	-0.668	-4.015	-3.620	-1.616	-1.081	1.597	4.767	-0.079	1.414	0.367
$ln(d)$	0.834	1.901	1.721	1.147	1.462	1.819	0.402	1.158	1.357	1.216
G					-0.062	-0.381	-0.317	-0.115	-0.305	-0.144
R^2	0.242	0.492	0.357	0.543	0.480	0.530	0.244	0.235	0.450	0.558
S_f	0.143	0.150	0.154	0.119	0.099	0.168	0.122	0.289	0.139	0.126
$S_e\%$	14.4	15.1	15.5	11.9	9.9	16.2	12.2	29.5	14.0	12.7

Constant = a_0 (in equation [2]) + average of fixed annual growth effects ($v_1, v_2, \ldots, v_n$); R^2 = coefficient of determination; S_f = Residual standard deviation; $S_e\%$ = Relative standard error of the estimate.

The residuals were examined separately for each stand with regard to the independent variables of the models and relative tree size (d_r). No trends in the residuals were observed with respect to the examined variables.

The basal area reference growths of fertilized trees were calculated using model [2]. When model [2] was applied to predict the annual reference growths for fertilized trees, the observed values of stand and tree characteristics at the beginning of the year in question were used as the independent variables. Thus, the annual reference growth of fertilized tree was estimated separately for each year regardless of the growth predictions of the previous years.

Growth response model

Relative annual basal area growth response, $\Delta(p_g)$, was chosen as the dependent variable of the response model. It was calculated on the basis of observed tree basal area growth (i_g) and the predicted reference growth ($\hat{i}_g$).

$$\Delta(p_g) = \left(i_g - \hat{i}_g\right) / \hat{i}_g, \qquad [3]$$

The temporal distribution of response following nitrogen fertilization was modelled using the Weibull function. The three-parameter Weibull distribution can be expressed as

$$f(X) = \frac{\chi}{\beta}\left(\frac{X-\alpha}{\beta}\right)^{(\chi-1)} \exp\left[-\left(\frac{X-\alpha}{\beta}\right)\right]^{\chi}, \text{ when } (\alpha \le X < \infty) \qquad [4]$$
$$= 0, \text{ otherwise}$$

where α = location parameter
β = scaling parameter (> 0)
χ = shape parameter (> 0)

When model [4] was applied to describe the distribution of growth response over time, it was multiplied by coefficient k referring to the total growth response caused by fertilization. Location parameter (α) was set to zero assuming that fertilization starts to increase tree growth already in the first growing season following nitrogen application. The modified Weibull model is given by equation [5]:

$$\Delta\hat{p}_g(t) = k\left\{\frac{\chi}{\beta}\left(\frac{t}{\beta}\right)^{(\chi-1)} \exp\left[-\left(\frac{t}{\beta}\right)\right]^{\chi}\right\}, \text{ when } (0 \le t < \infty) \qquad [5]$$

where $\Delta\hat{p}_g(t)$ = relative basal area growth response in year t after fertilization
t = year after fertilization
β, χ, k = parameters

To examine the effects of stand-level characteristics on growth response, model [5] was fitted separately to each fertilized plot. Accordingly, the average growth response of trees was calculated for every fertilized sample plot. Next, the relationships between stand characteristics (the amount and the type of fertilizer, site type, stand density and stand age) and parameters of the Weibull modell were examined. The relationships were formulated so that k, β and χ were expressed as a function of the nitrogen dose and stand characteristics.

Type of fertilizer, nitrogen dose and site index were the stand-level characteristics that correlated with coefficient k and parameter β. Further, parameter β and coefficient k were positively correlated. The shape parameter χ did not correlate with the studied stand-level variables, neither was it closely correlated with β or k.

The effects of tree characteristics on the growth response (coefficient k) were studied by calculating the total response of every sample tree. It was computed by summing up the annual responses of the study period. Annual responses were calculated according to equation [3]. The relationships between total response and tree diameter (d) as well as relative tree diameter (d_r) were studied. There was no significant interdependence between total relative growth response and studied tree-level variables.

The final, nonlinear growth response model can be expressed as follows:

$$\Delta(\hat{p}_g) = k\left\{\frac{\chi}{\beta}\left(\frac{t}{\beta}\right)^{(\chi-1)} \exp\left[-\left(\frac{t}{\beta}\right)\right]^{\chi}\right\}, \text{ in which}$$

$$k = \left(\frac{a_2}{a_1}\right)\left(\frac{H_{100}}{a_1}\right)^{(a_2-1)} \exp\left(-\left(\frac{H_{100}}{a_1}\right)^{a_2}\right)\left(a_3\left(\frac{FN}{10}\right) - a_4\left(\frac{FN}{10}\right)^2\right) \qquad [6]$$

$$\beta = a_5 + a_6 k$$

$$\chi = a_7,$$

where $\Delta(\hat{p}_g)$ = relative annual basal area growth response

t = year after fertilization

H_{100} = site index, m

FN = nitrogen dose applied, kg N/ha

$a_1, \ldots, a_7$ = parameters

In the final response model [6], coefficient k is depicted as the function of site index (H_{100}) and nitrogen dose (FN). Scaling parameter (β) in the Weibull model is stated as a linear function of coefficient k. Shape parameter χ is independent of fertilization factors and stand characteristics.

Model [6] was fitted separately for OS- and U-fertilizers (Table 3). The model was based on the data that included annual growth responses of all sample trees growing on the fertilized sample plots. The time period covered the studied years following the fertilizations. All the parameters were estimated simultaneously using an iterative nonlinear regression program (BMDP 3R) with the Gauss-Newton algorithm (Jennrich 1990).

The residuals were studied separately against the independent variables of model [6] and against stand density (G), tree diameter (d) and relative tree diameter (d_r). Residual variance was evenly distributed over time, except for the first two years after fertilization. The model resulted in slight overestimation in the first year, followed by the underestimation in the second year after fertilization. The Weibull model appeared to be too robust for describing the sudden increase in growth response during the first two years after fertilization. The residuals were evenly disrtibuted with respect to other studied variables.

TABLE 3. Parameter estimates of the relative tree basal area growth response model [6].

Os fertilization			Urea fertilization		
parameter	estimate	asymptotic standard deviation	parameter	estimate	asymptotic standard deviation
a_1	22.225	0.107	a_1	23.301	0.201
a_2	4.561	0.134	a_2	3.868	0.163
a_3	3.390	0.139	a_3	2.574	0.144
a_4	0.016	0.003	a_4	0.005	0.002
a_5	2.976	0.110	a_5	3.230	0.135
a_6	0.569	0.022	a_6	0.649	0.035
a_7	2.466	0.036	a_7	2.611	0.048
Mean of the dependent variable: 0.317 Residual mean square: 0.284 Degrees of freedom: 11323			Mean of the dependent variable: 0.245 Residual mean square: 0.270 Degrees of freedom: 10952		

According to the model, relative basal area growth response varies with nitrogen dose and the type of fertilizer. Within the range of variation of nitrogen doses used in the study material (80 - 450 kg N/ha), the response increased with increasing dose. The year of maximum growth response also varied according to the dose of nitrogen. When dose increased from 50 to 400 kg N/ha the maximum response increased respectively from three to six years after fertilization. With Os fertilizer the response, on average, was 30 % greater than after application using the same amount of urea fertilizer.

An increase in the site index increases the response until it reaches the maximum level at the site index of 21 - 22 m, thereafter the response decreases as the site becomes more fertile.

APPLICATION OF GROWTH RESPONSE MODEL

When model [6] is applied to growth simulation of a fertilized tree, it can be used only in combination with the tree basal area growth model of unfertilized tree by which the reference growth for fertilized tree is predicted. The relative annual growth response can then be calculated using model [6] and added to the predicted reference growth. Simulation is carried out year by year. Stand basal area and tree diameters are updated every year after computing the annual growths and growth responses. Thus, both the reference growth model and the growth response model affect the final, absolute growth response caused by nitrogen fertilization (Fig 1.).

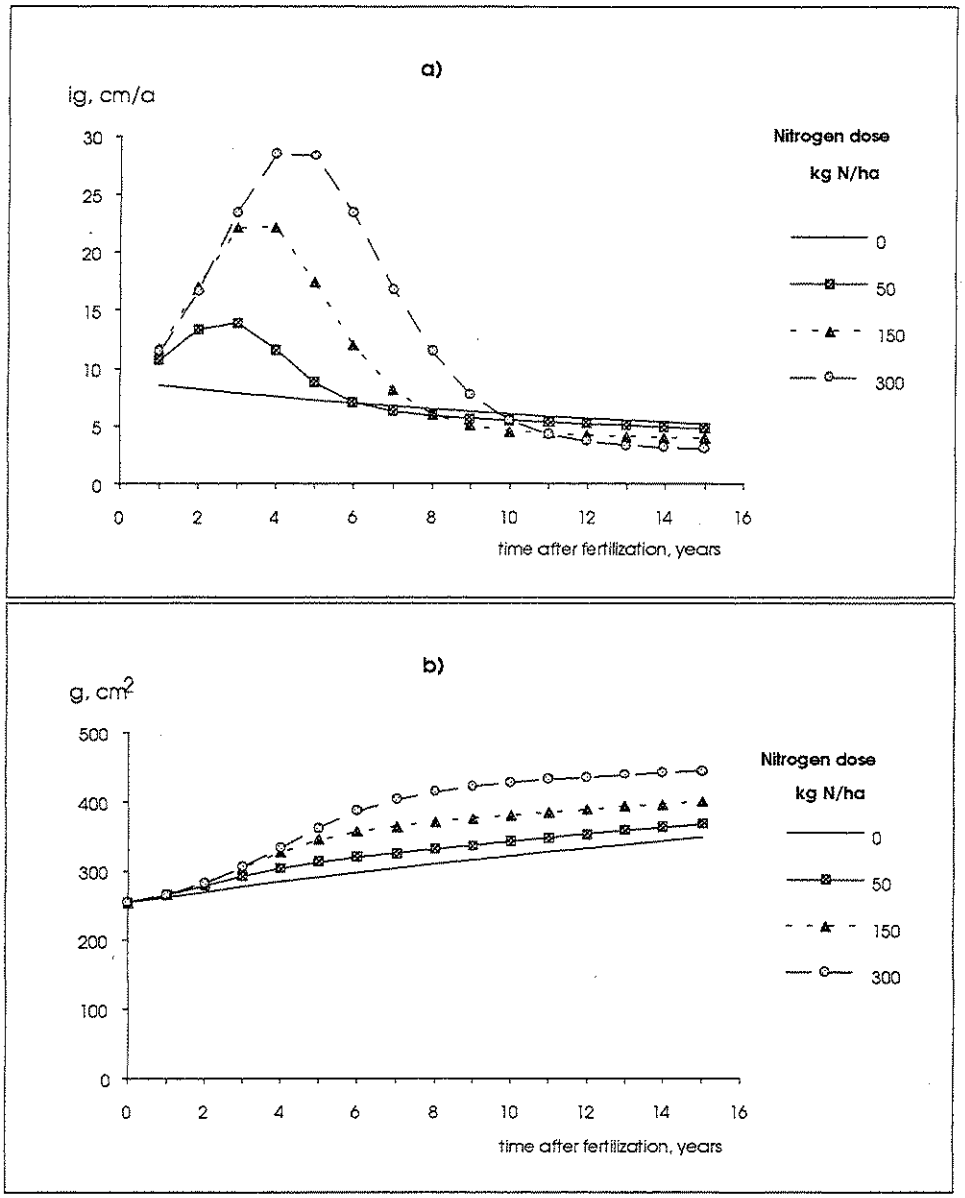

Figure 1. An example of simulated development of a fertilized tree. Annual tree basal area growth (a) and basal area development (b) following fertilization with varying nitrogen doses. Reference growth is predicted using basal area growth model for exp. 336.

VALIDATION OF THE MODELS

Because the response models were based on sample trees in experimental plots, stand-level simulations were done to test the models against data including all trees in experimental stands. Furthermore, the models were tested against the independent data. The list of tree diameters at the time of fertilization was used as the input data for simulation. Annual stand basal areas and mean diameters (weighted with basal area) of the sample plots were calculated from the predicted basal areas of trees. For every

fertilized plot, predicted stand basal area growth and mean diameter increment were compared with the observed values. The following characteristics were calculated to describe the reliability of the model:

$$b = \sum_{i=1}^{n} (y_i - \hat{y}_i) / n \qquad \text{(systematic error)} \qquad [7]$$

$$b_r = \sum_{i=1}^{n} [(y_i - \hat{y}_i) / \hat{y}_i] / n \qquad \text{(relative systematic error)} \qquad [8]$$

$$RMSE = \left[\sum_{i=1}^{n} (y_i - \hat{y}_i)^2 / n \right]^{0.5} \qquad \text{(root mean square error)} \qquad [9]$$

$$RMSEr = \left[\sum_{i=1}^{n} [(y_i - \hat{y}_i) / \hat{y}_i]^2 \Big/ n \right]^{0.5} \qquad \text{(relative RMSE)} \qquad [10]$$

where y_i = observed value in stand i

$\hat{y}_i$ = predicted value in stand i

At stand-level, simulations with the study material resulted in a relative bias of 1.01 % in the estimated annual stand basal area growth and a relative bias of -0,59 % in the annual mean diameter increment. The test against independent stand data showed that the models underestimated annual stand basal area growth by 6.8 % and mean diameter increment by 5.4 % on average (Table 4).

TABLE 4. Statistics describing the reliability of the models in stand-level growth prediction as tested against the study material and independent test material.

	Stand basal area growth, m^2/ha/a		Mean diameter increment, cm/a	
	Study material	Test material	Study material	Test material
Mean of the estimate	0,394	0.705	0,339	0.342
b	-0.001	0.003	-0.006	0.011
b_r, %	-1.01	6.79	-0.58	5.45
RMSE	0.049	0.091	0.053	0.036
$RMSE_r$, %	13.33	13.35	13.82	10.50

Most of the sample plots included in the test material were located in considerably younger and denser stands with faster basal area growth than the stands included in the study material. It was noticed that the model underestimated growth response most in youngest stands with rapid basal area growth (Fig. 2). As regards mean diameter increment, no such trend was to be noticed.

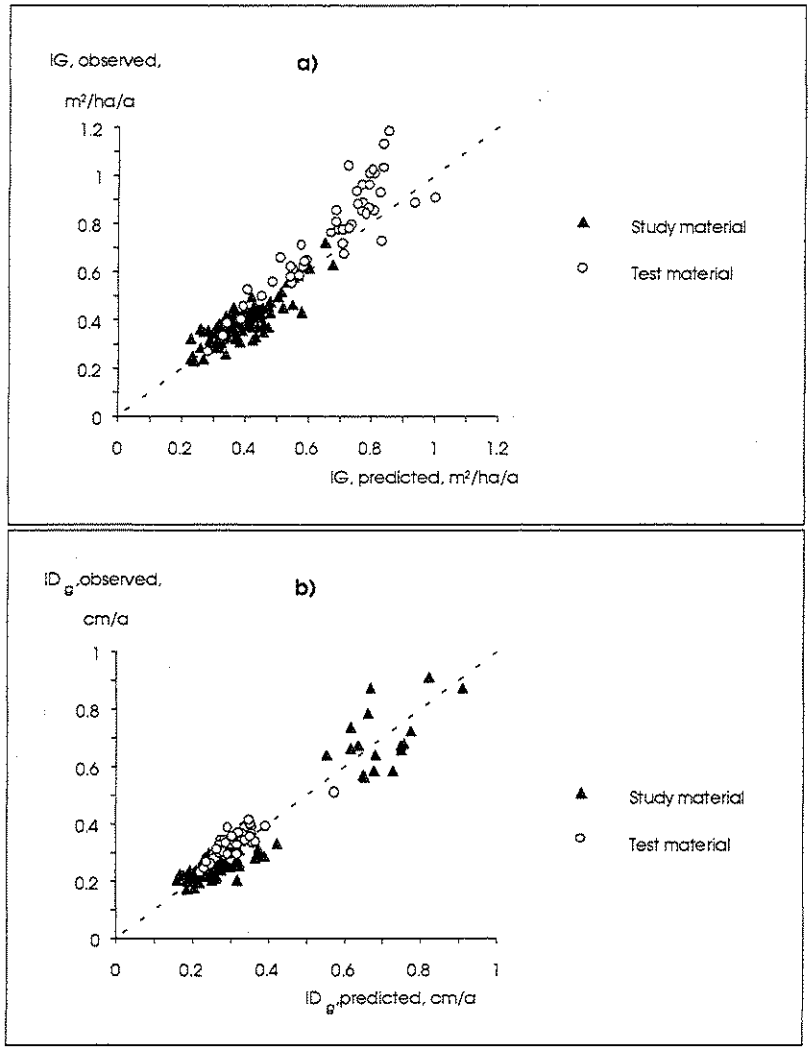

Figure 2. Observed and predicted mean annual stand basal area growth (a) and mean annual diameter increment (b).

At tree-level, the models were tested against independent test material. The residual variances of the predicted basal area growth responses were examined with regard to the variables of model [6] as well as tree and stand characteristics. The results showed that the model slightly underestimated the growth response in general, and especially in the stands fertilized with nitrogen doses over 450 kg N/ha. The residuals plotted against stand density, stand age and site index were evenly distributed. In young stands, after the growth response had levelled off, the models overestimated tree growth. This result indicates that there might be a negative aftereffect of nitrogen fertilization on tree growth. Furthermore, in young pine stands, the relative growth response of the smallest trees in the stands were slightly underestimated, while simulation resulted in overestimation of growth among the biggest trees.

DISCUSSION

Tree basal area growth response was modelled using the Weibull function. The parameters of the Weibull-function describe the size, location and the shape of the distribution. Whereas the Weibull parameters were expressed as functions of stand variables, the relationships between the characteristics of the distribution and stand variables are easy to interprete. Scaling parameter, β, was expressed as a function of coefficient parameter k because of the high correlation between k and β. The connection between these parameters in model [6] prevents irrational combination of the parameter values, and thereby the unrealistic shape of the disribution, even if the model is applied into stands with characteristics beyond the stands of the study material.

The growth response models developed in this study are based on data collected from managed, even-aged pine stands between the stand ages of 60 - 120 years. The study material represents the stands at that stage of development when fertilization is most profitable. Today, forest fertilization in Finland is mostly consentrated in mature pine stands with large-sized growing stock. The findings concerning the features of growth response in mature Scots pine stands with varying nitrogen doses and stand characteristics support the results of the earlier studies (Gustavsen and Lipas 1975, Rosvall 1980, Kukkola and Saramäki 1983).

The results obtained using the test material suggest that there are some uncertanties as to behaviour of the response model in young and dense pine stands. Firstly, applying the Weibull function to describe the temporal distribution of the response following nitrogen fertilization presupposes that the response is always positive. Therefore, the model fails to predict correctly those situations where fertilization has negative growth effects. It has been observed that nitrogen fertilization alters a trees internal growth ratios by decreasing the root:shoot ratio (e.g. Köstler et. al. 1968). It can be supposed that when the effect of fertilization terminates, the root:shoot ratio will be restored, and the growth will be allocated into roots at the expense of growth in the stem and crown. The results based on the test material showed that this kind of negative aftereffect is possible in young trees. Secondly, according to the basal area growth response model, the relative response is independent of tree size and stand age. This assumption is likely to hold in middle-aged and mature stands, where trees have enough growing space. Nevertheless, the results on young and dense stands included in the test material indicate that the assumption may not be valid. Therefore, the models should be applied very catiously in young and dense Scots pine stands.

Nitrogen fertilization accelerates the development of stand density, which leads to increased competition for growing space between trees. While stand density increases, the growth rate of single trees may decrease. In a fertilized stand, once the trees have used up the applied nitrogen, individual trees may grow more slowly than trees in an unfertilized stand because of increased stand density. In this study, the effect of stand density has been taken into account in the reference growth model. Consequently, the negative aftereffect of fertilization caused by increased stand density can be described with the models developed in this study (see Fig. 1).

The growth response model can be included in a simulator in which basal area growth is predicted using individual-tree growth model. To fulfill the presumptions underlying the response model, the basal area growth model should meet certain requirements. According to the response model, relative growth response is independent of stand density and tree size. Nevertheless, these variables affect absolute tree growth and so they should be included in the tree basal area growth model.

In this study, only the model for tree basal area growth response was developed. To predict the volume growth in fertilized stands, also height growth response model should be developed. Such a model could not be developed in this connection, because the study material did not contain annual height growth data. Also, the combined effect of fertilization and thinning, as well as the effect of repeated fertilizations, on tree growth await further study. A method introduced by Kukkola and Saramäki (1983) for predicting stand-level growth response in repeatedly fertilized stands is likely to find use to individual-tree growth response modelling as well.

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CHARACTERIZATION OF SHRUB AND HERBACEOUS VEGETATION FOLLOWING SILVICULTURAL TREATMENTS WITH IMPLICATIONS ON MODELLING PINE RESPONSE

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ABSTRACT

Forests in the lower coastal plain of the southeastern United States are intensively managed to produce pine fiber. Loblolly (Pinus taeda L.) and slash (Pinus elliottii Engelm. var elliottii) pine response to complete control of competing vegetation has been shown to be as large or larger than the response to other silvicultural treatments. However, both costs and pine response to operational vegetation control treatments are variable due to spatial and temporal characteristics of competing vegetation. Complete vegetation control treatments remove variation due to speciation, density, and recolonization, but operational treatments must contend with these variables. Pine response differs by life-form of vegetation controlled and by duration of control. Non-crop vegetation can compete for resources made available by silvicultural treatments. Planned experiments identify limiting resources and methods of manipulating these resources. Modelling can be used to describe use of resources or can be used to estimate yield. Yield models would be more useful if they provided information on 1) what variables need to be measured to predict future yield from silvicultural treatments, 2) how soon after treatment stands can be assessed to incorporate reasonable estimates of treatment response into yield predictions, and 3) the variability of predicted yields based on early assessments.

BRANCH SIZE RESPONSE TO NITROGEN FERTILIZATION IN YOUNG DOUGLAS-FIR

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ABSTRACT

A shift in crown developmental pattern is a fundamental response of trees and stands to silvicultural practices. This response, in turn, is functionally related to a wide range of silvicultural effects, from changes in growth rate to alterations in wood quality. One major component of the latter, particularly in regard to strength properties of dimension lumber, is branch size and branch distribution.

Maguire et al. (*in press*) have constructed a prediction system for describing the basal diameter and vertical distribution of primary branches on young Douglas-fir, given the dbh, total height and crown length of the tree. A major component of this system was a model that estimated maximum attainable branch diameter for a specific depth into crown. The first versions of the maximum branch diameter model did not explicitly incorporate the effects of any silvicultural manipulations; however, indirect effects are reflected by response of dbh, height and/or crown length to silvicultural treatment. A series of analyses were therefore conducted to test for any direct effects of nitrogen fertilization on maximum branch diameter patterns.

Trees were sampled from six plots on each of two installations established by the Pacific Northwest Stand Management Cooperative. Both installations had a pair of 0.2-ha plots at three different initial spacings; one plot of each pair was fertilized at a rate of 220 kg/ha as urea, and the other was left unfertilized. At the time of treatment, the first installation (Ostrander) had an average tree height of 8.8 m and a tph range of 306 to 2084. The other installation (Copper Creek) had an average tree height of 5.2 m and tph range of 217 to 904. Height and diameter of all branches up to approximately 7 m were measured four years after fertilization on five trees from each Ostrander plot and two trees from each Copper Creek plot.

The first analyses were based on the original segmented polynomial (Maguire et al., *in press*), which assumed a join point located at 10% of crown length from the tree tip; however, an indicator variable for fertilization was also introduced, as were terms representing the interactions between fertilization and the other variables already in the model. A random coefficients version was also fitted to address autocorrelation within a tree.

The second set of analyses applied the same basic segmented polynomial form but assumed that the join point location corresponded to the height of maximum

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branch diameter. A separate equation was developed to predict this latter height from tree dbh, height and crown length.

Finally, other model forms were tested for their relative flexibility in describing the vertical trends in maximum branch diameter, and feasible generalized least squares was explored as an alternative for addressing autocorrelation among error terms.

The general conclusion reached in these efforts to model the response of branch size to nitrogen fertilization was that, after incorporating tree dbh, height, and crown length into the model as covariates, virtually no direct effect of fertilization was apparent. In other words, fertilization did not appear to alter the allometric relationship between the vertical trend in maximum branch diameter and a given combination of dbh, height and crown length in young Douglas-fir.

MODELING GRASS, SHRUB AND TREE INTERACTIONS: A PROCESS BASED APPROACH

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ABSTRACT

The increasing demand for predictive capability regarding the consequences of silvicultural practices within the general context of an ecosystem approach to forest management has prompted the Inland Northwest Growth and Yield Cooperative to embark on a modeling effort that more explicitly incorporates fundamental processes. Especially important are questions regarding stand development patterns following: (1) control of herbaceous vegetation, and (2) partial cutting.

The proposed design of the individual tree model projects development of all vegetation on a site. Inputs are derived from standard timber inventory procedures augmented with observations of percent cover and height of grasses and shrubs. The vertical distribution of foliage is estimated from biomass and crown geometry equations and canopy zones defined for attenuating light. Operating on a daily time step, topographically adjusted, local climatic events, soil nutrient status, and site water relations are used to drive the processes of photosynthesis, transpiration, respiration, and carbon allocation. Life form phenology and stand structure combine to affect availability of light and water to individuals. Photosynthesis and allocation of carbon to leaf, stem, and root components are affected. Allometric relationships and such mensurational tools as taper equations are used to update the dimensions of individuals given an increment in component carbon. Mortality is controlled at the individual level through a growth/respiration relationship, and at the stand level through reference to a site specific equilibrium leaf area. Regeneration is a function of current site occupancy relative to equilibrium leaf area, temperature and moisture conditions of the air and soil, and available species and their phenological characteristics.

EFFECTS OF NITROGEN FERTILIZATION TREATMENTS ON WITHIN-STAND RELATIVE SIZE-GROWTH RELATIONSHIPS

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ABSTRACT. The distribution of within-stand basal area growth following fertilization treatments was investigated using a relative size-growth (RSG) function. The magnitudes and signs of the correlations among three coefficients of the RSG function, and the patterns of the relationships between the three coefficients were nearly identical for different fertilization treatments. Statistical tests of the RSG function indicated that fertilization does not alter the characteristic relationships between tree size, stand density, stand structure, and the relative distribution of growth across size classes within a stand. The contribution of an individual tree's response to total stand fertilizati on response depends on its relative size in the stand. Further, the RSG function can be used to disaggregate additional stand growth due to fertilization to individual trees.

INTRODUCTION

Nitrogen has been identified as a growth-limiting nutrient for interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn) Franco). For past 10 years, the Intermountain Forest Tree Nutrition Cooperative (IFTNC), located at the University of Idaho, has established a series of nitrogen fertilizer trials for Douglas-fir and other species throughout the inland Northwest. The studies have shown that nitrogen fertilization can significantly increase basal area and volume growth following treatments (Mika and Vander Ploeg 1991, Moore et al. 1991). Further, efforts to quantify growth response to fertilization treatments for inclusion in growth and yield simulation models have

focussed at both the whole-stand (e.g. Heath and Chappell 1989) and individual tree (e.g. Shafii et al. 1990) levels. Other investigators have used statistical distributions to model silvicultural treatment effects on tree diameter distributions (e.g. Bailey and Da Silva 1987, Bailey et al. 1989). Shafii et al. (1990) found that nitrogen fertilization impacts the absolute change in diameter growth distribution across tree size classes within a stand. Initial tree size and initial stand density produce significant interactions on an individual tree's response to fertilization. However, there remains a need for more general quantitative understanding of response distribution within a stand, and fertilization treatment consequent effects on dynamics and development of stand structure.

Zhang et al. (1993) developed a disaggregation function, the relative size-growth (RSG) function, to distribute stand total volume growth to individual trees in unfertilized stands. The RSG function is formulated as a quadratic equation relating relative tree growth to relative tree size. The shape and curvature of the RSG function determine future stand structure, dynamics and development (Figure 1). The RSG approach (1) avoids assuming that tree size follows a particular statistical distribution, (2) reflects competition effects among individual trees on dynamics of stand structure, and (3) predicts the relationship between tree growth and tree size based on current stand condition and structure. We therefore believe that the RSG function would also be a useful analytic tool for studying fertilization treatment effects on within-stand distribution of growth. Thus, the objective of this study was to investigate if fertilization treatments influence the relationships between tree relative size and relative growth.

DATA

The data were obtained from 94 installations established by IFTNC, representing even-aged, managed and predominant single-species Douglas-fir stands in the inland Northwest, USA. The study area covers northern Idaho, western Montana, northeastern Oregon, and eastern Washington. Each installation consisted of two blocks of three plots based on similarity of stand features to minimize among-plot variation. Three fertilization treatments, 0, 200, and 400 lb N/acre (1 lb = 454 g, 1 acre = 0.405 ha), were included in the IFTNC region-wide experiment. All live trees were measured for diameter (to the nearest 0.01 inches) for a 6-year growth period. Most of these stands had been thinned 5-12 years prior to fertilizer treatments between 1980 and 1982; other stands were unthinned, but naturally well-spaced. The data cover a wide

range of stand densities, tree ages and sizes, and site productivities (Table 1). Pretreatment stand characteristics of the three fertilizer treatments were essentially identical.

RESULTS AND DISCUSSION

The RSG Function for Basal Area Distribution

Since fertilization treatments may influence tree stem profile, we decided to work with basal area relative size-growth (RSG) relationships rather than volume RSG relationships. Relative basal area growth (RBAG) is defined as the ratio of individual tree basal area growth to stand total basal area growth (i.e. the sum of the individual trees) on a unit area. Relative basal area (RBA) is defined as the ratio of individual tree basal area to stand total basal area on a unit area. Since the frequency distributions of tree volume and basal area have similar patterns, but different degrees of skewness (Hara 1984a, 1984b), the RSG relationships for tree volume and basal area should be similar. Thus, the relative size-growth (RSG) function for tree basal area distribution was expressed as a quadratic equation relating relative basal area growth (RBAG) to relative basal area (RBA):

$$RBAG = \beta_0 + \beta_1 * RBA + \beta_2 * RBA^2 \qquad (1)$$

where β_0, β_1, and β_2 are coefficients to be estimated for each plot. This form is analogous to the RSG function for volume in Zhang et al. (1993).

Characteristics of the RSG Relationship

The relative size-growth (RSG) function (Equation (1)) was fitted to the 6-year growth data of 564 Douglas-fir plots, 188 each for control (unfertilized), 200 lb N/acre, and 400 lb N/acre treatments, respectively. The Pearson's correlation coefficients between the three coefficients of the RSG function for the three treatments are given in Table 2. The results showed nearly identical Pearson's correlations between the β_0, β_1, and β_2 of the RSG functions for the three fertilization levels. Correlations between β_0 and β_1, and between β_1 and β_2 were strongly negative. The positive correlation between β_0 and β_2 was relatively weak. More importantly, the relationships between the RSG function coefficients for 0, 200 and 400 lb N/acre plots were also nearly identical (Figures 2, 3 and 4). Generally, if β_1

Table 1. Averages and ranges of stand characteristics at the beginning of a 6-year growth period for Douglas-fir sites.

Characteristic	Mean	Minimum	Maximum
---------- Control ----------			
Site index (ft @ 50 year)	69	39	105
Stand total age (year)	63	12	100
Trees per acre	309	90	1640
Top height (ft)	73	33	118
Basal area (ft^2/acre)	141	24	267
Quadratic mean diameter (in.)	10	3	17
Coefficient of variation of basal area distribution	56	23	129
---------- 200 lb N/acre ----------			
Site index (ft @ 50 year)	68	41	96
Stand total age (year)	65	27	100
Trees per acre	269	105	745
Top height (ft)	73	39	114
Basal area (ft^2/acre)	141	44	283
Quadratic mean diameter (in.)	10	6	16
Coefficient of variation of basal area distribution	53	18	103
---------- 400 lb N/acre ----------			
Site index (ft @ 50 year)	69	41	97
Stand total age (year)	65	27	100
Trees per acre	269	88	650
Top height (ft)	74	42	119
Basal area (ft^2/acre)	142	42	275
Quadratic mean diameter (in.)	10	6	18
Coefficient of variation of basal area distribution	52	14	100

equals one, both β_0 and β_2 are nearly equal to zero; if β_1 is less than one, both β_0 and β_2 are positive; and in contrast, if β_1 is larger than one, both β_0 and β_2 have negative values. The above relationships represent three basic shapes of the relative size-growth (RSG) function for tree basal area distribution: linear, convex, and concave, determining the future frequency distribution of tree basal area to be symmetric, positively skewed and negatively skewed, respectively (Zhang et al. 1993).

Table 2. Pearson's correlations between the three coefficients of the RSG function (Equation (1)) for the three fertilization treatments.

Contrast	Treatments		
	Control	200 lb N/a	400 lb N/a
β_0 versus β_1	-0.86	-0.89	-0.87
β_0 versus β_2	+0.58	+0.55	+0.54
β_1 versus β_2	-0.88	-0.85	-0.85

Statistical Tests for the RSG Relationship

Statistical analyses were conducted to test the effects of fertilization treatments on the RSG function: (1) Analysis of variance was performed separately on the three coefficients of the RSG function from all unfertilized and fertilized plots. The F tests were all statistically non-significant (Table 3). (2) Multivariate analysis of variance was also performed simultaneously on the three coefficients of the RSG function. The p-values for F approximations of Wilks' Lambda, Pillai's Trace and Hotelling-Lawley Trace were 0.63, respectively (Table 3). (3) Analysis of covariance (test for heterogeneity of slopes) was also conducted to test the differences of the RSG relationships among the three fertilization treatments. The RSG function (Equation (1)) was fitted to combined observations of three plots within a block. Fertilization treatment was coded as an indicator variable. For 92% of the installations, F tests were statistically insignificant (α=0.05) for the three coefficients of the RSG function.

Table 3. Analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA) for the three coefficients of the RSG function (Equation (1)) for the three fertilization treatments.

ANOVA			MANOVA		
β_0	F=0.73	p=0.48	Wilks' Criterion	F=0.72	p=0.63
β_1	F=1.00	p=0.37	Pillai's Trace	F=0.72	p=0.63
β_2	F=0.77	p=0.46	Hotelling-Lawley Trace	F=0.72	p=0.63

CONCLUSIONS

The statistical analyses indicated that fertilization treatments had no significant effects on the relationships between relative tree basal area growth and relative tree basal area at the time of fertilization. Fertilization increases stand total growth and accelerates tree differentiation and thus speeds up the rate of crown differentiation, but does not affect the distribution of tree basal area growth within a stand. The contribution of an individual tree's growth to stand growth is a function of its relative size in the stand. A tree's response to fertilization depends on its initial size, since larger trees in a stand produce more absolute growth response than smaller trees (Shafii et al. 1990). However, the characteristic patterns of within-stand growth depend on stand conditions such as density and structure. Our results suggest that if a tree is growing relatively well prior to fertilization, its response after treatment will be proportional to its prior relative growth. The absolute growth effects of these silvicultural treatments would need to be first estimated at the stand level. Growth could subsequently be distributed to a list of individual trees using the RSG function.

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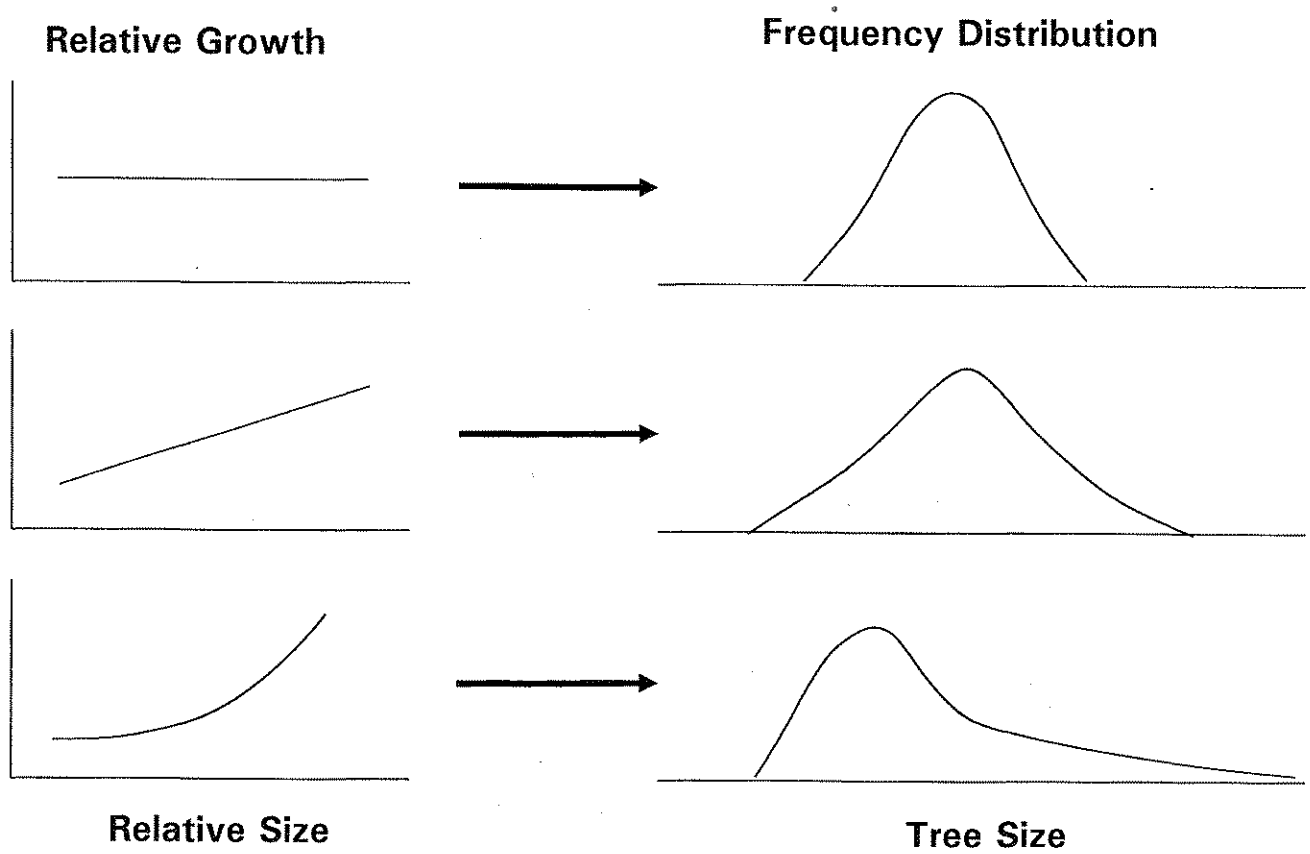

Figure 1. Relationship between the relative size-growth function and the frequency distribution of initial tree size

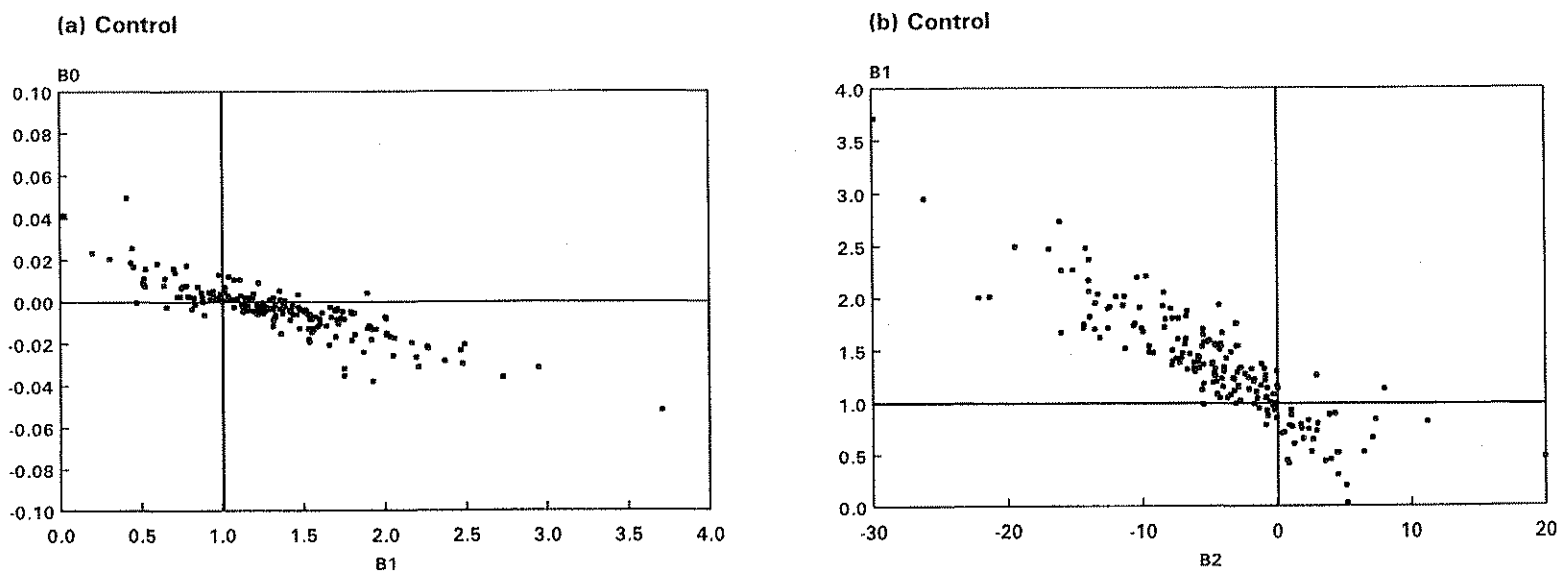

Figure 2. Relationships between the relative size-growth function coefficients for the control plots: (a) B0 versus B1, (b) B1 versus B2.

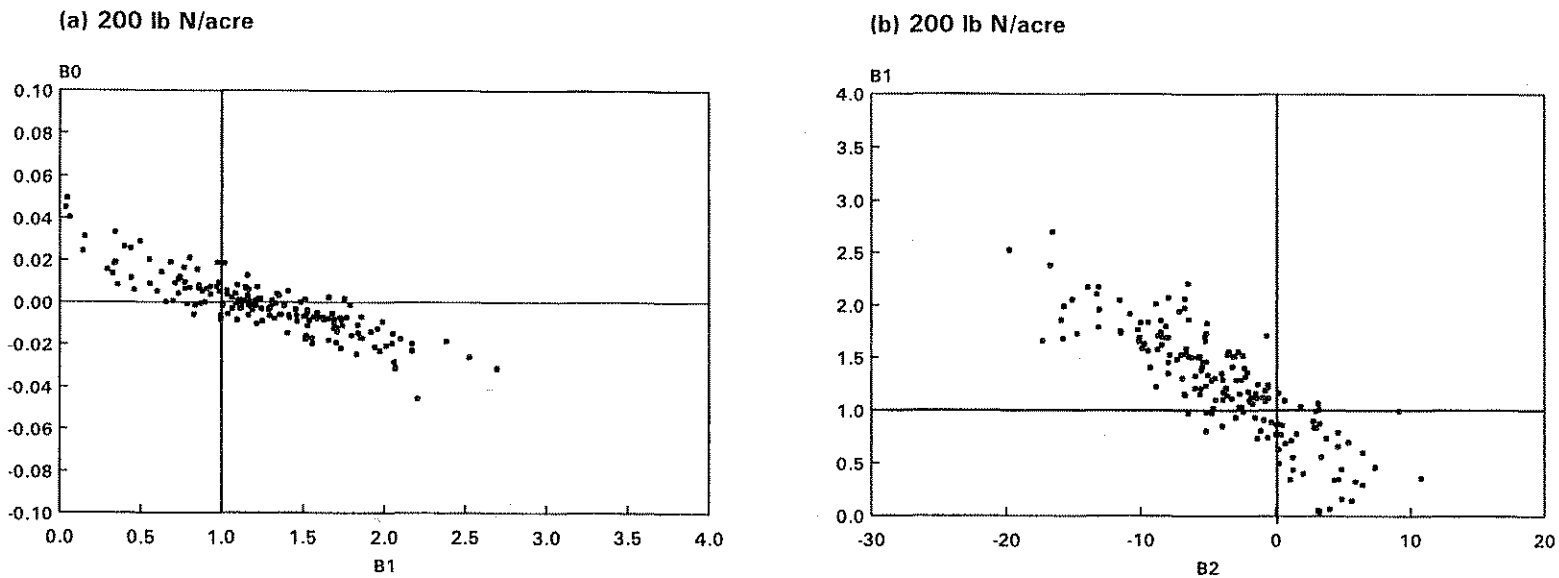

Figure 3. Relationships between the relative size-growth function coefficients for the 200 lb N/acre: (a) B0 versus B1, (b) B1 versus B2.

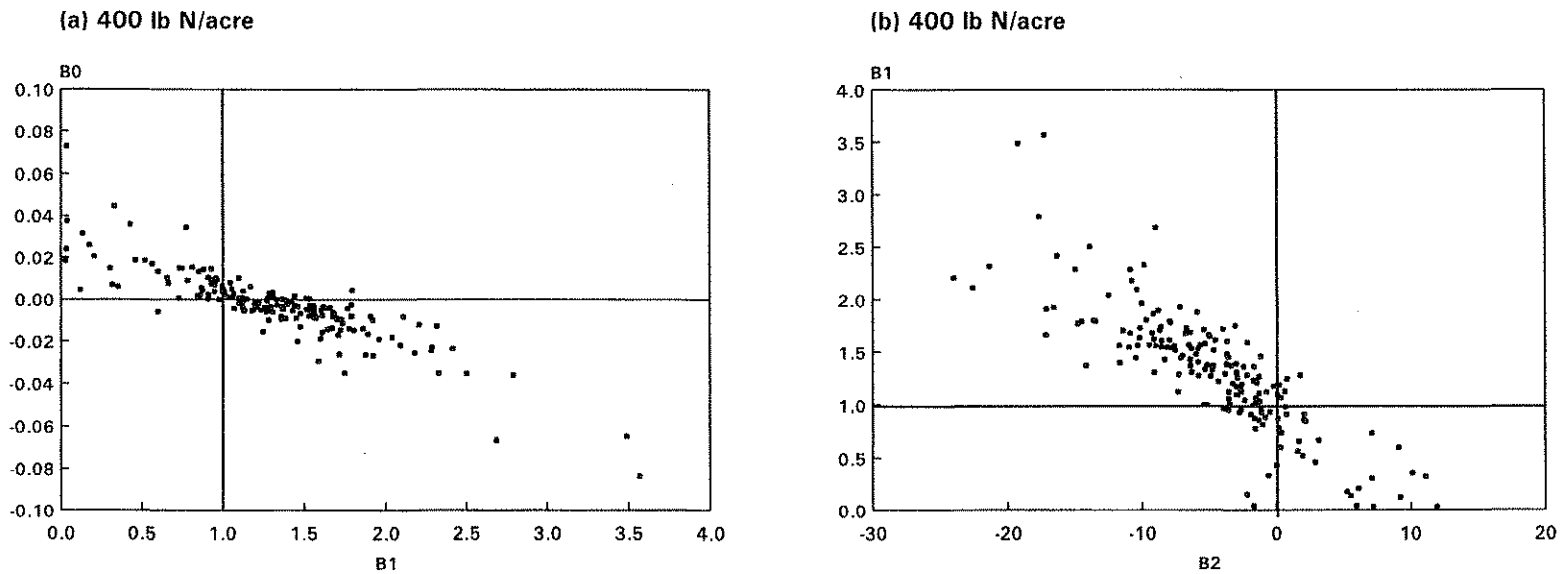

Figure 4. Relationships between the relative size-growth function coefficients for the 400 lb N/acre: (a) B0 versus B1, (b) B1 versus B2.

BASAL AREA PREDICTION FOR THINNED PLANTATIONS

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ABSTRACT

A model form that is consistent with empirical evidence is proposed for the prediction of per-acre basal area in unthinned plantations. Predictor variables are plantation age, average dominant height, and number of surviving trees. For thinned plantations in which thinning intensity is specified as number of trees to harvest or to leave, a general model to predict the basal area harvested by different thinning methods, is proposed. And, to predict basal area growth in thinned plantations, a general model is proposed based on the assumption that the basal area in the thinned plantation will converge on that of an unthinned plantation of the same age, that has the same number of surviving trees. Within a realistic range of planting densities and thinning intensities, the rate of convergence depends on the level of suppression in the thinned plantation, relative to the unthinned one, as expressed by an index of suppression. An example is given of the proposed models fitted to data from the South African Correlated Curve Trend experimental plots for Pinus elliottii Engelm.

Introduction

Plantation management regimes that include one or more thinnings are often implemented or contemplated. Analysis of this decision problem requires information on yields expected from different planting densities as well as the growth response to thinnings.

An ideal data base from which to develop the required prediction models would represent a wide range of planting densities and sites, where some plots were never thinned, while others were thinned at different ages with different intensities and thinning methods. No such data base exists, but a considerable number of so-called spacing and thinning studies have provided information that can be used to develop reasonable prediction models. The proposed strategy is to use a general prediction model for unthinned plantations as the basis for developing a model for thinned plantations.

Basal Area Growth in Unthinned Plantations

Results from spacing or planting density studies reported in the forestry literature provide the basis for the following generalizations. For a range of

planting densities considered realistic for timber production, say from 200 to 1200 per acre, and otherwise similar site conditions:

1. Average height of the dominant canopy is not affected significantly by differences in planting density, as illustrated in Figure 1.a.

2. The number of surviving trees per acre approaches a common lower asymptote at maturity, as illustrated in Figure 1.b.

3. Basal area per acre approaches a common asymptote at maturity, as illustrated in Figure 1.c.

4. At a given age, basal area per acre increases as the number of surviving trees increases, as in Figure 1.c.

5. At a given age and number of surviving trees per acre, the basal area increases as average dominant height increases.

6. At very young ages, average dbh is unaffected by differences in planting density, but at progressively older ages the average dbh of progressively lower planting densities will exceed those of higher planting densities, as illustrated in Figure 1.d.

Basal Area Prediction Model for Unthinned Plantations

Basal area prediction models for unthinned plantations must accommodate the generalizations identified above. An example is given below of such a model fitted to data from a Pinus elliottii planting density and thinning study in South Africa with planting densities ranging from 150 to 1200 per acre at the same location, and periodic measurements from age 5 through age 30.

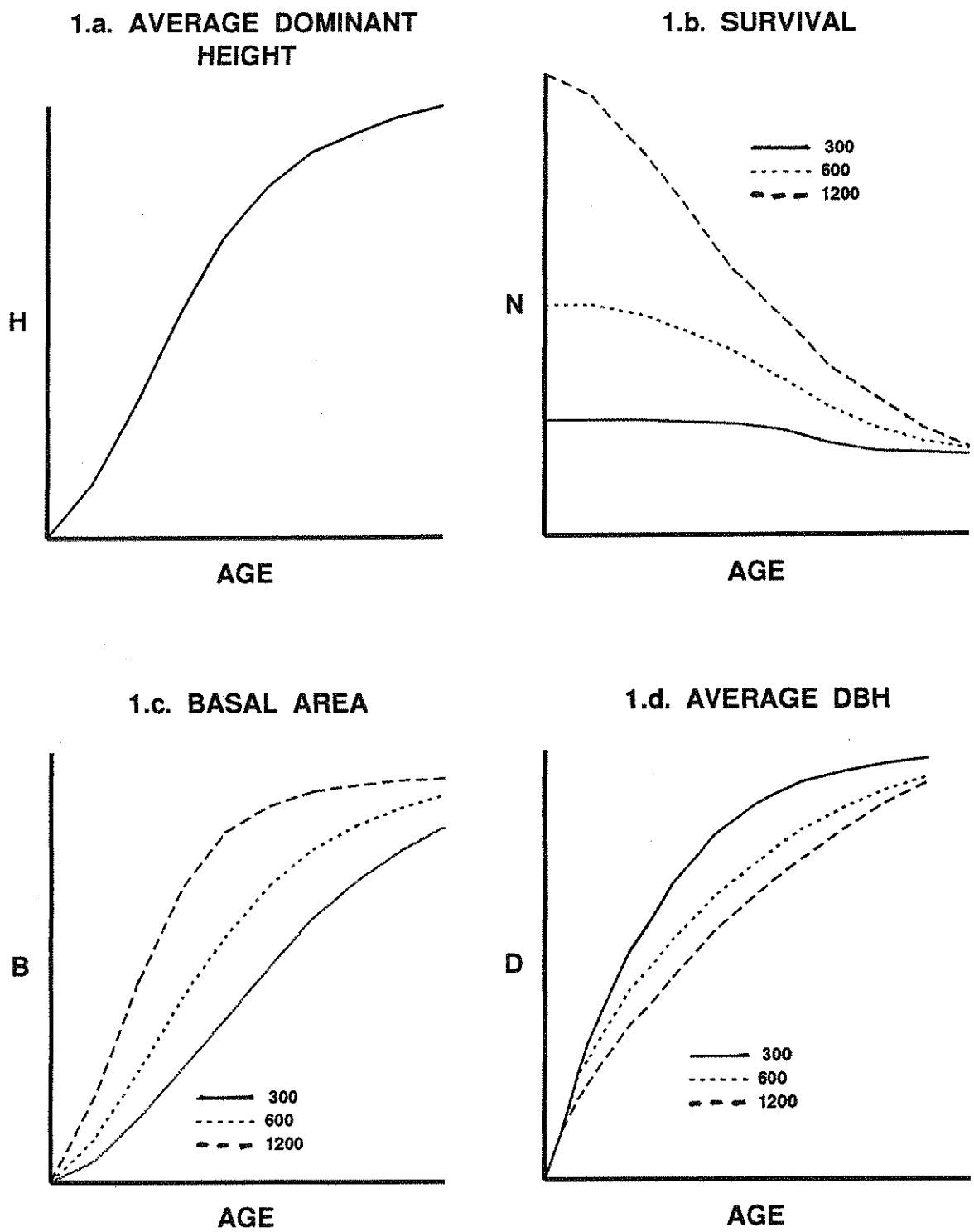
$$B = e^{-27.146(1/A)} \; H^{1.027 + 2.622(1/A)} \; N^{0.139 + 3.000(1/A)} \qquad \textbf{(1)}$$

observations = 102 $\qquad R^2 = 0.99 \qquad$ St. error = 6.3 sq ft

This model predicts basal area per acre, B, with plantation age A, average dominant height H, and number of surviving trees N, as input variables. Basal area will be asymptotic to the extent that both H and N are. The model also allows for a possible interaction of H and age, and of N and age. That is, the effect of a given increase in H or N on basal area may depend not only on their current values, but also on the age of the plantation.

A basal area prediction model such as equation 1 can be used to predict future basal area of an existing plantation if estimates of future survival and average dominant height are available.

Figure 1. Illustration of the general effects of planting density on plantation development.



For average dominant height a flexible growth model, such as the Chapman-Richards growth model (Pienaar and Turnbull, 1973), has proven satisfactory. This model can be fitted in the usual form to pairs of (H, A) observations. For the planting density study mentioned earlier, the following parameter estimates were obtained:

$$H = 115.1(1-e^{-0.0392\,A})^{0.9194} \tag{2}$$

observations = 102 $R^2 = 0.99$ St. error = 1.7 ft

It is commonly assumed that individual dominant height growth curves are proportional within the same climatic and physiographic region. That is, they differ only in the asymptote parameter, so that, for any given growth curve:

$$H_2 = H_1 \left[\left(1 - e^{-0.0392\,A_1}\right) / \left(1 - e^{-0.0392\,A_2}\right)\right]^{0.9194} \tag{3}$$

where H_1 and H_2 are average dominant heights at ages A_1 and A_2 respectively.

A survival model to fit the trends shown in Figure 1.b. is also needed. As an example, the flexible Weibull distribution function, with the shape parameter a function of planting density, and an assumed lower asymptote, can be used as the basis for such a model. Data from the planting density study were used to estimate the parameters.

$$N = N_0 - (N_0 - 200)(1 - e^{-0.00275\,A^{1.3709 + 0.0004\,N_0}}) \tag{4}$$

observations = 51 $R^2 = 0.098$ St. error = 28

where N = number of surviving trees per acre
N_0 = planting density as trees per acre
A = plantation age.

Basal Area Growth in Thinned Plantations

For operational convenience, thinning intensity is commonly specified in terms of the desired number of trees to leave. The thinning operation can be performed in a manner that is not selective for size, such as harvesting every n^{th} row, and in such cases, it is assumed that the proportion of trees removed is equivalent to the proportion of basal area (or volume) removed. On the other hand, the objective of thinning often results in selectivity for size, thus complicating the estimation of the amount of basal area removed. A logical and

simple prediction model was suggested by Field and others (1978). Data from the Pinus elliottii planting density and thinning study, where all thinnings were selective from below, at ages ranging from 6 to 22 years and intensities ranging from 25 to 80 percent of the trees harvested, were used to estimate the parameter:

$$B_t = B_b \left(\frac{N_t}{N_b}\right)^{1.2419} \tag{5}$$

observations = 42 $\quad R^2 = 0.98 \quad$ St. error = 4.1 sq ft

where B_t, N_t = basal area and trees per acre removed in thinning.
B_b, N_b = basal area and trees per acre before thinning.

The value of the parameter will depend on the thinning method: it equals 1 when thinning is not selective for size, such as row thinning; it is greater than 1 when thinning is selective from below, removing a larger percent of the trees than of basal area. If the thinning method is a combination of row and selective thinning a more general model form is required to predict the basal area removed, namely,

$$B_t = B_b\left[\frac{N_r}{N_b} + \left(1-\frac{N_r}{N_b}\right)\left(\frac{N_s}{N_b-N_r}\right)^{1.2419}\right] \tag{6}$$

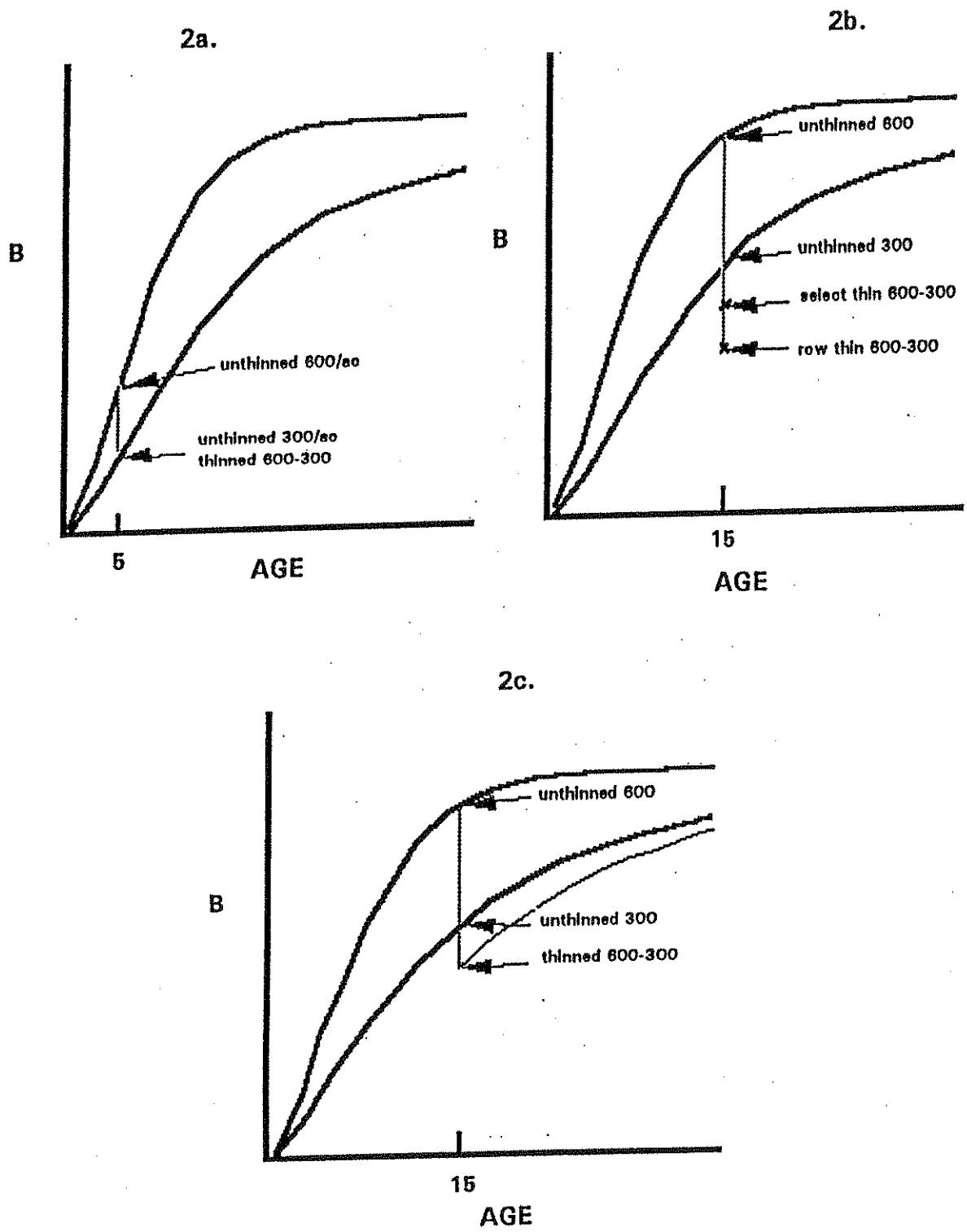
where N_r and N_s are the numbers of trees per acre removed in row thinning and in selective thinning from below respectively.

Information required for the formulation of basal area prediction models for thinned plantations is available from numerous thinning studies, particularly those that included different planting densities and thinnings at the same location. Generalizations gleaned from these studies have an important bearing on model formulation.

1. When a plantation is thinned and the remaining stand is compared with an unthinned plantation of the same age, on the same site, and with the same number of surviving trees per acre as remain in the thinned plantation, and found to have the same basal area (average tree size), basal area growth after thinning is expected to equal that of the unthinned plantation.

For example, a plantation with 600 trees per acre at age 5 that is thinned to 300, and has the same basal area as an unthinned plantation on the same site that is also 5 years old and has 300 trees per acre, as shown in Figure 2.a. Since the higher density prior to thinning had not had a measurable effect on average

Figure 2. General effects of thinning on basal area relative to unthinned plantations.



tree size compared to the unthinned plantation at the lower density, subsequent growth is expected to be the same for both plantations, as in Figure 2.a.

2. On the other hand, if a plantation with 600 trees per acre at age 15 is thinned to 300 and the remaining 300 trees have less basal area than an unthinned plantation on the same site that also has 300 surviving trees at age 15, it is not expected to have the same growth after thinning as the unthinned plantation, as shown in Figure 2.b. The magnitude of the difference in basal area depends on the thinning method. The largest difference is associated with nonselective (row) thinning, the smallest difference with selective thinning from below, while a combination of row and selective thinning will result in an intermediate residual basal area. For any given thinning method, the difference in basal area increases as the thinning intensity increases, within reasonable limits. For example, a plantation thinned from 1200 to 300 at age 15 will have less basal area than one thinned from 600 to 300, which will have less basal than an unthinned plantation with 300 trees per acre at age 15.

3. These generalizations imply that the same basal area prediction equation based on age, a measure of site quality such as average dominant height, and the number of surviving trees, is inappropriate for unthinned as well as thinned plantations.

4. Basal area in a thinned plantation will approach that of its unthinned counterpart with the same number of trees at maturity. For example, the basal area in the plantation thinned to 300 per acre at age 15 will, over time, approach the basal area in the unthinned plantation that had 300 trees at age 15, as shown in Figure 2.c.

Basal Area Prediction Model for Thinned Plantations

The difference in basal area per acre (or average basal area) between a thinned plantation and an unthinned one of the same age, on the same site and with the same number of surviving trees, is a direct indicator of the effect of the higher level of competition that the thinned plantation had experienced relative to the unthinned one. O'Connor (1935) proposed an index of suppression as the difference in basal area between the thinned and unthinned plantations, relative to the basal area in the unthinned counterpart. If B_{at} is the basal area in the thinned plantation, and B_u the basal area in the unthinned counterpart, the index of suppression is defined as:

$$IS = \frac{B_u - B_{at}}{B_u} = 1 - \frac{B_{at}}{B_u} \qquad (7)$$

The implication of the generalizations as stated earlier is that IS, over time, will approach zero. Data from the combined Pinus elliottii planting density and thinning study provided the following estimate for a simple prediction model of the expected trend:

$$IS_2 = IS_1 e^{-0.1079(A_2 - A_1)} \tag{8}$$

observations = 31 $\quad R^2 = 0.91 \quad$ St. error = 0.046

where IS_1 and IS_2 are indices of suppression at ages A_1 and A_2. Basal area in the thinned plantation at age A_2 would then be estimates as

$$B_{t2} = B_{u2}(1 - IS_2) \tag{9}$$

where B_{t2} and B_{u2} are basal areas in the thinned and unthinned plantations at age A_2. The degree of selectivity in the thinning would be reflected in the value of IS, thus obviating the need for an additional variable.

Example

To illustrate application of the proposed prediction models for thinned plantations, consider 2 unthinned 12-year-old plantations; one with 600 trees per acre, the other with 300, and both with average dominant height of 48 ft.

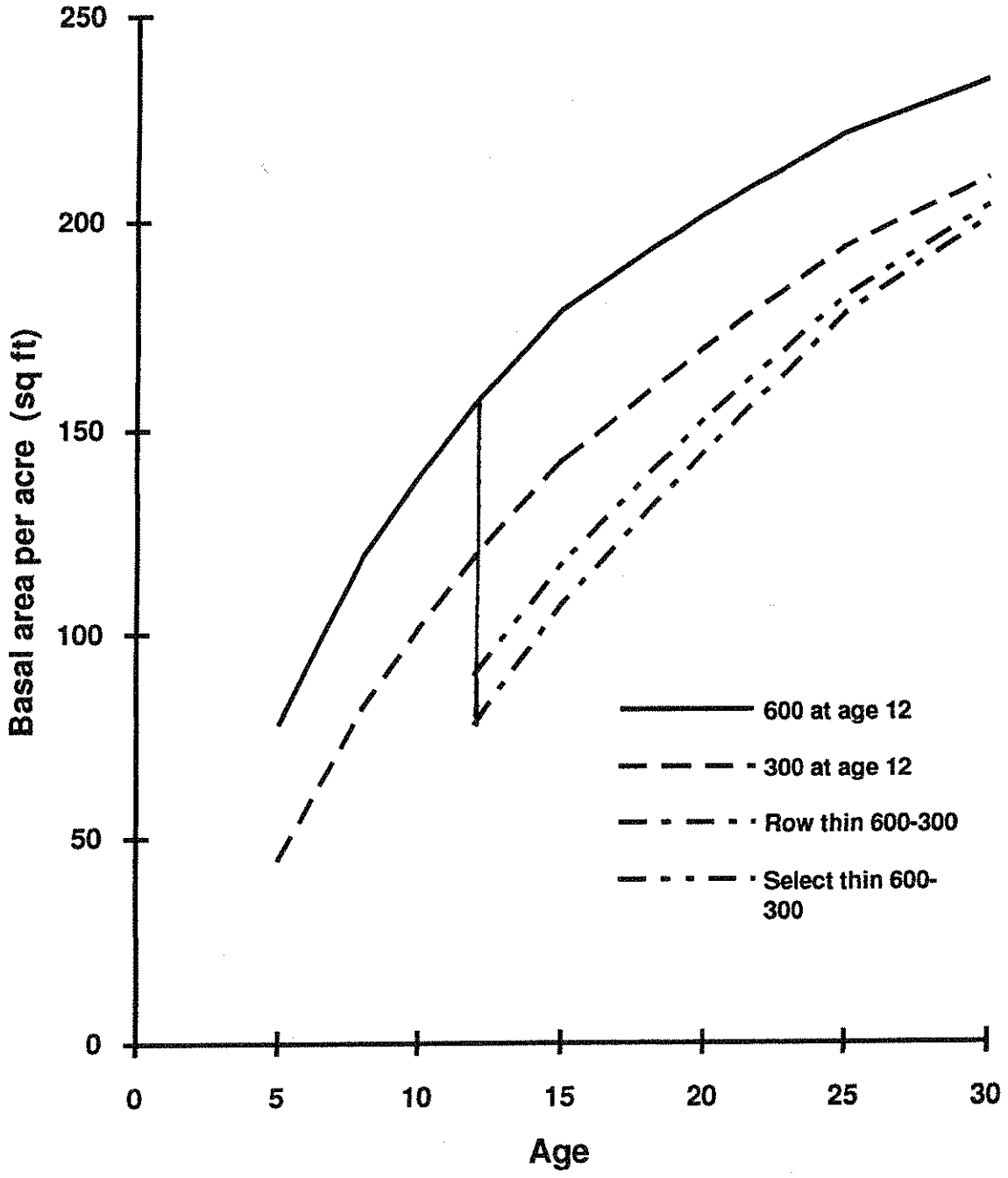
Basal area at age 12 is predicted with equation 1 as 156 and 119 sq ft per acre respectively. Equation 4 is solved for N_0, given N = 600 and 300 at age 12. Future average dominant height is predicted with equation 3 and survival with equation 4, so as to predict future basal area with equation 1. Predicted basal area development for these 2 unthinned plantations from age 12 to age 30 are shown in Figure 3.

Now suppose the plantation with 600 trees per acre is thinned to 300 at age 12:

1) With row thinning (every other row).
2) Selectively from below.
3) With every 4th row removed, the rest selectively from below.

Basal area before thinning was predicted as 156 sq ft. Basal area removed in thinning is predicted with equation 6 as:

Figure 3. Basal area growth in thinned and comparable unthinned plantations.



Basal area harvested (B_t)	Basal area remaining (B_{at})
1) 78 sq ft	1) 78 sq ft
2) 66 sq ft	2) 90 sq ft
3) 69 sq ft	3) 87 sq ft

Indices of suppression at age 12 are calculated with equation 7 (B_u = 119 sq ft) and projected to age 30 with equation 8. Basal area at age 30 is predicted with equation 9 (B_{u2} = 210 sq ft)

$IS_{age\ 12}$	$IS_{age\ 30}$	$B_{age\ 30}$
1) 0.3445	1) 0.0494	1) 200 sq ft
2) 0.2437	2) 0.0349	2) 203 sq ft
3) 0.2689	3) 0.0386	3) 202 sq ft

Predicted basal area development after thinning is shown in Figure 3.

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BASAL AREA GROWTH OF INDIVIDUAL TREES IN THINNED, EVEN-AGED STANDS OF LONGLEAF PINE

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ABSTRACT

An individual tree basal area increment (BAI) model for naturally regenerated, even-aged longleaf pine (*Pinus palustris* Mill.) is presented. The model was derived from data collected from 202 permanent measurement plots located in central and southern Alabama, southern Mississippi, southwest Georgia, and northern Florida. Most plots were installed between 1964 and 1967 and measured at five-year intervals from the year of installation. At the time of installation, a target basal area was assigned to each plot. Following each measurement, plot basal was calculated. If plot basal area was 7.5 ft^2/acre or greater than the target basal area, the plot was thinned from below to reduce basal area to the target basal area.

The model is an intrinsically non-linear equation, which is constrained so that it performs within the bounds of biologically reasonable outputs for any combination of values for the independent variables. All parameters in the equation were estimated simultaneously. This is a departure from the more traditional potential-times-modifier approach in which parameters for the potential growth function are estimated from a sample of trees exhibiting the fastest growth. Independent variables used to describe BAI are stand basal area, the competitive position of an individual tree within the stand calculated as the sum of the basal areas of all trees larger than the subject tree, mean age of dominant and co-dominant trees, and individual tree diameter outside-bark at breast height. Noticeably absent from the model is an independent variable that explicitly characterizes site differences. No consistent under- or over-estimations of residuals were evident when plotted against percent basal area removed or actual basal area removed in thinning operations.

A MODEL FOR THINNING REACTION

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ABSTRACT

The report describes a way to model the effect of thinning on Pinus kesiya. Modelling is based on first modelling mean basal area development of undisturbed stands and then defining the thinning reaction as the difference when compared to the undisturbed situation. The thinning reaction is also modelled. The model was built using inadequate data from thinnings. However, it seems to provide logical results. It enables the study of the effects of thinning time, number of thinnings, and thinning type on the growth and yield.

INTRODUCTION

In southern Africa, growth and yield models for plantation trees have been largely based on the so-called " Correlated Curve Trend " principle (CCT), first presented by O'Connors (1935). He was able to carry out quite large experiments in order to test the hypothesis. O'Connors (1935) started with three principles:

1)In any given locality, the size attained by a tree of a particular species at a given age must be related to the growing space previously at its disposal; all other factors influencing its size are fixed by the locality.
2)Trees planted at a given espacement will, until they start competing with each other, exhibit the absolute or normal standard of growth for the species and locality.
3)Trees planted at a given espacement and left to grow unthinned will exhibit the absolute or normal standard of growth for the species, locality, and the particular density of stock in question (Bredenkamp 1984).

Later this hypothesis was extended by Marsh & Burgers (1973) to concern thinned stands: "The increment of thinned stands is equivalent to that of unthinned stands of the same stocking (stems/ha) and density (m^2/ha or m^3/ha), but of younger age (i.e. the age at which they had the same basal area or volume per unit area)". This hypothesis has been validated with several subtropical species and appears to give accurate and unbiased estimates of growth after thinning, provided that growth is measured over a period of at least three years (Alder 1980).

When using the CCT principle once the results of the basic espacement trials are available, no more thinning trials are needed. In Europe and North America this hypothesis has attracted scant attention (see Smith & Hafley 1987). This might be due to the use of much longer rotations in boreal forests than in the tropics, and the much greater difficulty in producing a basic series of espacement trials.

Mitchell (1975) presented a very detailed dynamic yield model for Douglas fir (Pseudotzuga menziesii), which consists of models for tree foliage development and its effect on volume growth. The model enables the simulation of the effects of thinning, fertilization, animal browsing, and tree breeding on the yield of a stand.

Thinning reaction

The response of trees to thinning, and possible shock immediately after thinning, have caused problems for growth and yield modellers. Vuokila (1960, 1965) stated that positive response to thinning at breast height can change to a negative reaction at a higher position along the bole of the tree. He also confirmed the earlier statement that thinnings cannot improve the total production of forest stands. Marsch & Burgers (1973) solved the problem of modelling thinning reaction by further developing the CCT theory. Harrington & Reukema (1983) found an occurrence of thinning shock in Douglas fir which reduced height growth. After 15 to 25 years, at all thinning intensities, this negative effect had changed to positive, the best height growth being at wider spacings. Diameter growth at breast height increased following thinning and the rates in diameter growth between spacings increased with time. Saramäki & Silander (1982) have also found a reduction in height growth immediately after heavy thinning.

In many growth models, thinning is taken into account indirectly, as some measure of density is always included as an independent variable. Stand density changes with thinning and causes changes in the independent variables when post thinning growth is predicted. The type of thinning is often difficult to describe. However, inclusion of some measure of the relative size of removed trees compared to the size of remaining trees seems sufficient in describing the type of thinning (see e.g. Alder 1980). The effect of thinning is reflected in the competition index in distance-dependent treewise equations, even though a general competition measure like basal area provides almost the same information in plantations (Martin & Ek 1984, see also Pukkala 1988).

Thinning causes changes in the order of trees by releasing more resources to some trees than to others. However, within a quite short period after thinning the order stabilizes again. By studying only stable situations, the position of the tree at a future point in time can be estimated. When the ordinal of the tree is assumed to remain unchanged, it remains only to predict its percentile or change in percentile from one time to another.

The aim of the study

The thinning reaction of Pinus kesiya had to be solved as part of the larger growth and yield study (Saramäki, 1992). The aim of this report is to describe how thinning

effect was taken into account when predicting growth and yield of thinned stands.

MATERIALS

All the commercial P. kesiya plantations in Zambia are located in the Copperbelt province (13 S, 28 E, 1200 - 1300 m a.s.l) The material used in this study was collected from three different sources, and one source was divided into two submaterials according to the number of measurements.

Main data were collected from permanent sample plots established in the commercial compartments (Control Plan 5/3/1, 1969) and measured from four to ten times. This material is later called basic or original material. 114 permanent sample plots were used, including 766 assessments. Treatments of the compartments varied, but all were thinned at least once. The maximum number of thinnings was four. All the stands were pruned according to the pruning schedule. These data were used to find the shape of functions for mean basal area, variance, and skewness of diameter distribution. This material was used only for finding the shape of the main models, and not for the calculation of parameter values, because the range of treatments was narrow. However, it was used for the estimation of models for site index, mortality and thinning reaction.

The second source material, called test material, consisted of 125 permanent sample plots, which were measured only two or three times, making a total of 360 assessments. These data were used only for testing the equations and the whole model.

The third data source, called inventory material, was from the plantation inventory data (Saramäki et al. 1987). It included 3260 temporary sample plots. Inventory data were used to derive final parameters for mean basal area, variance and skewness functions as well as for height equations. This material represents a statistically sound sample for all plantations and thus, guarantees the usefulness of the model in operational planning.

The fourth source material (Control Plan 2P/7/6), espacement trial material, was a trial of nine spacings from 12048 stems/ha to 137 stems/ha with five replicates. These data were used for finding the shape of mortality and mean basal area functions. This is the only material where the original density varies and it gives valuable information on the effect of density on the growth and yield.

For more details on the materials used see Saramäki (1992).

CALCULATION OF THE THINNING EFFECT

Parameters of the basal area model:

$$\ln(g_m) = a + b/T^c$$

where

$\ln(g_m)$= natural logarithm of mean basal area,

T = age of the stand,
a,b,c= parameters that depend on site and density of the stand (Saramäki 1992),

were solved using observations where the amount of time from the latest thinning was not exactly known. When using the basic material(see Saramäki 1992), where thinning times were known, measurements allowed a prediction interval of three years; the first three years after every thinning were estimated separately. This was done by modelling the difference in basal area increment between the model without after-thinning years and measured values in this material (Fig. 1). This difference is later called thinning reaction, as it shows how much the increment deviates from the increment of an undisturbed stand with the same stocking.

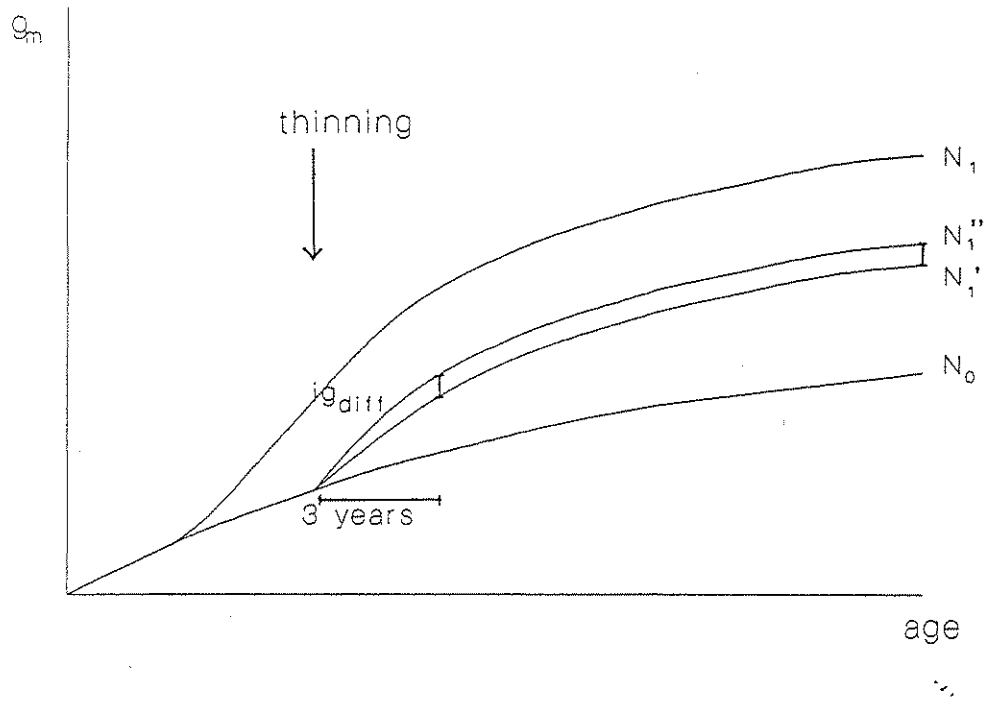

Figure 1. Schematic picture of the development of mean basal area after thinning from stocking N_0 to N_1. N_0 = development with stocking N_0 without thinning; N_1 = development with stocking N_1 without thinning; N_1' = development if no thinning reaction; N_1'' = development with thinning reaction; ig_{diff} = thinning reaction (Saramäki 1992).

All the stands are planted using the same stocking, 1330 stems/ha, so that competition starts at about the same time in all stands. The time at which competition starts also depends on the site. In this material, site variation was so small that differences were insignificant. In young stands (age<=7), no reaction to thinning was seen. Instead, thinned stands grew like stands which have grown from planting-out in the after-thinning stocking. Some signs that heavy early thinnings might decrease growth for a few years were observed. In all cases, heavy thinnings seem to cause only very little thinning reaction, if any (Fig. 2). As the material did not include information on thinnings from very old stands, the thinning reaction had to be partly estimated from heuristic values.

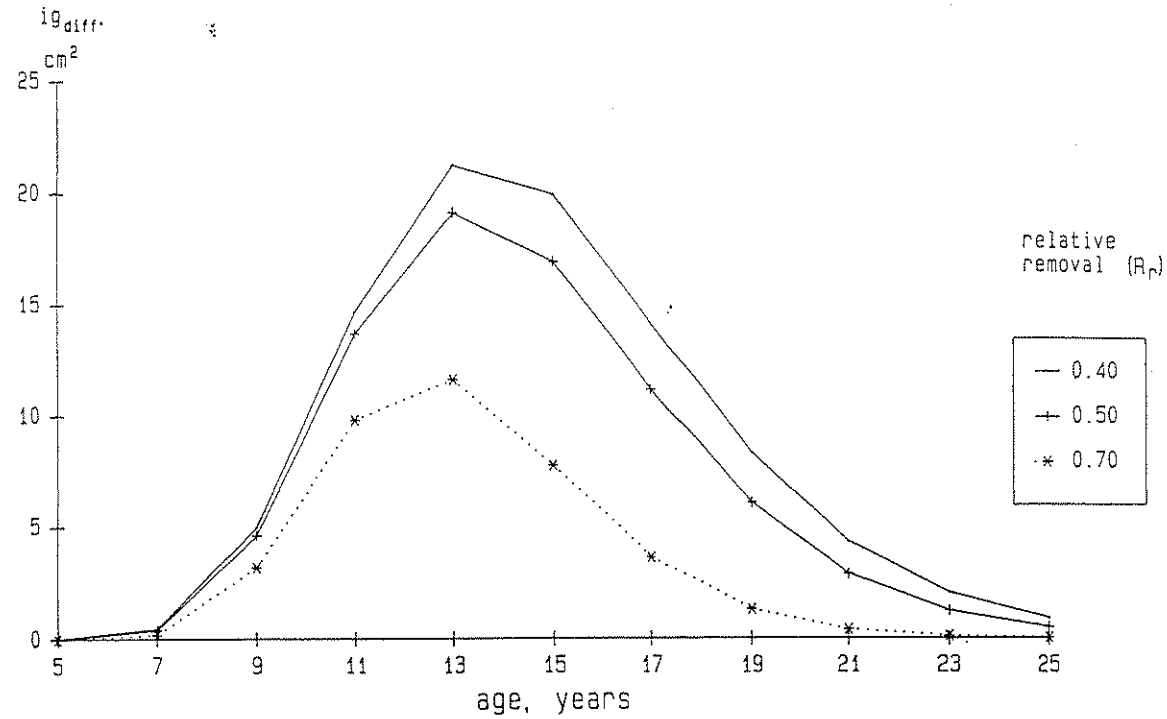

Figure 2. The shape of the thinning reaction model according to Saramäki (1992).

Thinning reaction was estimated in two steps. Firstly, the reaction was estimated for each thinning intensity separately, based on age only. The parameters a, b and c of the function

$$ig_{diff}=e^{(a+b\cdot lnT+c\cdot(lnT)^2)}$$ (Saramäki 1992, p 32)

where

ig_{diff} =difference of actual and estimated mean basal area increment during three years after thinning from predicted mean basal area increment, cm^2,
T = age of the stand, years,
a,b,c = parameters,

are closely correlated, and parameter b could be explained by relative removal (R_r). Parameters a and c were then found by regressing them against parameter b.

Relationships between parameters are partly based on assumptions, as not enough data were available at the older ages. Having fixed the relationships between parameters, the level of thinning reaction was scaled according to the data. On average, the model removes the systematic deviation caused by thinning, but the residual variation is considerable.

The mean basal area for the first three years after thinning is calculated by first using Eqn. (24) from Saramäki (1992 p 22), and then adding the value from above function. If measured information is available, the difference between the logarithms of measured and predicted mean basal areas is added to asymptote a in Eqn. (24) (Saramäki 1992), to balance out the equation to the correct level.

The effect of thinning on mean basal area development was assumed to last for three years, this being the length of time needed for the tree to change its entire foliage. It can be argued that especially in older stands the effect might last longer. This hypothesis was tested, but the present material did not support such a theory. As there were only a few observations at older stand ages, the function was forced to approach zero when stands were more than 20 years old.

The whole thinning reaction, as defined in this study, does not greatly affect total growth within the rotation. The difference between treated and untreated stands arises mainly from differences in the growth rate at different densities.

The thinning had to be spread into diameter distribution. In the simulation, the diameters of trees were fixed to predicted Weibull function, and that percentage point was kept fixed as long as there was no thinning. The parameters of the Weibull function were dependent on mean basal area, age, stocking (stems/ha) and site(see Saramäki 1992). After thinning, new Weibull was formed using new parameter values. Then, known diameters of the remaining trees were fixed to that Weibull. The thinning affected the growth of different sized trees via mean basal area.

In most thinnings there is a systematic as well as a selective component. The systematic component is a random sample from the diameter distribution and its proportion of total removal depends on the harvesting system. Thinning was assumed to be defined by the number of stems removed and by 'thinning type'. Thinning type means the ratio between mean basal area after and before thinning. If the ratio is one, thinning is random; if greater than one, thinning is from below; and if less than one, thinning is from above. A regression equation was calculated in each case to give the relative removal from each diameter class. Because of the discrete nature of the diameter distribution, trees were removed from or added to both ends of the removal in order to obtain the number of trees removed equal to the given values.

As no information was available on the rate of change of growth after thinning, the effect was set to last three years. The reaction was added to the basic curve so that mean basal area development was parallel with the original curve (see Fig. 1.). When better data about thinning become available, the time taken to reach the basic curve and the shape of the approaching curve can be determined more accurately. However, the total effect cannot deviate greatly from the assumed.

DISCUSSION

The inclusion of measured data provides more reliable estimates for short term prediction. It is not known for how long the assumption of the constant percentage point is valid. After thinning the diameter distribution changes and also causes temporary irregularities in growth. In operational use, it is recommended to measure diameter distribution after

thinning, and avoid the problems of increment prediction over thinning time. Thinning reaction has been inadequately studied and needs more attention. The method used in this study, where thinning reaction is defined as deviation from the growth rate of an unthinned stand with the same stocking, seems to provide a good basis for predicting total increment after thinning. The thinning reaction is only a small fraction of the total increment after thinning. Possible error remains small in all cases.

Although thinning reaction is not fully described in the study material, the simulation system, which is fully described in Saramäki (1992), makes it possible to simulate a large range of thinning regimes. The system as such allows both thinnings from above and below as well as systematic thinnings, but the data does not include thinnings from above. However, the model seems to also work logically in the case of thinnings from above. The effects of thinning time, number of thinnings and thinning type can be studied with this system.

The thinning function had to be based on permanent sample plot material. However, this produced quite a representative result. As the observations in the thinning data are autocorrelated, their error structure cannot be fully described.

Thinnings are simulated using quite a simple method. If simulated thinning types and intensities deviate greatly from practice, the output from simulations can be misleading, especially where sawlog production is concerned. Even if thinning effect may have been inadequately modelled, the influence on total yield is very small. Another practice would have been to use separate parameters after each thinning, as presented in Knoebel et al. (1986). However, this requires many more equations, and the whole variation in inventory material could not have been used. Although previous studies contain experiences of the effect of thinning on height growth (eg. Saramäki & Silander 1982, Harrington & Reukema 1983), no corrections were made to the predicted height growth in this study. It was assumed that in ordinary thinnings the effect is small, with no need for correction.

The most part of increase in growth after thinning can be explained by changing stocking or density. Nevertheless, detailed information on the type of thinning requires tree level data. By carefully selecting the tree increment function, compatibility with the distribution level function (Daniels & Burkhart 1988) can be ensured. In tropical plantations, the modelling of thinning reaction also requires annually measured data material, which was not available in this study.

Pukkala et al. (1990) define thinning removal in different diameter classes by removing a decreasing or increasing proportion from neighbouring diameter classes. The change in proportion defines the type of thinning. The specified thinning intensity is found iteratively. Knoebel et al. (1986) specified a function that estimates the amount of basal area to be removed from each diameter class. Parameters of the function were derived from empirical data and as such are dependent on the base material. The method used in this study is independent of the data, and is a modification of the method of Pukkala et al. (1990). The method makes it possible to simulate both thinning from above and thinning from below as well as systematic thinning. It also guarantees that no contradiction exists between the diameter distributions before and after thinning. In many thinnings there is also a systematic component. This can also be taken into account in the present system by defining, in the thinning situation, the proportion of the systematic part which is removed

first. This system also allows extreme thinning types, but the mean basal area, variance, and skewness functions may cause bias in the predictions.

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DEVELOPING A VARIABLE-DENSITY GROWTH AND YIELD MODEL BASED ON A NORMAL YIELD TABLE

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ABSTRACT

Silvicultural prescriptions and forest management decisions often rely on yield tables that do not model the effects of spacing and thinning regime on either stand or individual tree growth. These shortcomings can severely limit the potential of decision analyses. Forest managers and forest planners are usually not in a position to construct new growth and yield models, but often results from spacing and thinning experiments, or similar information are at hand. In this paper, a method is described that can be used in such situations as a "first aid" to improve on an inadequately formulated or outdated yield table. A subjectively fitted and graphically formulated yield table for Norway spruce (*Picea abies* L.) on former Atlantic heathland in western Denmark (West-Nielsen 1950) is used as an example to illustrate the technique.

From the original yield table only the height-age based site classification system and the relationships between stand height and total volume production are kept to form the basis of a revised and variable-density model. Results from spacing experiments are utilised for modelling natural mortality in the period until the first thinning. Results from thinning experiments are utilised for modelling further stand and mean tree development. Stand height rather than time is the driving variable, and thinning regime (timing and intensity) is defined by relative spacing. All parts of the resulting model, including the growth and yield functions are algebraically fully compatible. The model is open for incorporation of local experience regarding natural mortality, beating up, or effects of thinning regime on stand growth and yield.

The background to this work is a forest management analysis comprising 46,000 ha of national forests on former heathland (Skovsgaard & Jensen 1993). A comprehensive version of this paper is under preparation for the journal **Forest & Landscape Research**.

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ESTIMATION OF LONG TERM EFFECTS OF ESTABLISHMENT PRACTICE FROM EARLY MEASUREMENTS

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ABSTRACT

Forest managers need reliable estimates of the long term effects of experimental silvicultural treatments to give them confidence in implementing them into general practice. One approach is to fit growth curves to data from control and treated stands and then estimate future growth by extrapolation. This can be inadequate because i) the choice of the mathematical form of the growth curve (including any constraints) can have a marked effect on the reliability of extrapolation; ii) major fluctuations in climatic factors, e.g. severe droughts can result in data which precludes being described by smooth functional forms; and iii) there is frequently too few data to make reliable estimates of the coefficients for the growth curves. An alternative approach is to directly model the behaviour of the growth responses, i.e. the differences between the treatments. This paper shows that i) the behaviour of responses through time can have a simpler mathematical form than that required to describe growth; ii) the cumulative response is little perturbed by climatic factors; and iii) reponses often exhibit asymptotic behaviour within a few years of treatment. These principles are illustrated with data from long term experiments with *P.radiata* and *P.elliottii.*

Two basic patterns of response can be identified. Some treatments, such as weed control during plantation establishment, result in a short term change in growing conditions. The associated growth responses (called Type I responses) are of short duration but in the long term reduce the time for the forest stand to reach a given stage of development or maturity. Other treatments, such as addition of fertilizer to a nutrient deficient site, can have a long term effect on growing conditions. The associated growth response (Type II) is characterised by a long term change in the general level of productivity which may extend into subsequent rotations. The Type 1 response is characterized by a short period during which stage of stand development is advanced and the initial difference in size is established. Thereafter the size difference (response) increases until after the culmination of current annual increment and is maximised when the increment of the advanced stand in the descending phase of the current increment curve equals that of the standard stand which is in the ascending phase of the current increment curve. Thereafter the difference between the treatments declines. This behaviour can be usefully described by a monomolecular curve which rises to meet a descending 'asymptote'. The Type II response is multiplicative. Once a logarithmic transformation is taken, its behaviour is closely similar to that of the Type I response and can be modelled accordingly. These principles can be easily extended to the examination of factorial combinations of treatments and to quantitative treatments.

DIFFICULTIES IN THE ANALYSIS AND INTERPRETATION OF THINNING EXPERIMENTS AND THINNED EXPERIMENTS

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ABSTRACT

Initial spacing or thinning have important effects on the state of a forest stand and on its future behaviour. Consequently, great care needs to be taken when specifying thinning regimes for experiments designed to compare different methods of thinning and particularly when thinning is applied to existing experiments in which growth responses have been obtained. In the first case plots representing a single population are treated to obtain two or more populations with different characteristics. Since the populations differ from the outset of the experiment, traditional analyses of variance of yield statistics may give biassed or confounded results. The consequences of thinning existing experiments where the treatments have resulted in a series of populations with different characteristics can be even more complex.

Recommendations are made and illustrated for i) modelling plot growth in spacing or thinning trials by sigmoid or orthogonal polynomial functions followed by statistical analysis of treatment effects on the coefficients; ii) the incorporation of prior growth data as covariates; and iii) the use of multivariate techniques to assist interpretation. This type of analysis is illustrated with data from a New Zealand experiment. The paper also uses data from an Australian experiment to illustrate how thinning can affect the retention of prior treatment differences and their magnitude.

INTRODUCTION

The initial spacing of a forest stand has major effects on operational costs, on risks of damage by pests, diseases and wind, and most importantly on the growth, form and quality of the trees in the stand. Increasing the spacing in older stands by thinning is also important for maintaining growth without competitive mortality and to improve value of individual tree stems. Consequently a common type of forest field experiment is that concerned with spacing or thinning. Different initial spacings can be formed (for example, 2 x 2 m, 2 x 3 m) by planting (Buford 1991, Cromer & Pawsey 1957) or by thinning to waste at an early age (Woollons & Whyte 1989). In older stands different spacings are achieved by thinning to waste or by production thinning (Hamilton 1976, Wiley & Zeide 1988). Typically, four or five residual stockings are created then the performance of these treatments are monitored over some decades by periodic remeasurement of the experimental plots.

Given the number of these spacing and thinning trials that have been assayed, it might be assumed that analyses of them are routine, easily extracted from any appropriate text. In our opinion this assumption is not justified; indeed the opposite is the case. To extract the maximum information inherent in a thinning experiment requires application of quite sophisticated or specialised statistical techniques. Woollons (1985) has defined the problems associated with the analysis of experiments containing both thinned and unthinned stands, and has recommended various procedures for their statistical analysis. In this contribution we extend those methods to the case of multiple levels of thinning or spacing and illustrated them with data from a thinning trial in New Zealand.

We also address the problems involved when existing experiments are thinned. The importance of thinning in forestry practice is held in such high regard that there is often a temptation to thin existing long term experiments. By the time of thinning the various treatments, e.g. initial spacing, fertilization, weed control etc., in these experiments would usually have resulted in growth differences. Little attention has been paid the consequences of thinning such trials. Matheson and Raymond (1984) showed that simulated selective thinning altered estimates of genetic and phenotypic variances and their ratio - heritability. Snowdon and Waring (1984) suggested that responses to treatments which have no sustained effect on the forest site, e.g. weed control, could be easily eliminated at the time of thinning whereas responses to treatments which have an enduring effect on the forest site, e.g. rehabilitation of a nutrient deficiency, might be expected to enhance growth following thinning. In this paper we examine the effects of thinning an Australian initial spacing trial.

ANALYSIS OF SPACING AND THINNING TRIALS

Problems in analysis

In establishing a series of replicated experimental plots comprising of different densities (stems/ha) the researcher is essentially interested in studying the respective yield trajectories through time, as represented by various traits, for example basal area/ha, top-height or live stems/ha. Measurement or estimation of these may be annual or periodic, that is, the intervals between measurements may or may not be, constant.

At first inspection, it might be assumed analyses of variance or covariance, using yields at chosen time periods, will provide a satisfactory analysis, but this is not so. *A priori,* the experimental treatments are (deliberately) set at contrasting densities, so future basal area/ha must be distinct between treatments; significance testing in this respect is therefore almost irrelevant. Covariance analysis is also compromised, in that the usual covariates for growth, e.g. initial basal area or top height, are strongly correlated with treatments so that adjusted yields become meaningless.

A suggested analysis

The data structure outlined above is typical of a repeated measures design (Winer 1971), but the likelihood of the presence of many (say > 10) remeasurements, probably at

uneven intervals, makes a normal repeated measuresanalysis difficult to assay. A satisfactory and thorough exploration of the data, however, may be achieved as follows:

1. Model each plot sequence by a suitable yield-time function. For data over an appreciable age range, a sigmoid formulation is relevant; for shorter datasets, it is sufficient to express the data in terms of linear, quadratic, and cubic coefficients, through orthogonal polynomials (Ostle & Malone 1988). If uneven time intervals are present, calculation of the coefficients is still straightforward, although protracted without a computer routine (Carmer & Serf 1963).

2. Analyse the sigmoid or orthogonal coefficients singly and jointly through univariate and multivariate analyses of variance. Further insight may be obtained through a canonical analysis of the coefficients, discriminating between thinning treatments. Differences in yield paths can be estimated and demonstrated by calculating generalised squared distances, or plotting canonical scores resultant from the first two canonical variables.

Experimental

These analytical approaches can be illustrated through data extracted from a thinning experiment in the northern region of the North Island of New Zealand. The trial was established in a first rotation *Pinus radiata* stand at Forsyth Downs under the propietry of Carter Holt Harvey Forests, Ltd. In 1987, at age 5, four residual stockings (200, 350, 500 and 1200 stems/ha) were created in four randomised blocks, the blocking undertaken through proximity of experimental plots. Plot size was 0.1 ha, with an outer 0.4 ha buffer. Prior to thinning the breast height diameters of ~11 plot trees were measured. Thinning, *per* se. was very largely assayed from below, but with some recognition of form.

Diameter breast height and tree height measurements have been taken annually for all experimental trees and plots.

Analyses and results

For brevity, attention will be limited here to top-height development; top height ($\bar{h}_{100}$) is defined as average height of the top 100 trees/ha by diameter.

Preliminary analyses revealed a strong relationship between pre-thinned basal area/ha and subsequent top-height growth, suggestive of variable productivity within the experiment. The association was especially significant ($p < 0.0001$) at the time of thinning then becoming relatively weaker thereafter but not independent until four years after thinning. Accordingly, top-heights of each plot were adjusted through covariance, using a separate coefficient for each year of growth. Figure 1 illustrates the consequent height development for the four treatments over 1987-1992.

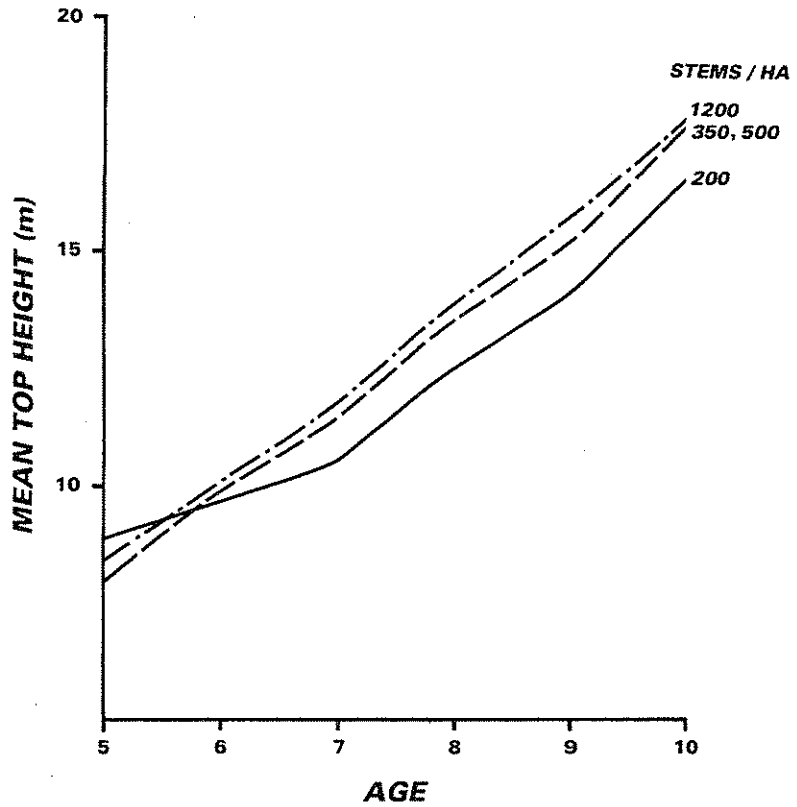

Figure 1: Effect of stocking on development of top height of *P. radiata.*

These data strongly suggest the 200 stems/ha regime is on a lesser height yield path relative to the other stockings. To test this hypothesis, each plot was modelled over time, by expressing the annual measurements in terms of linear, quadratic, and cubic orthogonal polynomials. (with only six measures available, fitting of a sigmoid function is not practical.). Individual analyses of variance for these response variables are summarised in Table 1.

Table 1: ANOVAs for orthogonal polynomial coefficients for modelling height growth.

SOURCE OF		LINEAR		QUADRATIC		CUBIC	
VARIATION	df	SS	P>F	SS	P>F	SS	P>F
Blocks	3	15.8	0.38	13.4	n.s.	50.6	n.s.
Treatments	3	332.5	0.0001	25.4	n.s.	30.8	n.s.
Linear	1	276.8	0.0015	10.3	n.s.	83.1	0.3
Deviations	2	360.4	0.0001	32.9	n.s.	4.7	n.s.
Error	9	13.7		13.9		13.9	

n.s. not significant, $p<0.05$

From Table 1, it is clear that the linear, and to some extent, the cubic orthogonal coefficients differ significantly by treatment. A joint canonical discriminant analysis of the three components refines these results. A generalised squared distance matrix for the four stockings is given in Table 2.

Table 2: Generalised distances between spacing treatments.

STEMS/HA	200	350	500	1200
200	0	21.7	29.8	20.2
350		0	2.5	0.8
500			0	5.9
1200				0

Table 2 confirms that if the four stockings are ranked from smallest to largest, the 200 stems/ha treatment is overtly "furthest distance" from the other three treatments. This can be seen even more readily by plotting the first and second mean canonical scores for the four treatments (Figure 2): the circles represent 95% confidence regions (Mardia *et al.*, 1979). Thus, it can be substantiated that in the early years of this experiment, the 200 stems/ha treatment top-height development is on a lower yield-path than the other three stockings.

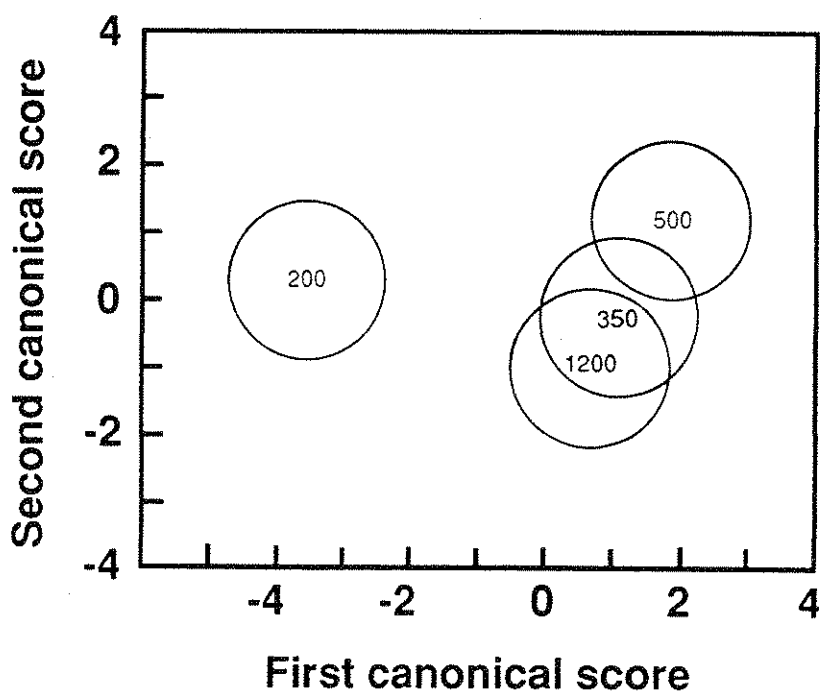

Figure 2: Mean canonical scores for orthogonal coeficients describing top height growth.

ANALYSIS OF THINNED EXPERIMENTS

Experimental

The analysis of thinned experiments is illustrated with an Australian initial spacing trial located near Canberra, A.C.T.(M.L. Benson, CSIRO Division of Forestry, pers. comm.) The experiment used three randomised blocks to test six stocking rates: 2990, 2200, 1680, 1330, 1080 and 890 stems/ha. By 16 years of age basal area on individual plots varied from 33 to 62 m^2/ha. At this time all plots were thinned from below but with regard to spacing and form to retain very nearly 25 m^2/ha. Breast height diameters were measured on seven occasions subsequent to thinning. The growth trajectories for basal area and mean diameter before and after thinning are shown in Figure 3.

Analyses and results

Basal area growth on each plot after thinning was adequately modelled with a straight line equation. There were no significant effects of initial spacing treatments on basal area growth after thinning ($F < 1.0$). Diameter growth was modelled in a similar fashion Analyses of variance (Table 3) showed that the only significant effect of initial treatments was on the intercepts. A generalised squared distance matrix for the six stockings is shown in Table 4.

Table 3: ANOVAs for intercepts and slopes used for modelling diameter growth.

SOURCE OF VARIATION	df	INTERCEPTS SS	INTERCEPTS P>F	SLOPES SS	SLOPES P>F
Blocks	2	2.18	n.s.	0.027	n.s.
Treatment	5	14.80	0.0056	0.014	n.s.
Error	10	2.22		0.036	

n.s. not significant, $p<0.05$

Table 4: Generalised differences between spacing treatments for diameter.

STEMS/HA	890	1080	1330	1680	2200	2990
890	0	1.0	7.5	26.6	31.3	77.2
1080		0	4.2	19.5	23.7	65.3
1330			0	5.8	8.1	36.6
1680				0	0.2	13.4
2200					0	10.3
2990						0

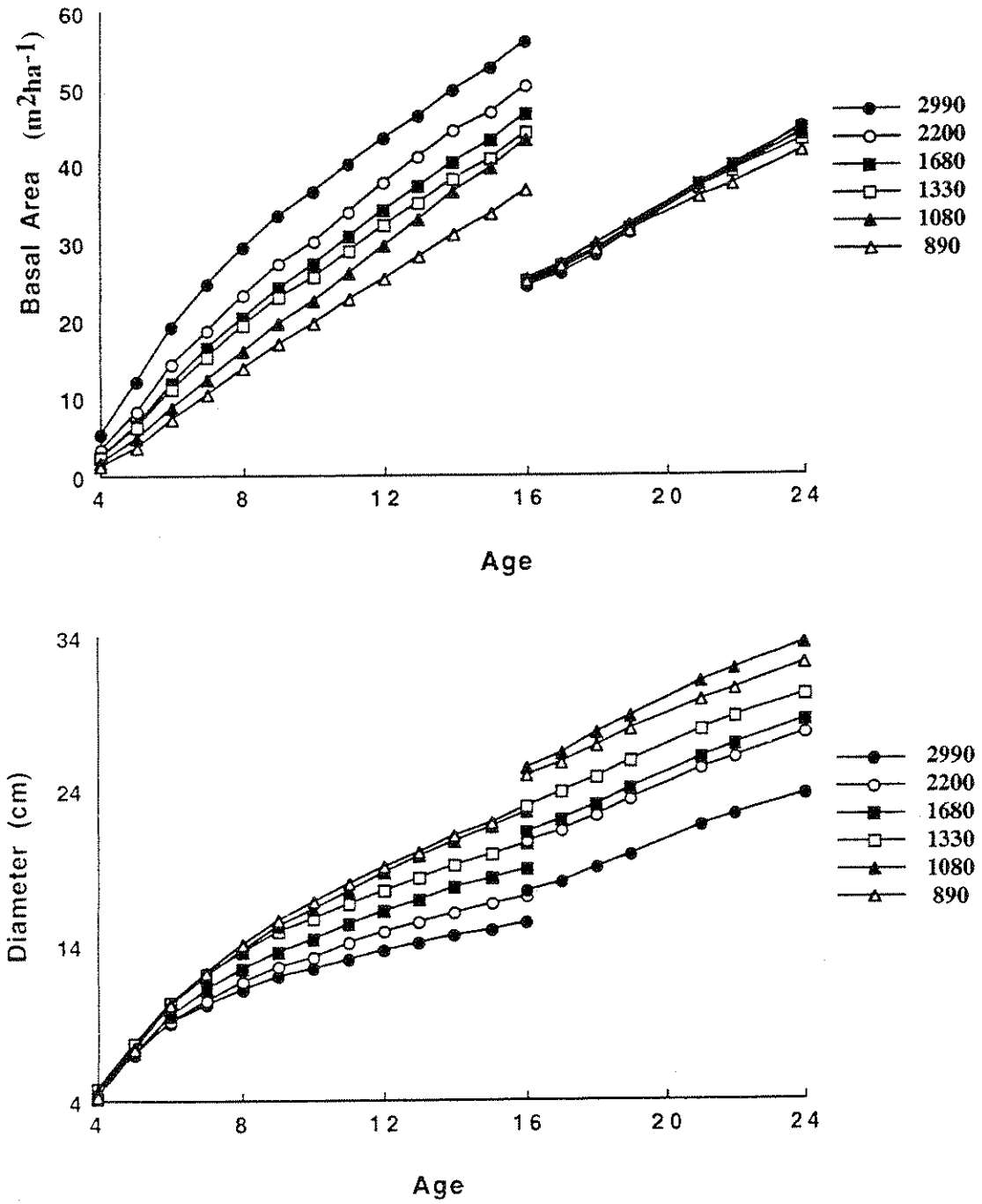

Figure 3: Effect of initial stocking (stems/ha) and subsequent thinning on basal area and diameter growth of *P. radiata.*

These results demonstrate that some components, in this case stand basal area, of a Type I response can be eliminated by thinning. Diameter differences, however, were maintained in a modified form.

DISCUSSION AND CONCLUSIONS

Thinning and spacing trials

Thinning and spacing experiments are inevitably large and are therefore costly. This is compounded by a need to maintain the experiments over decades. It is thus imperative that the maximum amount of information is extracted. This process is not necessarily straightforward.

Analyses of variance or covariance of yields at chosen points in time, are not especially informative, nor really necessary, since significance is ensured by the treatments used in the experiment. In our view, a major objective of thinning experiments is to identify, (if present,) differences in growth paths, and here a repeated measures approach is invaluable, especially so as to utilise all available data simultaneously. Multivariate analysis is not utilised to unnecessarily complicate the issue. While the multivariate tests of hypothesis do formalise the detection of differences in growth, we see the biggest advantage in the analysis being its ability to give an excellent visual summary of the treatments moving through time.

The results summarised here have some ramifications with respect to trial design and rneasurement scheduling. It is our experience, researchers frequently overlook to secure a measure of total plot growing stock before thinning; this can often be strongly linked to subsequent growth and without being taken, could lead to appreciable bias in estimation of basal area/ha and top-height projection.

Thinned experiments

Snowdon and Waring (1984) defined two basic patterns of response to silvicultural treatment: Type I responses due to treatments such as weed control which lead to a short term improvement of growing conditions and Type II responses due to treatments such as fertilization which have a sustained effect on site productivity. Accordingly, at any particular time an experiment will consist of stands at different stages of stand development or of different site qualities. Under ideal conditions forest managers alter the time of first thinning, thinning intensity and thinning interval according to the degree of stand development and for differences in site quality (e.g. Lewis *et al.* 1976). In order to conform with this practice the different treatments (and plots) in an experiment would need to be thinned at different times. This would present considerable practical difficulties and,depending on the thinning regime, could introduce heterogenous variances into the experiment (see Woollons 1985). The alternative is to thin the experiment at a single time in which case some treatments will be thinned too early with respect to existing practices while others will be thinned too late.

Systematic methods of thinning usually result in thinning intensities proportional to the productivity of the treatments but characteristics such as mean diameters (e.g. Snowdon and Waring 1990), diameter distribution or heritabilities (Matheson and Raymond 1984) will be little changed. By comparison, selective methods of thinning are often partly defined by the quantity of growing stock to be retained after thinning. If experiments are thinned in this way then the intensity of thinning will vary with each treatment (and plot). Moreover, mean diameters and diameter distributions will be markedly changed. Differences between treatments for some response variables will be eliminated while those for other response variables might be enhanced.

In effect thinning an existing experiment marks the beginning of a new experiment in which each new treatment is a unique combination of the initial treatment with the particular thinning schedule which has been applied.

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MODELING THE DEVELOPMENT OF FOREST STANDS IN THE NORTHEAST USING ECOLOGICAL SITE CLASSIFICATION

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ABSTRACT

Recent trends in forest management philosophy, such as the approach to ecosystem management adopted by the U.S. Department of Agriculture, Forest Service, indicate that forest growth modeling efforts need to be broadened to reflect stand attributes related to succession, biodiversity, wildlife habitat, and forest esthetics, in addition to timber yields. Site index, the most common measure of site productivity in growth models, predicts tree and stand growth accurately but provides little basis for modeling ecological processes. FIBER 3.0 uses habitat classification to reflect ecological dynamics for the major tree species in the forest stands of the Northeast. Growth projections for a young aspen-birch stand reveal the differing successional trends characteristic of six habitat units. Projections for hypothetical stands of several species show differences among the habitats in species dominance due to growth, mortality, and ingrowth functions, and competitive interactions. Modeling, based on ecological land-types, should provide the forest manager with a broader range of information necessary to meet multi-resource demands.

INTRODUCTION

Growth and yield models traditionally provide estimates of timber volumes over time. Although useful in the past, most management problems, on both public and private properties in the Northeast, require estimates of a broader range of stand attributes to meet wildlife, biodiversity, and esthetic objectives, in addition to timber yields. For example, the ecosystem management approach recently adopted by the USDA Forest Service, places emphasis on maintaining the natural ecological dynamics of the stands comprising a forested landscape. Currently, the most common measure of land productivity used in growth models is site index which is based on the height of dominant trees at a given base age (usually 50 years). Site index is useful in estimating tree and stand growth, but does not adequately represent the ecological dynamics of a stand. Many forested ownerships are beginning to use multifactor classification systems to represent ecological potential. It follows that growth models should begin to utilize such systems if they are to provide meaningful prediction that can be used in solving the on-the-ground problems now facing modern forest managers. To help meet the need for an ecologically based growth model, FIBER 2.0 (Solomon, et al. 1986) was revised using an ecological site classification approach to reflect land productivity. The purpose of this paper is to describe the site classification approach used in FIBER 3.0 and to illustrate its application in predicting successional trends and species performance.

The ecological classification system on the White Mountain National Forest, New Hampshire, uses a multifactor approach based on landform, glacial process, and potential vegetation. The basic planning unit is the ecological land type, an area of up to a few hundred acres in size. These units can be subdivided into land-type phases (locally called habitats), stand-sized units based on topography, soils, and apparent climax tree species (Leak 1982). These habitats are used in planning vegetative management activities for timber, wildlife, and esthetic purposes because they provide a means to predict individual species success through natural successional trends.

FIBER 3.0 predicts stand development based on habitat classification in contrast to site index that was utilized in the previous model (Solomon et al. 1987). Briefly, using an algorithm based on species composition, the basic growth, mortality, and ingrowth data were sorted into six habitats: sugar maple-ash, beech-red maple, hemlock-spruce, spruce-fir, cedar-black spruce-tamarack, and oak-white pine. These species mixes are late successional or climax types found throughout the Northeast and tend to occupy unique soils, landforms, and climatic regimes. These sorted data sets were then used to calibrate and test model parameters.

METHODS

Two types of stand conditions were modeled over time with FIBER 3.0 on each of the six habitat classifications. First: To demonstrate the successional capabilities of FIBER, the development of a young stand was simulated for 120 years. The stand composition was 20 square feet basal area each of aspen, paper birch, and the predominant species associated with each of the six habitats separately. Trees in the 5- and 6-inch class were used as initial input typical of stands on each habitat following complete clearcutting in New England forest types.

Second: To demonstrate habitat suitability for different species, red maple, yellow birch, sugar maple, white pine, and red spruce were modeled separately over time on each of the habitats. The stand basal area was divided evenly between the species of interest and the predominant species in the habitat. The purpose was to demonstrate the result of trying to grow species on sites where they are unsuited and to depict those species sensitive to site conditions. This type of stand is typical of those where partial cutting forces a mixed stand toward a dominant single species in the residual stand.

The majority of commercial species found in New England were used to develop FIBER. However, only the predominant species, together with the successional species that follow, were used as examples of stand development on each of the different habitats (Figs. 1-6).

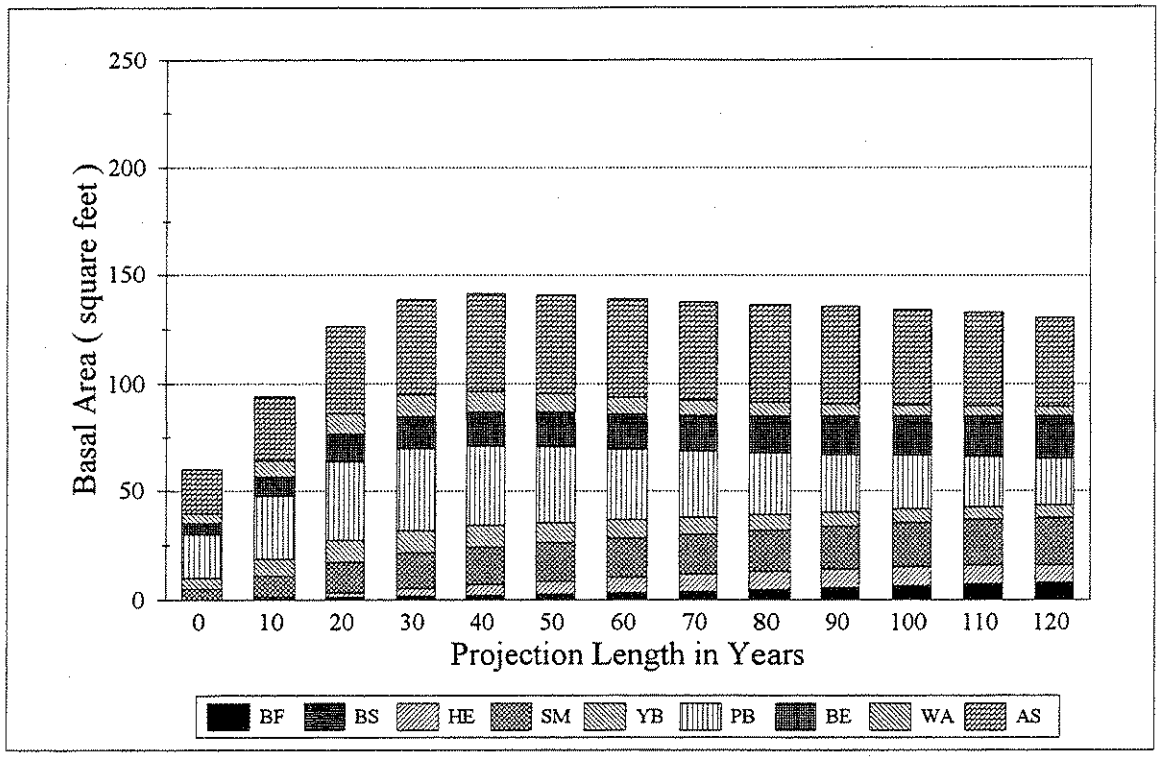

Figure 1. Species composition development in square feet of basal area over 120 years for an initial aspen-birch stand on sugar maple-ash habitat.

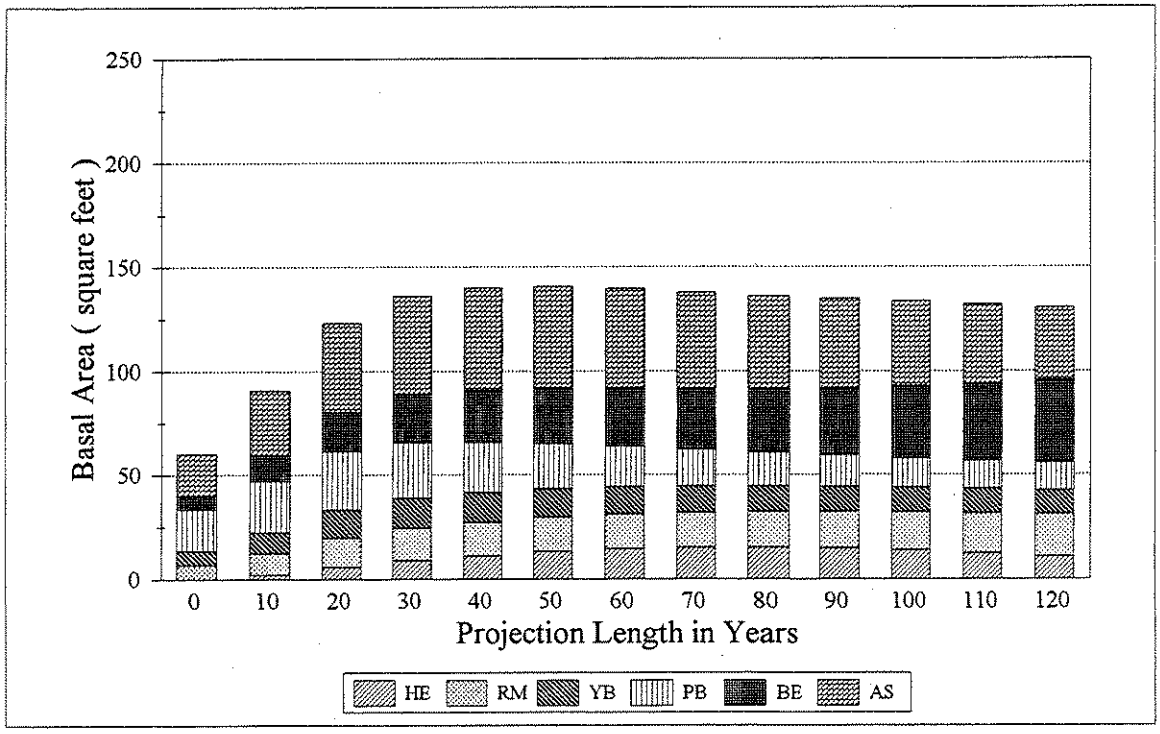

Figure 2. Species composition development in square feet of basal area over 120 years for an initial aspen-birch stand on beech-red maple habitat.

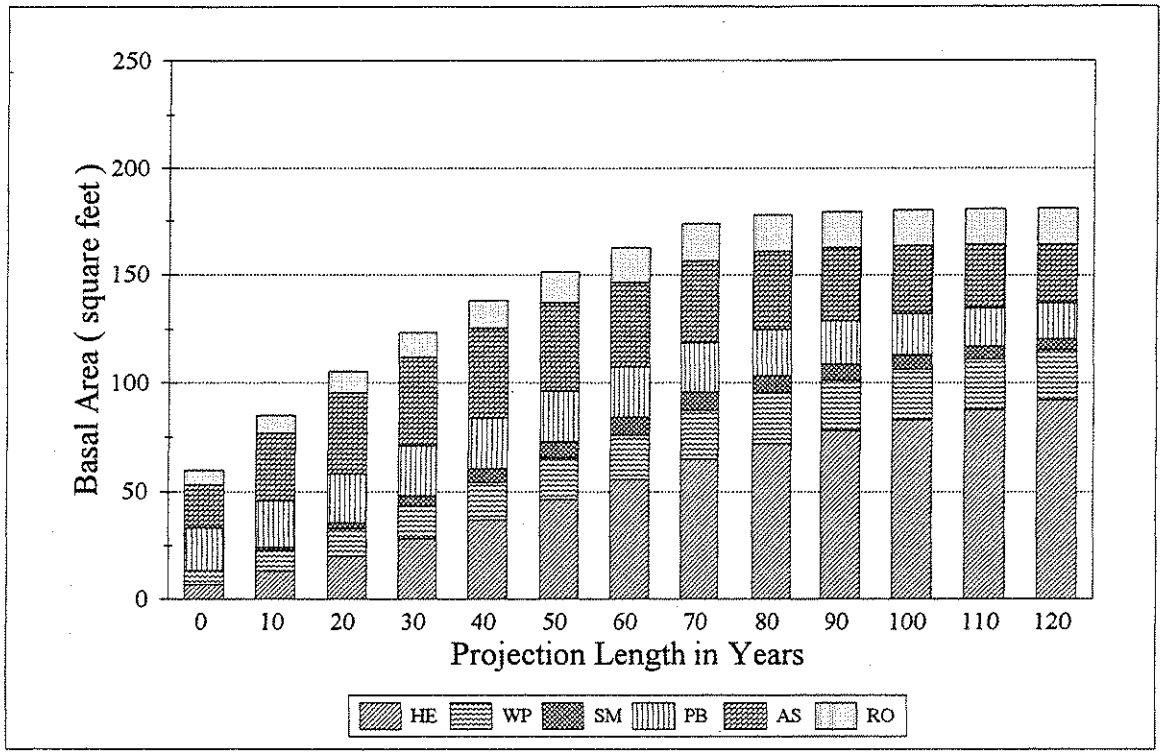

Figure 3. Species composition development in square feet of basal area over 120 years for an initial aspen-birch stand on oak-white pine habitat.

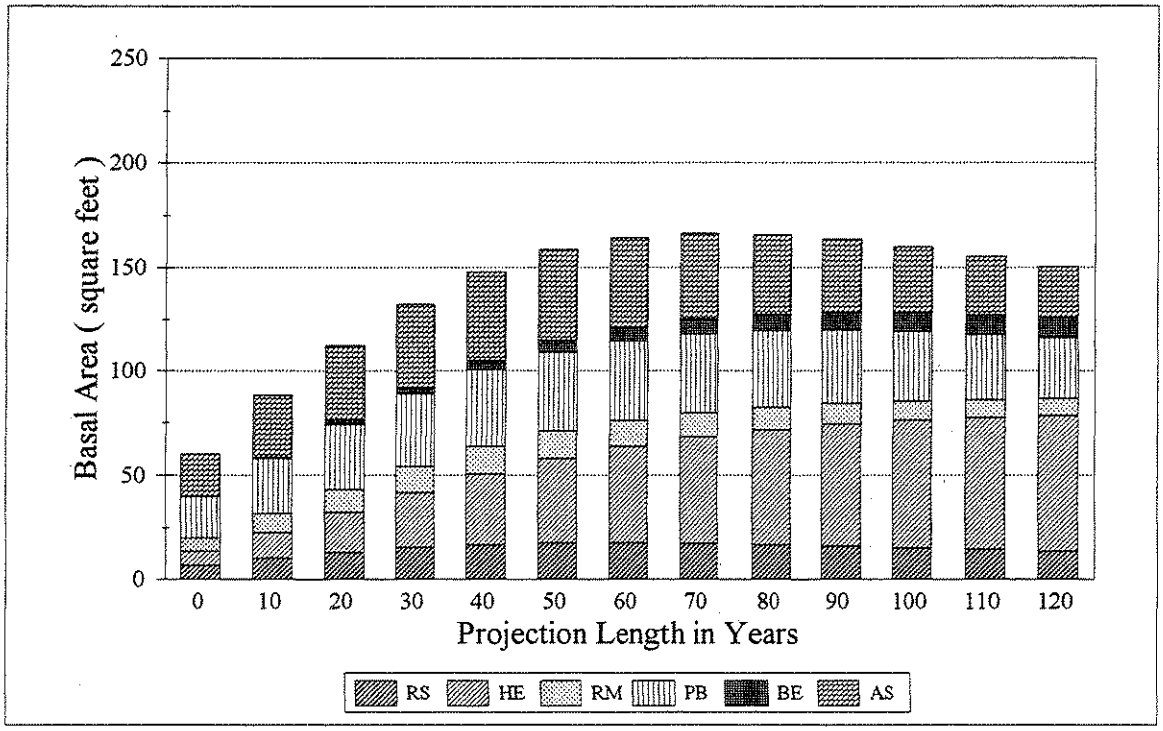

Figure 4. Species composition development in square feet of basal area over 120 years for an initial aspen-birch stand on hemlock-red spruce habitat.

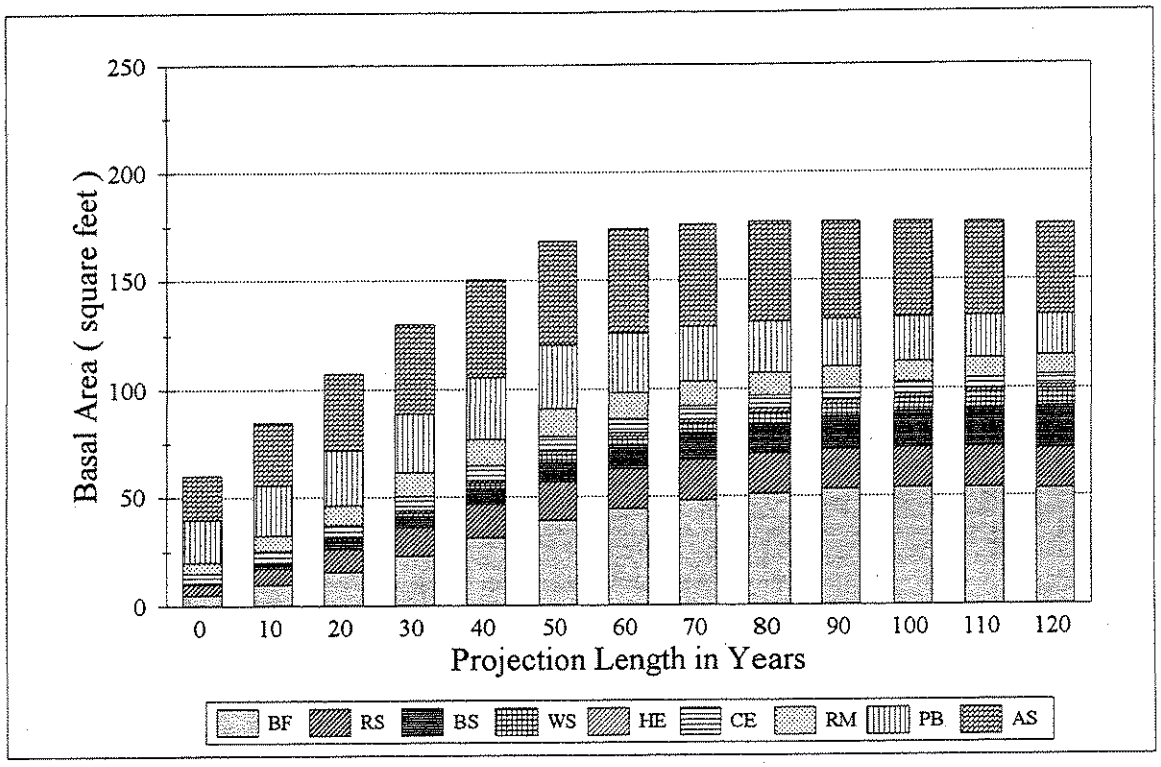

Figure 5. Species composition development in square feet of basal area over 120 years for an initial aspen-birch stand on spruce-fir habitat.

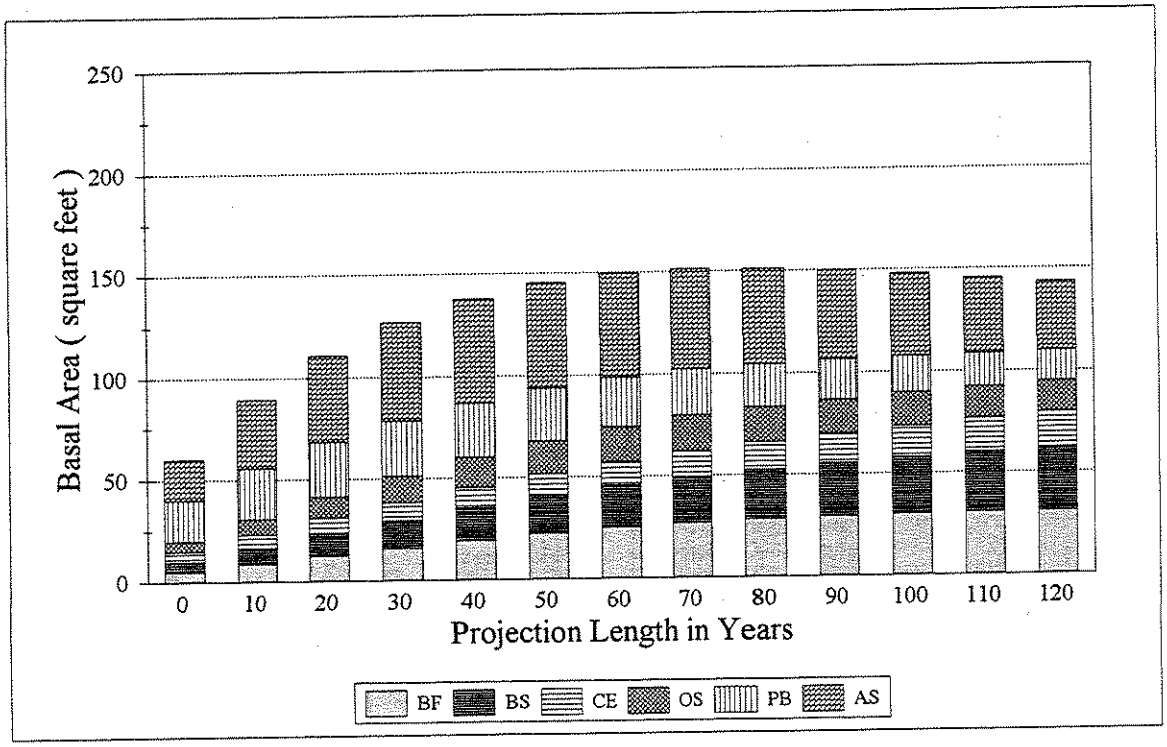

Figure 6. Species composition development in square feet of basal area over 120 years for an initial aspen-birch stand on cedar-black spruce habitat.

RESULTS

Beginning with a young aspen-birch stand, successional trends over time varied greatly among habitats (Figs. 1-6). On the hardwood habitats, late successional hardwoods increased to the point where they comprised about half the stand. On the softwood habitats, the tolerant softwoods--hemlock, spruce, and balsam fir, or both--made up approximately half the stand at the end of the 120-year period. These findings generally are consistent with available successional information in New England, which suggests that climax species may comprise 30 to 60 percent at ages of 140 years, and over 70 to 80 percent after 200 to 250 years (Leak 1991). On the oak-white pine and hemlock-red spruce habitats, hemlock increased substantially and appeared to take over as a predominant climax species. Successional trends on oak-white pine are poorly documented in the literature. However, white pine-hemlock is a well-accepted forest type in New England (e.g. Frieswyk and Malley 1985), and hemlock is known to be an aggressive species on the dry sites that characterize the oak-white pine habitat (Leak 1982, Stout 1952). On the softwood habitats, such as spruce-fir, aspen maintained a strong compositional position over the 120 years. It has been found that through natural disturbance cycles typical of older softwood stands, a proportion of intolerant species, such as aspen and paper birch, can be maintained (Hill 1989, Leak 1975). On all habitats, aspen maintained its compositional position in the stand better than paper birch. This trend is in line with long-term observations in early successional stands that show that aspen will almost completely dominate associated stems of paper birch, due to its more rapid height and diameter growth (LaBonte and Leso 1990).

FIBER simulations with young stands dominated by either red spruce, white pine, yellow birch, red maple, and sugar maple show that the success of these mid-to-late species varies with habitat. Red spruce maintains a dominant position only on the spruce-fir habitat (Fig. 7) and a moderately dominant position on the other softwood habitats. On oak-white pine or hardwood habitats, the proportion of red spruce drops to about one-fourth of the stand or less (Fig. 8). Young stands dominated by white pine, maintained a major proportion of this species only on the oak-white pine habitat (Fig. 9). On all other habitats, the initial proportion of white pine declined over time--a trend that has been observed many times in old-field pine growing on hardwood or tolerant softwood habitats (Hibbs 1983, Stout 1952). Yellow birch and red maple are mid-successional species common on all the habitats represented by FIBER. In accord with their mid-successional status, these species show a gradual decline on all habitats, and neither will comprise a large proportion of the eventual climax stand. However, red maple especially is abundant on the beech-red maple habitat where it regenerates prolifically (Leak and Solomon 1975); and yellow birch is notably noncompetitive on the oak-white pine habitat where the species exhibits poor development on the characteristically dry sites. Sugar maple is one of the more demanding species in New England, second only to white ash.

Simulations with FIBER show that sugar maple dominates only on the fairly rich soils typical of the sugar maple-ash habitat (Fig. 10). On all other habitats, sugar maple declines over time. In general then, behavior of mid-successional and climax species on the six habitats represented in FIBER varies in predictable fashion, consistent with available published literature on silvical characteristics and site requirements of these species.

CONCLUSIONS

The FIBER model (version 3.0) now employs growth responses by habitat classification, to represent land capability or productivity. The advantages of habitat classification are that this method reflects successional trends and competitive ability of species on different sites. Thus, forest resource managers can utilize species succession of stands on different habitats to reach management objectives other than timber production. Simulations beginning with early successional aspen-birch stands showed how species composition tends toward tolerant softwoods on softwood habitats (spruce-fir, hemlock-red spruce, cedar-black spruce) and the oak-white pine habitat. On the other hand, hardwoods predominated over time on sugar maple-ash and beech-red maple habitats. Beginning with stands containing a single dominant mid-successional or climax species, FIBER simulated the effects of habitat on the success of that species. In all cases, species increased or maintained their dominance only on suitable habitats. For example, white pine retained a dominant position in the simulated stand only on the oak-white pine habitat, and declined in relative position over time on all other habitats. Sugar maple increased over time on the sugar maple-ash habitat. These results indicate that FIBER 3.0 should be useful in predicting not only timber growth but other stand attributes related to ecosystem management.

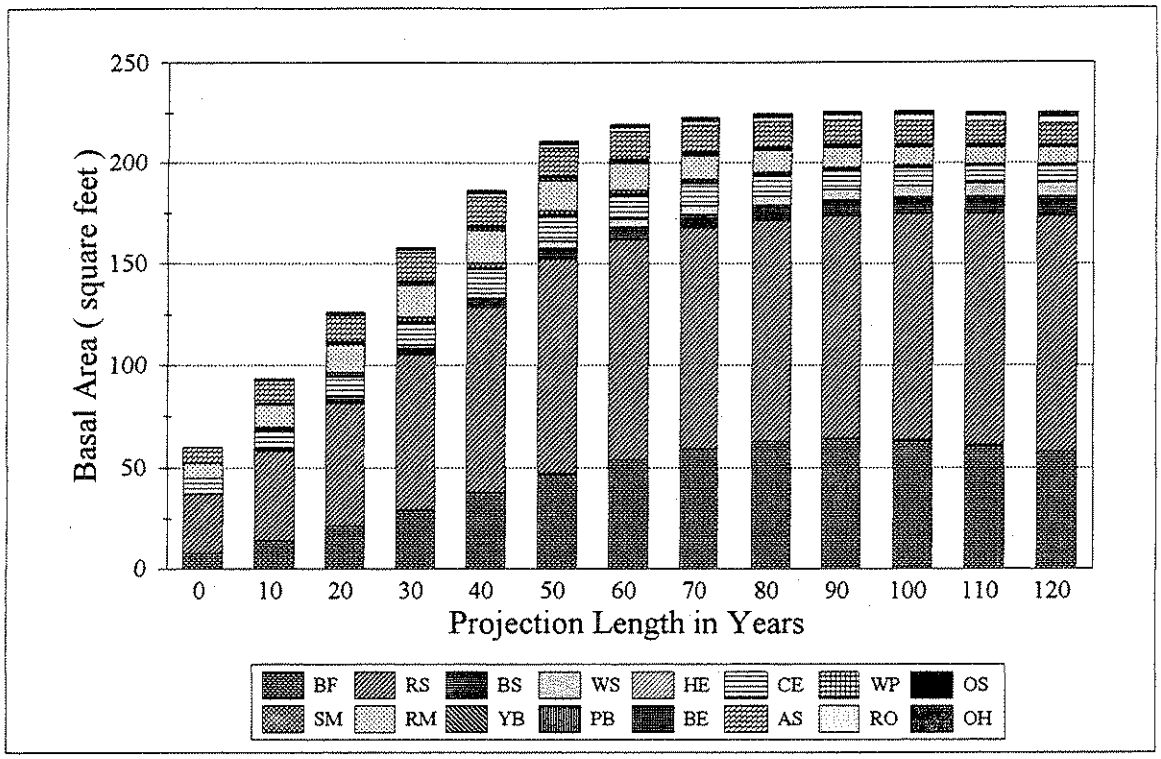

Figure 7. Species composition development in square feet of basal area over 120 years for an initial red spruce stand on spruce-fir habitat.

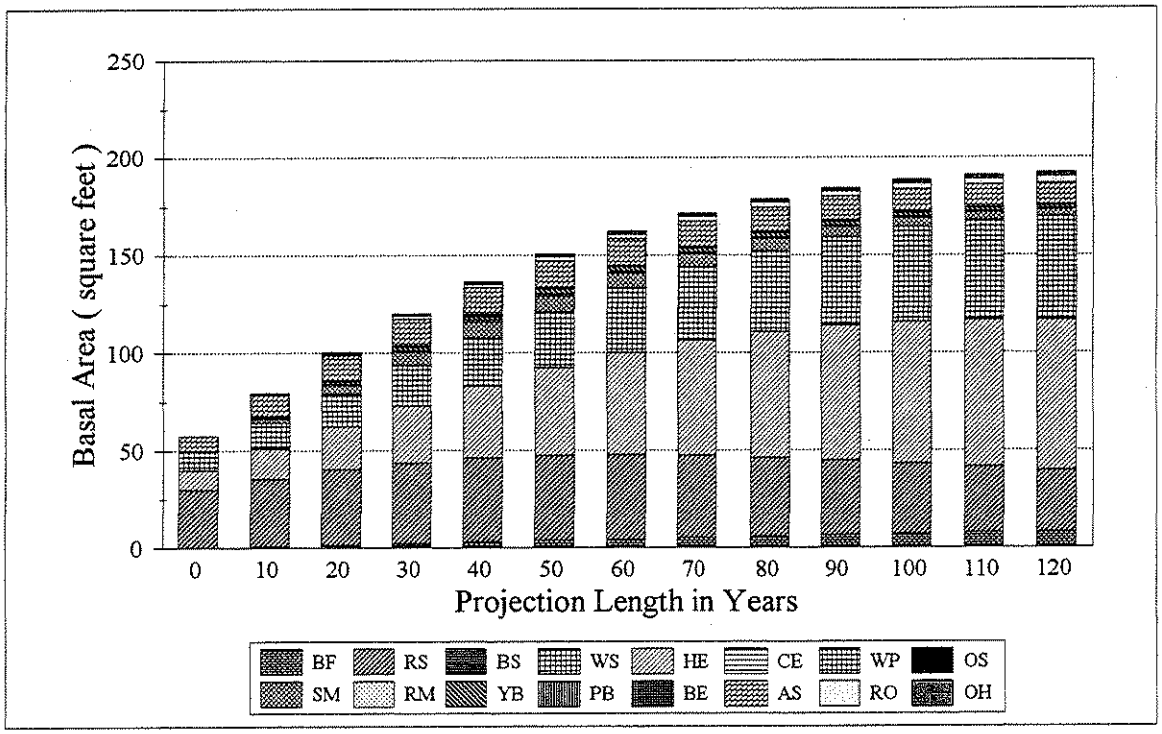

Figure 8. Species composition development in square feet of basal area over 120 years for an initial red spruce stand on oak-white pine habitat.

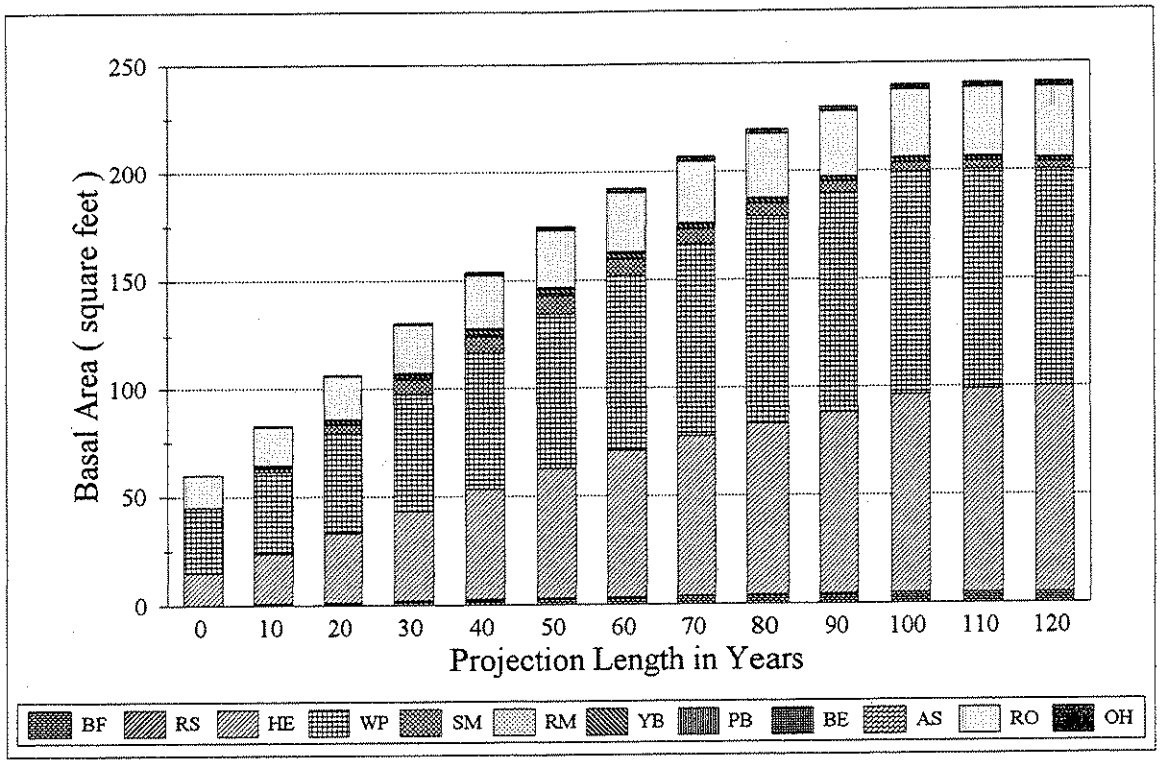

Figure 9. Species composition development in square feet of basal area over 120 years for an initial white pine stand on oak-white pine habitat.

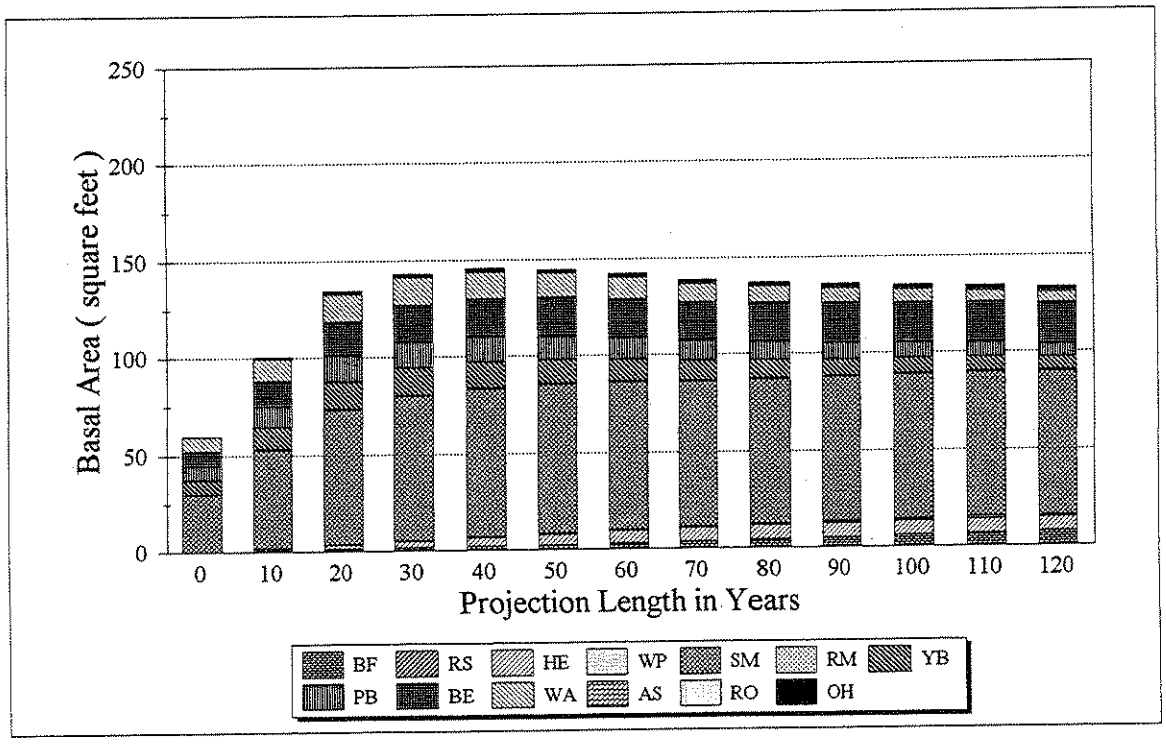

Figure 10. Species composition development in square feet of basal area over 120 years for an initial sugar maple stand on sugar maple-ash habitat .

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PROCEDURE FOR REPRESENTING SPATIAL VARIABILITY WITHIN DISTANCE-INDEPENDENT STAND GROWTH MODELS: An Application of Measurement Error Models

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ABSTRACT

In forest research, plots used to build forest growth and yield models commonly have been located in such uniform stands, and include large enough areas that they can be assumed to represent the population condition without error. However, when the models are applied to real stands, there is a hiatus between the conditions under which these models should be used, and the inventory and analysis needs of practicing foresters. The problem is especially acute when the silviculture to be modelled creates very heterogeneous, patchy stands. A solution to the problem is outlined. One component of the solution is a model of the variance of competition within the stand as a function of size of plots relative to tree size. The second component is the use of the variance of the competition variables in the statistical procedures for estimating parameters of the structural relation. The jóining of these two components into a forest stand growth simulator produces a growth model that can be applied to stands of very irregular structure.

INTRODUCTION

We are concerned with how to simulate the development of extensive, patchy stands. In the course of developing a method for modeling patchy stands, we also treat problems that arise when the stand is sampled with an inventory design that differs from the design used in the calibration of the model. Forest stands with a complex spatial pattern of tree sizes and species or in which complex patterns may be proposed by silviculturists pose real problems for modeling future growth. Although distance-dependent models that represent spatial positions of each individual have some possibility, they are too demanding of data to be feasible for large stands. On the other hand, distance-independent models as presently formulated lack spatial resolution. Lack of good solutions to this problem limit the capability of silviculturists to evaluate proposed treatments that create spatial aggregations of trees.

How one should approach the modelling of patchy aggregations of trees depends on the size of the patches in relation to the size of the trees. If the patches are relatively large, their development is little influenced by competition from surrounding patches. In this case, landscape models that are simply aggregates of independent stands so far as interstand competition is concened should suffice

(Crookston and Stage 1991). As patch size becomes smaller, it is possible to continue treating the patches as small stands, but with growth of a portion of the stand affected by competition from its neighbors (*e.g.* Crookston and Stage 1993). At the extreme, where stands are composed of homogeneous mixtures of age classes, either distance-dependent models or distance-independent models that use relations between individual-trees and stand measures of stocking to describe the socio-ecological status of the trees (e.g. Wykoff *et al.* 1982, Wykoff 1990) appear adequate. To fill the gap between this extreme and the patches-as-stands-with-border-competition is the purpose of the methods developed in this paper.

The methods we develop, although motivated by the need to model patchy stands, also solve a problem that arises when one models the growth of an inventory in which stand densities are based on samples of varying precision--especially when the precision is very different than that of the model calibration data.

Forest stand growth models using a multi-plot stand examination as input (*e.g.* Stage and Alley 1972) have been a useful part of silvicultural planning . However, Grosenbaugh (1955) argued long ago that stands were a poor choice of spatial unit for prescription and management record-keeping. Although his prescription system could treat variation internal to the unit of management, long-range planning was stymied by lack of a correspondingly capable system for growth analysis. For some silvicultural systems, growth models currently in use have been insensitive to stand clumpiness. One alternative is to maintain the identification of each record with the particular sampling point at which it was sampled, as proposed by Pukkala (1990). However, with this approach, variation between points increases markedly as the trees grow in size and decline in numbers. This increase is the consequence of a population of successively larger trees being "sampled" only on the original small plots. Although there is no bias in the stand average density, the density measured at each point is inappropriate for use as a point-centered measure of competition.

The lack of spatial resolution becomes especially troublesome when the growth simulation model adds regeneration to the inventory. The regeneration sub-model in the Prognosis Model for Stand Development goes part way toward modeling internal variability (Ferguson *et al.* 1986) This model uses sampling-point attributes to describe site and overstory structure within the stand. Then the model generates the equivalent of a new inventory as though new regeneration were sampled on numerous small (1/300-acre) fixed-area plots within the stand. However, when that inventory is projected forward in time, contributions of that new cohort must be averaged over the entire stand if realistic estimates of stand density are to be maintained throughout the span of simulated time.

In this paper, we prescribe a modification of the simulation procedure that resolves the problem just described. When this procedure is added to distance-independent models of stand development, their capability to represent clumpy stands, including representations of group-selection silviculture will be considerably enhanced. Yet the procedure avoids errors caused by aggregating parts of the stand likely to be treated differently and which will grow differently. Therefore, greater variation of density, species and age structure within the delineated stand boundaries can be tolerated without loss of resolution. Thus management information systems maintaining stands as record units can deal with fewer, larger units. An additional

benefit may also accrue when a common model is applied to stands that are characterized by competition variables measured with different precision from stand-to-stand.

The key to the approach we describe lies in solving the problem noted by Jaakola (1967). He observed that the relation between growth and stand density varied with the size of the inventory plot used to define stand density. The effect he noted is caused by the sampling error always inherent in a measure of competition. Indeed, the major reason why most modelers of stand growth insist that their data come from large, homogeneous plots is to reduce the measurement error of the competition variable to near zero. For only if independent variables are free of error can one use common regression techniques to obtain unbiased estimates of the underlying structural relations (Fuller 1987).

The first step of our procedure is to obtain estimates of the structural relation of growth to competition. If adequate data are available for calibration from large, uniformly stocked stands, then this requirement is easily met as previously noted. However, for many interesting and valuable data sets, it will be necessary to determine the measurement error of the competition variables. Then, we estimate the biases of the estimated coefficients of the competition variables so that the biases can be removed, leaving an unbiased estimator of the structural relation.

The second step is to model the measurement error of the variables representing competition. During the course of simulated time, the measurement error of these competitive effects will change as tree size changes in relation to the plot size used in the initial inventory (or in the simulated inventory of new regeneration) and as management modifies the spacing of trees and other vegetation.

Third, based on the current estimate of these combined sampling errors, re-insert an appropriate bias into the coefficients of the competition-effects model. Then the biased relation can be used to produce <u>unbiased</u> estimates of growth for the current time step (cf. Fuller 1987, example 1.6.1, pg 75). At each successive time step, a new estimate of sampling errors and a new regression coefficient must be computed. In addition, a measure of local relative density must be made available to guide prescriptions intended to modify spatial distribution of stocking.

Procedures for carrying out the first step are fully described in Fuller (1987). Therefore we will recount them only briefly. Procedures for the second step will be treated more fully because they require a greater degree of empiricism.

In this paper, we approximate the steps of the proposed procedures, imbed the approximate relations in the Prognosis Model for Stand Development, and then exercise the modified model to evaluate its sensitivity to the modifications.

ESTIMATION OF BIAS IN REGRESSIONS ON VARIABLES WITH KNOWN MEASUREMENT ERROR

The model, in vector notation is:

$$\begin{aligned} Y_t &= y_t + w_t \\ X_t &= x_t + u_t \\ y_t &= x_t'\beta + q_t \end{aligned} \tag{1}$$

$$(q_t, w_t, u_t)' \sim Ind[0, block\ diag(\sigma_{qq}, \sigma_{ww}, \Sigma_{uutt})]$$

where Y, X are the observed variables, y, x are the corresponding true, but unobservable variables. The vector q is the equation error and (w_t, u_t) is the vector of measurement errors.

Stage and Wykoff (in press) provide estimates of w_t for conifers of the Rocky Mountains. A model for Σ_{uutt} will be described in the following section of this paper.

Bias in regression coefficients introduced by error in the independent variable is well known for bivariate regression with constant measurement error:

$$\beta = \beta'[\ 1 + \sigma^2_{uu}/\sigma^2_{xx}] \tag{2}$$

where:

$\beta' = (X'X)^{-1} X'Y$ is the usual least-squares estimator
β = structural coefficient of x
σ^2_{uu} = variance of measurement error of x in the calibration data-set
σ^2_{xx} = variance of the explanatory variable x in the calibration data-set.

For example, Crown Competition Factor (*CCF*), which is closely related to basal area for Rocky Mountain species, was an important competition variable in Wykoff's (1990) model of diameter increment. The regression coefficient for *CCF* in the Douglas-fir model was -0.00039. This estimate was derived from a data set for which the standard deviation of *CCF* was approximately ± 52. If *CCF* were the only variable in the regression, we could approximate the bias of the least squares regression coefficient under the assumption that the measurement error was ± 20. Deducting the square of the measurment error from the total leaves an estimated variance of the x variable of 2304. Then the structural coefficient based on equation (2) would be about -0.0005254 or a bias of 26.8%.

The variances of the competition variables will vary from observation to observation, and will be functionally related to each other for the same observation. Procedures for estimating the coefficients for this more realistic case are given in Fuller (1987, eqn. 3.1.26).

With the measurment errors assumed known, a method of moments estimator for β is used to provide an initial estimator (Fuller 1987, pg 193) of the structural

relations for competition variables:

$$\tilde{\beta} = \hat{M}_{xx}^{-1}\hat{M}_{xy}$$

where:

$$(\hat{M}_{xy}, \hat{M}_{xx}) = n^{-1}\sum_{t=1}^{n} [(X_t'Y_t - \Sigma_{uwtt}), (X_t'X_t - \Sigma_{uutt}] \tag{3}$$

With this initial estimator of $\tilde{\beta}$, an improved estimator can be calculated:

$$\hat{\beta} = [\sum_{t+1}^{n} \tilde{\sigma}_{vvtt}^{-1}(X_t'X_t - \Sigma_{uutt})]^{-1} [\sum_{t=1}^{n} \tilde{\sigma}_{vvtt}^{-1}(X_t'Y_t - \Sigma_{uwtt})] \tag{4}$$

where:

$$\tilde{\sigma}_{vvtt} = \tilde{\sigma}_{qq} + \sigma_{wwtt} - 2\tilde{\beta}'\Sigma_{uwtt} + \tilde{\beta}'\Sigma_{uutt}\tilde{\beta} \tag{5}$$

CHOICE OF COMPETITION VARIABLES

Wykoff (1990) used two measures of competitive status of individual trees for the Inland Empire variant of Prognosis: Crown Competition Factor (*CCF*) (Krajicek *et al.* 1961), and basal area in trees of larger diameter (*BAL*). The *CCF* term introduced a general level of competition, and *BAL/ln(dbh+1)* represented the social status of the individual in relation to the number and sizes of its competitors in the overall stand. By dividing *BAL* by *ln(dbh+1)*, this variable is predominantly effective for relatively small trees. In this formulation, basal area and *CCF* are calculated for the stand as a whole. Comparable equations, but substituting various combinations of these two variables calculated at the point and/or the stand level have been fit for other geographic variants (Johnson and Dixon 1990). In these latter studies, choice was usually based on overall goodness-of-fit statistics which ignored the effects of measurement variance.

A preponderance of studies of individual-tree measures of competition leading to distance-dependent simulation models have shown that the largest spatial extent of the competition measure considered in each study has produced the highest correlation with increment. Causes of this effect are partly biological and partly statistical. The biological effect must decrease such that there is some distance beyond which the subject tree is indifferent to conditions. However, the statistical effect of decreasing measurement error with increasing distance has an opposite effect, causing the correlation with increment to increase with spatial extent. Our conclusion for a distance-independent model from these studies is that both local competition and effects of surrounding stand attributes must be considered. These conclusions have been confirmed empirically by Hensold (1989) who studied growth in ponderosa pine stands that had been managed by group selection through four cutting cycles. He found that new regeneration was not growing as well as would be expected for its age in a larger clear-cut, but better than would be expected in a comparable mix of tree sizes in a single-tree selection structure.

For competitive status of trees larger than 5 inches, we will use *BAL/ln(dbh+1)* based on the position of the tree in the diameter distribution of the

total stand, but using the basal area at the point. Basal area of the entire stand (*BA*) will be included as an additional variable to contrast point conditions with stand conditions.

Sampling errors of the competition variables depend on the inventory design, as noted by Jaakola. We will assume as a standard, the design used in inventories that were developed to reveal the silvicultural needs of the stand (USDA Forest Service 1962). Trees less than 5 inches dbh are sampled with a 1/300 acre circular plot and larger trees with a 20 *BAF* point sample. In this design, the area of influence is 6.8 feet for small trees and 1.944 feet per inch dbh for larger trees. This design was the same as used in the calibration data set for the diameter increment model (Wykoff 1990).

RELATION OF COMPETITION MEASUREMENT ERROR TO PLOT SIZE

Measurement errors of the variables describing competitive status depend on how the configuration of the internal plots used to sample the stand relates to the spatial variability of site and stocking. Even if we limit our procedure to circular plots, the common use of concentric plots to sample different size classes of trees with increasingly larger plots for larger trees must be considered. For example, basal area in trees larger than the subject tree (*BAL*) will have a measurement error that changes with tree size more or less abruptly at the tree size at which one changes plot sizes. Of course, with variable radius plots (horizontal point sampling) the change is a smoothly continuous function. In either case, measurement error for variables that sum competition over all tree sizes can be obtained from the same function representing the variance of BAL, but evaluated for the smallest tree in the population.

We are concerned with two scales of variation of the competition variables, the variance of the stand average, and the variance in the immediate neighborhood of each sampling point. At a particular point, however, there is only a single observation. Therefore, we must develop an estimate of the local variation on the basis of theoretical models of spatial variation.

Several reports have indicated that a plot-variance model proposed by Smith (1938) is of very general applicability to forest stand data. (Freese 1961, Wensel and John 1969, Sukwong et al 1971). The model, in its logarithmic form is:

$$\ln(V) = \ln(k) - b \ln(a) \tag{6}$$

where:

- V = variance of tree numbers per unit area,
- $ln(k)$ = intercept (logarithm of constant of proportionality,
- a = plot area, and
- b = constant representing stand heterogeneity.

Point Variance--Natural stands

The model we adopt for the local variation within natural stands is the Poisson, which assumes that the coordinates of each tree are random variates from a uniform distribution, and that the location of each tree is independent of the locations of all other trees.

In such a Poisson forest,

$$\sigma^2 = m$$

where m = mean number of trees per plot, and σ^2 = variance of trees per plot.

The effect of changing plot size is to change the mean count per plot:

$$m = Ma \tag{7}$$

where a is area of the plot and M is tree count per unit area.
Then, changing from statistics for the plot to statistics per unit area,

$$\begin{aligned} M &= m/a \\ V &= \sigma^2/a^2 \\ \ln(V) &= \ln(\sigma^2) - 2\ln(a) \\ &= [\ln(M) + \ln(a)] - 2\ln(a) \\ &= \ln(M) - \ln(a) \end{aligned}$$

which is the Smith variance function with b equal to unity.

Application to Basal Area

To derive the sampling distribution of basal area in a Poisson forest, define BA_i as the basal area in the ith diameter class, and its variance as VBA_i:

$$\begin{aligned} BA_i &= c\, d_i^2\, m_i/a \\ VBA_i &= c^2 d_i^4\, \sigma_i^2/a^2 \end{aligned} \tag{8}$$

where $c = \pi/[4(144)]$.

Point sampling with plot radius proportional to diameter is an efficient procedure for sampling competition within a stand. Furthermore, derivation of the Smith variance function is relatively simple for point sampling (Matern 1969). Therefore, it will be used as a point of departure for a more general treatment. If we divide the Poisson forest into very narrow diameter classes indexed by i:

$$\sigma_i^2 = m_i$$

In a point-sample, plot area for the diameter class is:

$$a_i = c\, d_i^2/BAF$$

where BAF is the basal area factor as commonly used. Then, from (8):

$$\begin{aligned} \hat{BA}_i &= BAF\ m_i \\ V\hat{BA}_i &= BAF^2\ \sigma_i^2 \\ &= BAF^2\ m_i \\ &= \hat{BA}_i\ BAF \end{aligned} \tag{9}$$

Because the sum of n Poisson processes is again Poisson (Johnson and Kotz 1969 pg. 93), the distribution of the sum has variance:

$$\begin{aligned} \sigma^2_{Total} &= \sum_i \sigma_i^2 = \sum_i m_i = m \\ \ln(\sum_i V\hat{BA}_i) &= \ln[\sum_i \hat{BA}_i] + \ln(BAF) \end{aligned} \tag{10}$$

In a point sample, m is proportional to stand basal area, so the sampling distribution of point-sample estimates of basal area in a Poisson forest is also Poisson!

The variance for fixed-area-plot sampling of a Poisson forest is not as elegant. However, we only need to recall that m_i in equation (8) is the count per plot, whereas the density values carried in the simulation model are on a unit-area basis (per acre): $M_i = m_i/a$. Therefore, the variance of the point basal area is the sum over all trees of equation (8):

$$\sum_i V\hat{BA}_i = [\frac{c^2}{a}]\sum_i M_i d_i^4 \tag{11}$$

In this form, the only difference between the variance for fixed-area plots given by (11) and the variance for a point sample is the point-sample variance would have the plot area changing with diameter.

We propose to represent the measurement variance of stand basal area by summing (11) over the n points in the stand. If we add a plot subscript (k) to the variables, then the measurement variance of mean stand basal area is:

$$Var[\frac{1}{n}\sum_k \sum_i BA_{ki}] = \frac{1}{n^2}\sum_k \sum_i V\hat{BA}_{ki} = \frac{c^2}{n^2}\sum_k \sum_i \frac{M_{ki}}{a_{ki}} d_{ki}^4 \tag{12}$$

Plantations

Persson (1964) compared the standard deviations of fixed-area, circular plots sampling both random and square-lattice spatial patterns. His calculations were for two plots sizes such that the expected number of seedlings per plot ranged from 0.5 to 4. As a very crude approximation, the lattice spatial arrangement had about half the standard deviation (1/4 the variance) of the random pattern. At densities greater than 3000/ha. the standard deviation declined for the larger plot size. However, in the field, there would seem to be little possibility of maintaining an exactly square spacing such that the periodicity would produce as low a variation as he calculated. Therefore we propose to use half the Poisson-based variance for plantations that were intended to have uniform spacing. In addition, one should also reduce the b exponent of area in the Smith variance function.

REVISION OF SAMPLING ERRORS DURING COURSE OF SIMULATION

Plot size is established for each tree record in the simulation by either the initial inventory design, or by the design of the regeneration submodel. Then the variance of the point basal area at each time step is given (11) with a_{ki} held constant at its initial value while d_{ki} changes during the simulation.

Percentile in the basal area distribution is being used as a stand variable. The variance for the ith tree in the kth point at each successive time step (t) is given by:

$$Var[p_{ik}] = p_{ik}(1-p_{ik})/r \tag{13}$$

where p is percentile/100 and r is the number of tree records in the stand inventory (Wilks 1962 p.271).

BAL is the product of p times the point basal area (*BAP*). We assume that percentile and *BAP* are independent. Therefore the variance of the product is:

$$Var[BAL] = BAP^2 var[p] + p^2\ var[BAP] \tag{14}$$

As used in the current model, basal area in larger trees than the subject is further transformed by division by $ln[dbh + 1]$. We will assume that this variable, although changing during the simulation is, at a given timepoint, a constant known without error. Therefore the measurement variance given by (14) is multiplied by the inverse of the square of the logarithm.

REVISION OF REGRESSION COEFFICIENTS DURING COURSE OF SIMULATION

At each successive time interval of the simulation, it is necessary to revise the coefficients of the competition variables. However, there is little precedent on whether it is necessary to consider the covariances of the recalculated measurement errors. The computationally most direct procedure is to use (2) for each variable, independently. This approach is analogous to rescaling the X variable. Its variance would be obtained from the $\hat{M}_{xx}$ of (3).

The alternative, to reverse the computations in (3), would be very cumbersome. For the purposes of this paper, we will evaluate the general sensitivity of projections to measurement errors using the former (2) procedure. If the effects are important, the more complex methods can be accomodated.

EFFECT ON PROJECTIONS

The sample stand to show the effects of these procedures will be generated by the Regeneration Establishment Model, version 2 for a typical site in the Douglas-fir habitat. Hence, each "tree" will be entered as though sampled on a 1/300th acre plot. Two management alternatives will be evaluated--with, and without a thinning from below at age 30 that removes 44% of the basal area. Effects of three sequential changes in the model will be displayed:

1. the original Prognosis model in which only stand average measures of competition are used.
2. *BAL* computed using basal area at each point, but assuming that the same regression coefficients still apply. This option corresponds to how some users of the model are projecting existing inventory locations consisting of a few small plots.
3. as in the previous set, but modifying the coefficients according to the relation between the measurement errors computed for each stage of stand development and the assumed measurement errors of the calibration data set.

These changes are made only in the sub-model for diameter increment of trees larger than 3 inches. Therefore, there will be little effect until there has been enough time following stand regeneration for trees to reach 3 inches. Because the Prognosis Model includes some stochastic components, we discuss results based on the mean of 20 replications of each combination of management and model formulation.

The most obvious result is that none of the three options cause large changes in projected basal area, top-height or quadratic mean diameter. However, the three versions of the model show successively larger increases in the growth of the thinned stand compared to the unthinned (figure 1). The difference in basal area thinning response at age 130 between the original model and the changing-coefficient model is about 10%.

The time-trends of minimum and maximum point basal areas for the three model formulations are shown in figure 2. Recall that these basal areas (per acre) represent the stand as if it were sampled with 1/300th acre plots. Shifting to a point measure of stand density (formulations 2 and 3) reduces the range of point densities. Making the coefficients change with measurement error mostly affects the growth of the dense points. The coefficients are closer to zero for the more variable plots with higher basal areas so there is less reduction in growth attributed to competition.

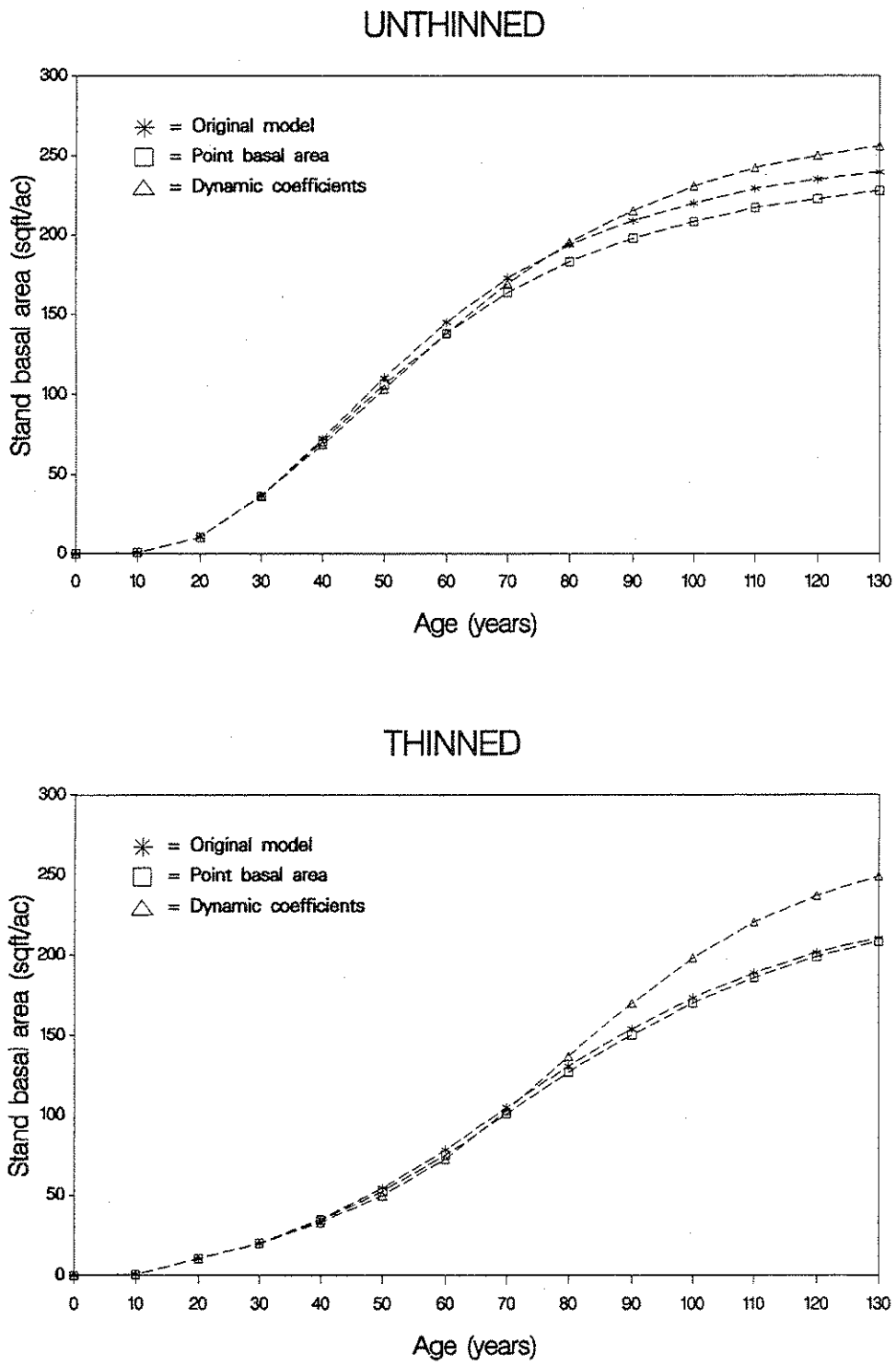

Figure 1. Effects of model formulation and management scenarios on mean stand basal area per acre. Means of 20 replicated simulations.

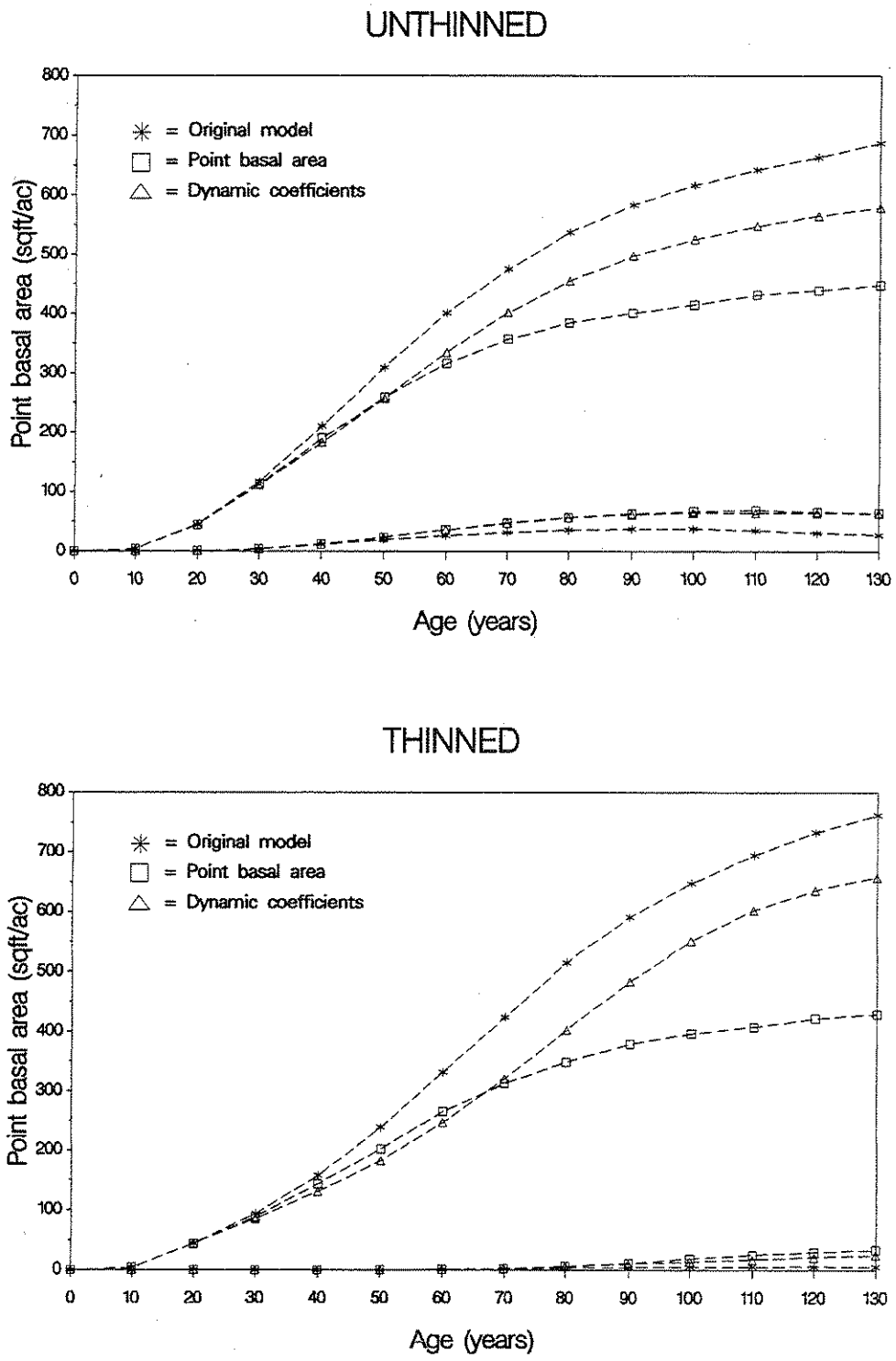

Figure 2. Effects of model formulation and management scenarios on maximum and minimum point basal areas per acre. Means of 20 replicated simulations.

CONCLUSIONS

With the methods we describe, simulation of stand development using individual-tree distance-independent models can better represent point-specific silvicultural prescription. In addition to the thinning methods described by Pukkala (1990), one could also simulate the creation of small clearings to implement group-selection forms of silviculture. Although there has been substantial interest in this capability, we have resisted implementing it in the Prognosis Model for Stand Development until the attendant statistical problems have been resolved. We believe the methods we describe are satisfactory, although there are inevitably further nuances to challenge further research. Our next step will be to extract growth data with the information for calculating measurement errors from extensive inventories. Then the methods described in this paper will be fully implemented and evaluated.

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EVALUATING REALIZED GENETIC GAINS FROM TREE IMPROVEMENT

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ABSTRACT

Tree improvement has become an essential part of the management of forest lands for wood production, and predicting yields and realized gains from forests planted with genetically-improved trees will become increasingly important. This paper discusses concepts of tree improvement and genetic gain important to growth and yield modelling, and reviews previous studies of the growth and yield of genetically-improved stands. Three types of studies that have been done include: (1) simulations in which assumptions have been made about key inputs into the models, (2) studies of genetic variation in stand productivity at the level of seed sources or families, and (3) actual comparisons of improved versus unimproved stands. Simulation studies indicate that genetic gains are highly likely, but how much gain is realized will depend on height-age trajectories after crown closure. Studies of genetic variation in stand productivity are ambiguous with respect to genetic variation in parameters of the height-age curve. Few studies have been published of actual comparisons of improved versus unimproved stands, although many such studies have recently been established. The design of a study to evaluate realized genetic gains from Douglas-fir tree improvement programs is presented.

INTRODUCTION

Tree improvement efforts began in earnest in the 1950's and 1960's in many regions of the world, and have become an essential part of the management of forest lands for wood production. Presently many forestry organizations are embarking on second and third generations of improvement. In the Douglas-fir region of the Pacific Northwest, tree improvement programs have been initiated over the last 30 years to provide improved trees for over 6.5 million hectares (Silen and Wheat 1979; Adams et al. 1990). These programs represent a cumulative effort of approximately 42,000 parent trees evaluated at over 1,350 progeny test plantations with an investment of approximately a quarter-billion dollars (Adams et al. 1990). Seed orchards are now beginning to produce large amounts of improved seed and landowners are now utilizing improved planting stock in their reforestation programs.

Despite large investments in tree improvement programs like those in the Pacific Northwest, fundamental questions about the interaction of genetics and silviculture and the use of genetically-improved stock remain unanswered. Specifically, it has not yet been demonstrated that expected genetic gains, which are based on growth

differences measured on individual trees in young progeny tests, are achievable as per-unit-area gains at rotation. Although forest geneticists are confident in the efficacy of tree improvement, they are less confident in their ability to predict with any certainty the level of achievable gains in stand productivity. Developing the techniques needed to predict the growth and yield of improved stands will require the integrated knowledge of geneticists, biometricians, silviculturists, economists, and land managers.

Several reasons exist for wanting to predict the final yield of improved stands (Flewelling and Talbert 1990). Besides providing justification for the large investment in tree improvement programs, knowledge of the productivity of genetically-improved forests will facilitate better-informed land management and economic decisions. These include establishing the allowable cut for sustained wood production, making decisions on establishing new mills and new markets, altering silvicultural treatments to best utilize the growth behavior of the improved stock, making decisions on how best to allocate improved stock to different sites, and making decisions on how much to invest in tree improvement versus other activities. In addition, understanding the biology of increased stand growth and yield may lead to changes in the selection process, including decisions concerning the competitive regimes of genetic tests (i.e., stand density and mixed versus pure family blocks) and the inclusion of physiological or morphological traits in selection criteria (Ford 1976; Cannell 1978).

The goal of this paper is bring together concepts of forest genetics and stand modelling important to the prediction of yield and realized genetic gains from genetically-improved forest stands. I will first review some concepts of tree improvement and genetic gain, and consider some of the factors important in determining expected and realized gains. I will then discuss growth and yield modelling of improved stands, including a review of past studies. In the final section, I will present the outline of a study recently initiated by the USDA Forest Service Pacific Northwest Research Station and members of the Northwest Tree Improvement Cooperative designed to evaluate realized genetic gains from Douglas-fir tree improvement programs.

EXPECTED VERSUS REALIZED GAINS FROM TREE IMPROVEMENT

The primary objective of most tree improvement programs is increased value production per unit area of land at rotation. Unfortunately, this trait is not easily measured. To get around this, tree breeders do several things. First, they measure and select multiple traits thought to be related to value, in particular, stem size, but also traits related to wood quality (e.g., wood density, stem straightness, branch characters) and adaptability (e.g., cold and drought tolerance, disease and insect resistance). The different traits are then combined by a variety of techniques, including index selection, independent culling levels, tandem selection and multiple population breeding, to select genotypes in one or more generations. Second, they

measure and select genotypes at a much younger age than rotation length. Although no studies exist relating early performance to performance at typical rotation ages, several studies suggest that correlations are sufficiently high to make early selection worthwhile (Lambeth 1980; Lambeth et al. 1983). Third, selection is done based on performance of individual trees rather than yield per unit area. At younger ages before appreciable competition, individual-tree yield and stand yield should be highly correlated after correcting for differences in survival. At older ages, however, relative family performance and estimates of genetic parameters may be influenced by differential responses to density and intergenotypic competition (Foster 1989; St.Clair and Adams 1991).

Realized genetic gains refer to those gains actually obtained from tree improvement. Realized gains in value or volume production per unit area at rotation are rarely tested due to the considerable expense and time commitment involved in establishing trials. Instead, expected genetic gains are predicted based on estimates of heritabilities and genetic values of parents from genetic tests. The primary objective of most genetic tests is to evaluate the relative performance of genotypes for purposes of selection. Estimating components of variance and covariance for purposes of estimating heritabilities, genetic correlations and expected genetic gains are usually only secondary objectives.

Genetic tests are usually established using a randomized block design with row or non-contiguous plots of a few trees (e.g., one to five trees). Several studies indicate that a test design using small, non-contiguous plots is the most efficient design for estimating family means, and designs using large, pure-genotype plots are the least efficient (Lambeth et al. 1983; Loo-Dinkins and Tauer 1987). Although family ranking for selection appears to be stable among different plot configurations, variance component estimates may differ greatly between large block plots, row plots and non-contiguous plots (Foster 1989). Intergenotypic competition among families may lead to much larger estimates of genetic variance, heritability, and expected genetic gain. In a seedling study of Douglas-fir, I found that the expected genetic gain for selection for biomass when families were evaluated in mixtures was 26%, whereas the same families tested in pure family plots resulted in estimates of genetic gain of only 8% (St.Clair and Adams 1991). Which estimate of gain is most appropriate is a question that is not easily answered. If genotypes are evaluated in pure stands (for example, to obtain estimates of yield per unit area), the gains calculated may not be appropriate if the improved material is to be deployed in mixtures in production forests. However, if genotypes are evaluated in mixtures, the mixture used in the genetic test will necessarily differ from the mixture of selected genotypes deployed in production forests. This may lead to reductions in realized genetic gains if selection in mixtures leads to selection of trees that are more competitive. This concern is the basis for ideotype breeding which attempts to select tree types that are less competitive and may lead to larger yields per unit area (Cannell 1978; Dickmann 1985).

Expected genetic gains predicted from genetic tests may differ from realized gains for

the reasons given above, that is, the trait of interest is not directly selected, juvenile-mature correlations may be less than perfect, and competitive interactions may affect relative performance and variances. Other factors that may be important include poor design and siting of genetic tests, pollen contamination in seed orchards, unequal contributions of parents to the improved population, and interactions between genotypes and silvicultural practices. Much research in forest genetics is aimed at addressing these concerns. However, establishing genetic gain trials and applying techniques of growth and yield modelling to existing genetic tests and improved plantations will be required if we are to be able to confidently predict yields and realized genetic gains from improved plantations.

GROWTH AND YIELD OF GENETICALLY-IMPROVED FOREST STANDS

Growth and Yield Modelling

Many different models have been developed to predict the growth and yield of forest stands. Growth and yield models are commonly classified as either stand-level models or tree-level models, dependent upon whether the stand or the individual-tree is the basic prediction unit (Clutter et al. 1983). Stand-level models use stand statistics as input variables, whereas tree-level models include at least some individual-tree statistics. Diameter distribution models are a type of stand-level model that produce some individual-tree outputs in the form of frequencies and average heights by diameter classes. Tree-level models include distance-independent models and distance-dependent models, which are distinguished by whether or not information on the positions and distances between trees are included. Data needed for input into models include height, diameter, and stand density at different ages. Given this data, modelers attempt to mathematically describe and interpret several important relationships. These include (Buford and Burkhart 1987; Foster 1992): (1) the development of height over time (the height-age relationship or site index), (2) the frequency distributions of height and diameter, (3) the relationship between height and diameter, (4) mortality trends over time, and (5) the relationship between individual-tree size and stand density (the self-thinning line). Some models may include other types of data such as information on wood quality, crown structure, or physiological variables.

Current genetic tests are ideal for initial development of models for predicting yields from improved stands. Information on height, diameter, and stand density at different ages is readily available in many genetic tests. Both stand-level and tree-level models may be used for predicting yields using genetic test data, since data is collected on an individual-tree basis. Inferences from current genetic tests, however, will be limited due to the unknown effects of intergenotypic competition.

Evaluating genetic effects on growth and yield involves several steps. First, the mathematical model that best describes the relationships of interest must be selected. Two mathematical functions commonly used to describe relationships of interest are

the Schumacher function and the Chapman-Richards function (Clutter et al. 1983). The Schumacher function includes an asymptote, or level, parameter, and a slope parameter, which defines curve shape. The Chapman-Richards function also includes an asymptote parameter, but curve shape is defined by two parameters, commonly referred to as shape and rate. The choice of mathematical model may be important to conclusions from the analysis (Knowe and Foster 1989; Sprinz et al. 1989). In the next step, genetic treatments are compared for differences in the parameters of the mathematical model. Ideally, comparison of genetic treatments should be between improved and unimproved populations. Alternatively, comparisons may be among different pure stands of genetic entities (clones, families, or provenances), but if pure stands are not used in operational plantings, extrapolation to mixing of selections involves assumptions of no effects of intergenotypic competition. Finally, growth and yield models are modified to accommodate differences between improved and unimproved stands. Once growth and yield models are developed for improved stands, they should be validated using independent data sets.

Past studies of genetic effects on growth and yield have been of three types: (1) simulations in which assumptions are made about key inputs into the models, (2) studies of genetic variation in stand productivity at the level of seed sources or families, and (3) actual comparisons of improved versus unimproved stands. These three types of studies are reviewed in the following sections.

Simulations of Improved Versus Unimproved Forest Stands

Studies involving simulations indicate that assumptions made about key inputs into the model are important to predictions of growth and yield from genetically-improved stands. For example, assumptions about the trajectories of genetic gains in height and diameter after crown closure may result in large differences in stand volume gains (Nance and Bey 1979; Du and Fins 1990; Rehfeldt et al. 1991). Rehfeldt et al. (1991) predicted genetic gains in stand volume for western white pine grown to two rotation ages and at two planting densities given three possible scenarios for the trends in levels of gains after crown closure. Initial genetic gains at 25 years were 5.6% for height and 6.1% for diameter, as estimated from three genetic tests planted at two sites in northern Idaho. After 25 years, genetic gains were either: (1) truncated and no further gains allowed to accumulate, (2) continuously accumulated throughout the rotation at annual rates equal to those observed during the first 25 years, or (3) augmented to a value of twice the annualized rate and allowed to accumulate continuously. Genetic gains at age 55 for stands planted at a high density were 5.0% assuming gains are truncated, 10.3% assuming gains are continuous, and 14.9% assuming gains are augmented. Genetic gains were also affected by choice of initial planting density and rotation age. Thinning may also be important for capturing gains.

Assumptions concerning phenotypic variances (frequency distributions of size) may also be important to predictions of stand yield from improved populations. Simulations by Mitchell (1975) and Nance and Bey (1979) indicate that reduced

phenotypic variance may result in reduced stand volume, presumably because large, vigorous trees must compete with each other to a greater degree. Phenotypic variance may be reduced by planting single family or single clone blocks, or, theoretically, as a consequence of genetic selection. Reductions in phenotypic variance from genetic selection, however, are likely to be small since environmental variation within a typical forest stand is large and considerable genetic variation still exists even within a single family. Buford and Burkhart (1985) found no significant differences in variances of height and diameter among eleven open-pollinated families and a woodsrun checklot of loblolly pine.

Simulation studies demonstrate the likelihood of achieving genetic gains from tree improvement. However, these studies require estimates of initial genetic gains before crown closure and assumptions about the trajectories of genetic gains after crown closure. Information from the second and third types of studies is needed in order to test those assumptions.

Studies of Genetic Variation in Stand Productivity

Studies of genetic variation in stand productivity require genetic tests with large, pure-genotype block plots, and of sufficient age to account for competitive effects. These types of genetic tests are rare. Provenance tests often involve large block plots, and, consequently, most studies combining genetics and growth and yield modelling have been at the seed source level. Most have involved one or more sites of the loblolly pine portion of the Southwide Pine Seed Source Study. Few genetic tests involve large block plots of families. This is the level of genetic variation of greatest interest to evaluating genetic gain from tree improvement programs.

Site index and the related height-age curves are among the most important input parameters of growth and yield models. Most studies of genetic effects on growth and yield consider genetic variation in parameters of the height-age curve. Conclusions from these studies are ambiguous. Nance and Wells (1981) and Buford and Burkhart (1987) found significant differences among seed sources and families in the asymptote of the height-age curve, but not in the shape. Thus, a simple adjustment in the level of site index may be sufficient to account for genetic differences in stand productivity for purposes of growth and yield modelling. However, results using the same set of seed sources, but considering only a single site in Arkansas, indicate that sources differ in the shape of the dominant height-age relationship, but not in the asymptote (Sprinz 1987; Talbert and Strub 1987; Sprinz et al. 1989). East Coast sources were tallest and yielded more than western and interior sources at the Arkansas site, but trends were beginning to converge at older ages. Knowe and Foster (1989) considered family variation in the same set of study material as Buford and Burkhart, but used the three-parameter Chapman-Richards function. Families differed significantly in the asymptote and rate parameters, but not in shape. Their results, along with those from Arkansas, indicate that different genotypes have different growth patterns relative to one another, and that simply adjusting the level of site index may not be sufficient for predicting growth and yield.

The study of Knowe and Foster (1989) illustrates how genetic differences in height-age curves may be used to study genetic variation in stand productivity. They incorporated family differences in height-age curves into a growth and yield model to predict stand yield for each family in their test. Expected genetic gain from selection of the top three families was then calculated based on the predicted stand yields. This estimate of expected genetic gain was highly correlated to the expected genetic gain estimated from observed family differences. Although these results do not tell us anything about the relationship between expected genetic gains and realized genetic gains, their technique does represent a unique method to estimate the genetic value of different families and the expected genetic gains from selection. For example, height-age curves could be determined for families in genetic tests involving row or non-contiguous plots and used to estimate expected genetic gain in volume per hectare at different rotation ages (assuming no intergenotypic competition effects on height growth).

Seed source variation in the size-density relationship was explored in two studies using material from the loblolly pine Southwide Seed Source Study. Results from both Schmidtling (1988) and Buford (1989) indicate that seed sources vary in the intercept of the self-thinning line, but not in the slope. Furthermore, strong positive correlations were found between the intercepts and the site indices of seed sources. These results indicate that loblolly pine seed sources differ in their carrying capacities at a given site. It would be of great interest to consider the morphological and physiological variables associated with these differences in carrying capacity.

The height-diameter relationship in loblolly pine was considered by Buford and Burkhart (1987) and Schmidtling and Clark (1989). Height-diameter relationships are used in growth and yield modelling to predict mean heights for a given diameter or diameter class, which in turn are used to predict stand volume and value. Buford and Burkhart found that the shape of the height-diameter relationship does not differ among families or seed sources, but the level does. Schmidtling and Clark found seed source differences in both shape and level. These results indicate that prediction equations for height and volume differ among seed sources and families due to differences in stem form. Although these differences may be important for predicting stand volume from different families or seed sources, they may not be large enough to be of practical importance to the relative ranking of families or seed sources for purposes of selection.

Comparisons of Improved Versus Unimproved Forest Stands

Few organizations have established designed studies to compare stand productivity of improved versus unimproved stands. Although studies have been initiated for Douglas-fir, western hemlock, radiata pine and loblolly pine, few studies have been published. Janssen and Sprinz (1987) compared improved and unimproved families of loblolly pine grown in pure family blocks. They found that improved families were

superior in individual-tree diameter and volume per hectare at 30 years of age. However, no estimates of the overall level of superiority are given, and no mention is made of what the criteria were for choosing improved and unimproved families. Eldridge (1982) reported on an Australian trial in which a radiata pine seedlot from an early seed orchard was compared with a control seedlot representative of the population from which the trees in the orchard were selected and typical of much of the early commercial seed. At 10 to 12 years of age, the realized genetic gain in volume per hectare at three sites was 9, 16, and 22%. Growth and yield parameters were not determined in this study, and no mention is made of trends in the results. Interestingly, genetic gains were smallest at the most productive site, possibly indicating decreasing genetic gains with increasing stand development and competition.

When designing studies to evaluate realized gains in improved versus unimproved forest stands, one must address the question of what is improved and what is unimproved. An improved population may be considered to be the seedlot from a typical seed orchard. However, the genetic composition of that seedlot may differ dependent upon orchard design and management, location of the orchard relative to potential sources of contamination, age of the orchard, and the particular year of seed collection. The genetic composition of the improved population may be controlled, however, by using controlled pollinations among the parents for which gain is to be estimated. Another problem with designating an improved population is that the level of improvement in a tree improvement program is a moving target. By the time data is collected to evaluate realized gains from an improved population, another round of selection has been completed. The realized gains and growth and yield models developed for the earlier improved population will not be appropriate for later populations. One solution to this problem is to develop a general relationship between realized genetic gains and the expected genetic gains as determined from genetic tests used for selection. The unimproved population is used as a standard for determining realized gains, but what is the appropriate standard to use? If your goal is to estimate response to selection, the appropriate unimproved population is the population from which the original selections were made. But if your goal is to estimate gains from tree improvement relative to alternatives, the appropriate unimproved population would be that which would be used if improved stock were not available.

EVALUATING REALIZED GENETIC GAINS IN DOUGLAS-FIR

Forestry organizations in the Pacific Northwest have recently become more concerned about their ability to predict realized genetic gains and productivity from the large number of stands planted with genetically-improved Douglas-fir. As a result, members of the Northwest Tree Improvement Cooperative asked the Genetics Team of the Pacific Northwest Research Station to help design and coordinate a region-wide study to look at the growth and yield of improved Douglas-fir stands. The two primary objectives of this study are: (1) to compare estimates of growth and yield

parameters among genetic populations having different expected growth potential, and (2) to develop a predictable relationship between expected genetic gain based on individual-tree growth characteristics and realized genetic gain in stand productivity.

Three different genetic quality types will be tested at six sites within the breeding zones of each of three different tree improvement programs. The large number of sites and inclusion of three different programs will allow us to test the generality of relationships across sites and across programs. The three genetic quality types include an unimproved control and two improved populations representing two levels of expected genetic gain. We chose to test two levels of genetic gain for each of three breeding zones in order to have a range of expected gains for developing the model to predict realized gains. Expected genetic gains are determined based on estimates of heritabilities and selection differentials from extensive progeny tests within each breeding zone.

The improved genetic quality types will be produced by controlled pollinations among 20 clones of the original parent trees. In one of the three programs, the mating design is single-pair matings among the 20 parents, while in the other two programs, the mating design is a polycross in which each selected parent is pollinated with a common mix of pollen from the other 19 selected parents. The "elite" genetic quality type aims for the highest level of genetic gain. It will include crosses among the best 20 parents in each breeding zone. The "intermediate" genetic quality type will include crosses among 20 parents targeted at a level of genetic gain of about half that of the elite genetic quality type. The unimproved genetic quality type will be a random selection of 50 to 100 "wild" trees that are well distributed throughout the breeding zone. The unimproved type is assumed to represent both the average genetic quality of seed that would be used for reforestation in the absence of tree improvement and the original base population from which selections were made. The genetic growth potentials of these two populations are probably equal since the average parent tree in progeny tests was essentially randomly selected from natural stands within each breeding zone.

Each test site will also include two different planting densities and an optional thinning treatment in order to test the effect of stand density. The low density treatment (772 trees per hectare) was chosen to represent operational conditions assuming no thinnings. The high density treatment (1250 trees per acre), besides allowing consideration of density effects, will provide early results by promoting stand competition effects at a relatively young age. Later, data from the low density plots can be used to verify the accuracy of information from earlier ages in the high density plots. The high density plots may be particularly valuable in providing timely information on genetic effects on self-thinning. The objective of the thinning treatment is to evaluate the role of intermediate cuttings in capturing potential gains in yield from genetically-improved stands. The hypothesis to be tested is that the magnitude of realized genetic gains will be larger in thinned versus unthinned stands due to the avoidance of competition effects (Talbert 1981; Switzer and Shelton 1981).

The experimental design at each site will be a split-plot design with density treatments occupying the whole-plots and the genetic quality types occupying the split-plots. Plot size will be 100 trees planted in a 10 tree x 10 tree square plot for the low and high density treatments. The thinning treatment will initially have 162 trees to be thinned to a final number of 81 trees per plot (9 tree x 9 tree). The number of trees per plot in this study are more than that used in previous studies of the genetics of growth and yield, and within the range of numbers recommended in a review by Curtis (1983).

This study represents a considerable effort by members of tree improvement cooperatives in the Pacific Northwest. However, we feel that the benefits from this study will greatly outweigh any costs. It is hoped that the results from this study will be generally applicable to a Douglas-fir tree improvement programs throughout the region, and will allow us to confidently predict the yield and realized genetic gains from genetically-improved Douglas-fir stands. Furthermore, we feel that results from this study will go a long way to establishing the value of tree improvement programs in the Pacific Northwest.

CONCLUSIONS

Tree improvement has become an important part of forest management throughout the world. Predicting the yields and realized gains from forests planted with genetically-improved trees will become increasingly important. Developing the techniques needed to do so will require the integrated knowledge of geneticists, biometricians, silviculturists, economists, and land managers. We can begin the task by applying techniques of growth and yield modelling to the analysis of data from genetic tests already in the ground. Much of the information needed for growth and yield modelling is available for many of these tests, although assumptions about the influences of intergenotypic competition may be required. Studies are needed to evaluate the effects and importance of density and intergenotypic competition, including comparisons of families or clones in pure plots versus in mixtures. Finally, we must establish new trials to compare realized gains and yield in improved versus unimproved forest stands. Such trials are now being established for Douglas-fir in the Pacific Northwest.

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THE IMPACT OF THE VARIATION OF POTENTIAL HEIGHT GROWTH ON THE PROJECTIONS OF A SINGLE TREE GROWTH MODEL

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ABSTRACT

Stem analysis data of 50 dominant trees of Norway spruce (*Picea abies, L. Karst.*) and Scots pine (*Pinus silvestris, L.*) give evidence to the fact that height growth deviates from the expectations of a site index system which was developed from stem analysis data by Guttenberg (1896). These deviations do not occur until about the year 1960. Part of the variation of height increment deviations from its predictions by Guttenberg's site index system afterwards can be explained by changes of monthly temperatures and precipitation. Additional effects of nitrogen deposition, increasing mineralization of raw humus layers through acid rain, increasing carbon-dioxide in the atmosphere can be suspected.

From the 20 years observations of plots in mixed species uneven aged stands of Norway spruce and Scots pine a single stem growth simulator had been parameterized using a simplification of Monserud's (1975) simulator FOREST. The parameterization had to take into account that the potential height growth model is altered by the findings of the stem analysis data (increased height increments). Using these parameters for one 30 years old stand six different scenarios of height increment change are simulated: One which assumes that the average height increment change found during the years 1971 - 1985 will last until the age of 80 years, one which assumes the same for the hiehgt growth deviations found between 1986 and 1991 and three others where a 15 years period of accelerated height growth like that in the period between 1986 and 1991 will start in ages 30, 45 and 60 years respectively. The sixth scenario where no deviations from Guttenberg's height growth curves are assumed severs as a control.

Resulting from these simulation runs we see that the accelerated height growth leads to higher final volumes with less stem numbers through higher mortality. The sooner the period of increased height growth starts the higher is the mortality of Norway spruce and the less is the mortality of Scots pine. Even when the height growth acceleration of Scots pine is greater than that of Norway spruce the mortality of Scots pine will increase and the resulting average stem volume of Scots pine will be lowered compared to that of Norway spruce. These results may at least partly explain the fact that in spite of reports about forest decline increased volume increments were found in the Austrian national forest inventory for 1986 to 1990.

INTRODUCTION

Many surveys of crown transparency of Norway spruce and Scots pine in central Europe report of forest decline for which air pollution is hypothesized to be an important reason (Krause et al. 1986; Smith 1985; Führer, 1990 and many others). On the other hand there is evidence of increased increments on a national scale in Austria (Schieler and Schadauer, 1993) and for several long term thinning experiments in Germany (Pretzsch,1985; Röhle,1985; Kenk and Fischer,1988). As causes for the latter fact nitrogen deposition, increasing mineralization of raw humus layers through acid rain, increasing carbon-dioxide in the atmosphere and changing climate are discussed. Whatever kind of interactions of all these effects may really take place they will result in a change of forest site quality and thus violate the main underlying hypothesis of site constance of all usual forest growth simulators. Those simulators the main parts of which consist of equations for "potential increments" and competition models which reduce potential growth to actual growth by competition factors or stand density measures seem to be appropriate for adjusting them to changing site quality by changing the potential increment functions.

The objective of this paper is to show how a simplified version of Monserud's (1975) single stem distance dependent simulator FOREST can be adopted to care for "changing site conditions" and then be used to study the effects of different scenarios of site quality changes on the growth of mixed species uneven aged stands of Norway spruce and Scots pine.

DATA

The area of the study is situated in the central Austrian part of the Bohemian Massif. The bedrock is built by gneiss and granite, the soils are all transitions between brown soils, podzolic soils and pseudogleys. Yearly precipitation is about 740 mm with a maximum in summer and mean annual temperature is about 6.8° C. The average snow cover lasts about 80 days.

To study the effect of changing site quality on growth 50 stem analyses of each, dominant Norway spruce and Scots pine were conducted. The stems had been harvested in 1992 and were about evenly distributed among good, medium and poor sites and ages between 60 and 150 years. Height increment of these trees were compared with the site index system developed by Guttenberg (1896) from stem analyses in the same region. The deviations of actual height growth from the predictions of Guttenberg's site index system were then correlated with the monthly precipitations and temperatures reported by a nearby weather station since 1901.

To determine the parameters of Monserud's simplified growth model the data of 21 plots in mixed stands of Norway spruce and Scots pine in the same region were used. These plots had been established in 1972 and remeasured in 1977, 1982, 1987 and 1992. The measurements taken comprised the coordinates of the trees, their heights, crown lengths and breast height diameters.

METHODS

The first target was to find a possibility to introduce short or long term variations of site quality into the growth simulator which was developed from Monserud's simulator FOREST in a simplified version and parameterized for even- and uneven-aged stands of Norway spruce and Scots pine (Sterba, 1982; Eckmüllner, 1990b; Sterba, 1992). The two main parts of this model which we intended to use for this study were

1. a model for potential height- and diameter growth, and
2. a competition model to describe the reduction of potential growth by competition

The model which we used for our single stem distance dependent growth simulator for more or less uneven aged mixed stands of Norway spruce and Scots pine is based on the philosophy of Monserud's (1975) simulator *FOREST*. Its derivation from this model needs shortly to be summarized:

The simulator WASIM

Potential height growth of the trees is calculated from site index systems built from stem analysis data. Given a site index for a certain stand, a "calculatory age" is derived for every tree by finding the age at which the actual height of the tree were reached. Potential diameter growth is derived by the height growth curves and a relationship between height and breast height diameter of open grown trees as it results from Sterba's (1987) modification of the competition density rule of Kira et al. (1953). The actual projections for height- and diameter increments are then found by reducing potential growth by competition.

1. The height growth model

$$\frac{ih}{ih_{pot}} = OVS \cdot CR^{b_6} \cdot SHIFT$$

with ih, the actual height increment, ih_{pot}, the potential height increment, OVS, the "overstocking multiplier", CR, the crown ratio and $SHIFT$ a multiplier that shifts the point at which maximum height growth occurs.
The "overstocking multiplier", OVS, depends on the "adjusted competition index, CIA":

$$OVS = \{ 1 - e^{-\frac{1}{b_4 \cdot CIA}} \}^{b_5}$$

The competition index, CI, is calculated according to Monserud's (1975) modification of Bella's (1970) overlap index. The adjustment of this index accounts for the shade tolerance of different species as it depends from the tree's height, h, and for the change in competition, ΔCI as it may result from died or removed neighbors:

$$CIA = 1 + 0{,}1 \cdot CI \cdot (1 - b_1^{h+1}) \cdot (1 + b_2 \cdot \Delta CI)^{-b_3}$$

The shift-multiplier, *SHIFT*, depends only on the height of the tree, accounting for the fact that higher and thus older trees may have a maximum height growth at a competition index other than zero, while in very small and young trees the maximum height growth may be at zero competition and stay at this maximum value until a certain competition index is reached.

$$SHIFT = 1 + [\, b_7 \cdot (1 - b_8^{h+1}) \,]^{CIA}$$

2. The diameter growth model

The competition model for diameter growth differs from the height growth model only in lacking the multiplier *SHIFT*.

So Monserud's competition model needs 8 parameters to be estimated in the height growth model and only 6 parameters for the diameter model.

3. The modifications of Monserud's Competition Model

Although Monserud's model is defined by 8 parameters for height growth and 6 parameters for diameter growth we found that several parts of the model were not significant in the nonlinear regression analyses. Even from Monserud's (1975) table of the coefficients it can be seen that several of them must have been set to certain bounds which were reached in the iteration process for different species. Thus many of Monserud's parameters had not been really estimated from his data but only by heuristic definition. Especially in the height growth model this must have been the case because there had been only very few really measured height data. The majority of the heights had been estimated by only one height diameter equation per species.

Because our data had repeated height-, crown length - and diameter-measurements for all trees in the plots, we simplified Monserud's model by using only those parts of his model which contributed significantly to the explanation of the variance of the dependent variables ih/ih_{pot} and id/id_{pot} respectively. So we ended up in a model with only three parameters for the height- and the diameter-model of Norway spruce (b_4, b_6 and b_2 in the above equations) and only two parameters in the height- and diameter model for Scots pine (b_4 and b_6). The way of their estimation, the parameter estimates and their statistical properties were given in Sterba (1992).

4. The mortality model

The mortality model of our study was a very simple one. We defined a threshold of diameter increment to which we added a normally distributed random variable to decide if a tree died within the next five years period or not. The diameter

increment threshold was chosen in a way that the resulting basal area of the simulated stands equalled to the "natural basal area" per hectare as it was defined by Assmann (1956) and evaluated according to Sterba (1987).

The modification of the potential increment model

Under the assumption that potential diameter growth's change is sufficiently described by the influence of an altered height growth in the relationship between potential height and diameter, it was only necessary to investigate if there are deviations from the potential height growth as is it described by Guttenberg's (1896) site index systems. To define these deviations, the site index of every stem of the recent stem analysis data set was determined using its height in 1970, two years before the establishment of the plots which should later be user to determine the parameters of the model WASIM. The deviations from the site index system were then defined as

$$q = \frac{ih_{obs}}{ih_{SIS}}$$

with ih_{obs}, the observed height increment from the stem analysis of the tree and ih_{SIS}, the height increment which is projected from the height growth curve from Guttenberg's site index system with the site index determined in 1970. Using stepwise regression analysis the deviations, q, were described as a function of climate, i.e. different transformations of the monthly precipitation and temperature data from the nearby weather station. The deviation, q, of the preceding year was used to account for the expected auto-correlations.

The parameterization of the competition model

Since Sterba (1992) could show that the estimates for the parameters of the competition model will be biased if the site index system doesn't describe real potential height growth, the potential height increment of Guttenberg's height growth curves was multiplied by the average q for the appropriate observation period before estimating the parameters of the competition model by nonlinear regression.

The simulation runs

To study different scenarios of changing height growth, one stand out of the 21 observed plots of this study was selected. Its average age in 1972 was 30 years, the site index (dominant height in age 100) was 42 m for Norway spruce and 36 m for Scots pine. In 1972 it had 4579 trees per hectare, the proportion of Scots pine was 28 % by volume but only 7 % by stem number. Six different scenarios, all of them with no thinning, thus assuming only natural mortality by competition, were simulated from age 30 to age 80. They were defined by different lengths of the period in which the height growth acceleration occurs. The amount of the height growth acceleration was once that which was observed in the stem analysis data between 1971 and 1985 and once between 1986 and 1991.

The deviations from the expected height growth

A comparison of the observed height growth of the stem analyses data and that of Guttenberg's height growth predictions is given in Figure 1 for Norway spruce.

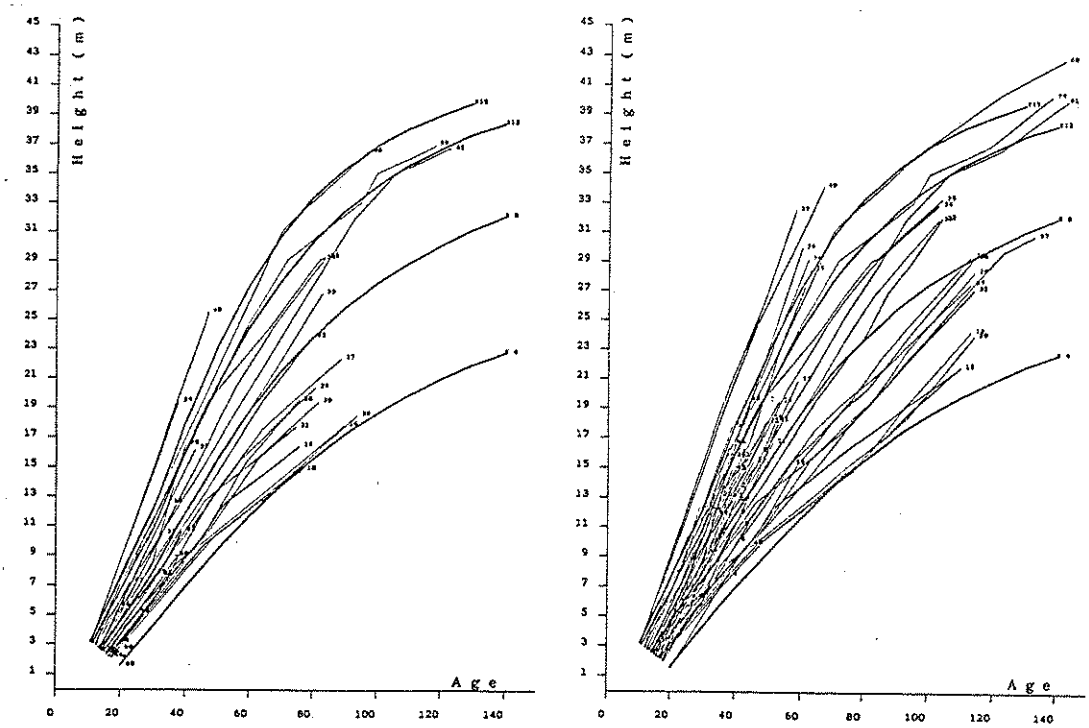

Figure 1: The height growth of 50 dominant Norway spruce stems harvested in 1992 (fine lines), compared with Guttenberg's (1896) height growth curves (thick lines). On the left picture the height increments of the last 30 years are omitted, on the right one they are added.

On the left side the last 30 years of all stem analyses were omitted. The site index system of Guttenberg describes the actual height growth on these sites quite well, the variations around the height growth curves seem to be only random. When the actual height growth of the last 30 years is added (Figure 1, right picture) the acceleration of the height growth becomes significant. The yearly averages of the deviations, q, are given in Figure 2.

There seem to be two different periods of growth acceleration. The first one lasting until about 1985 where both Norway spruce and Scots pine have about 65 % higher height increments than it would have been expected from the height growth curves. The second one from 1986 until the end of the observations in 1991 where the ratio between observed and expected height increments of Scots pine is distinctly higher than that of Norway spruce (2.16 compared to 1.80 as an average).

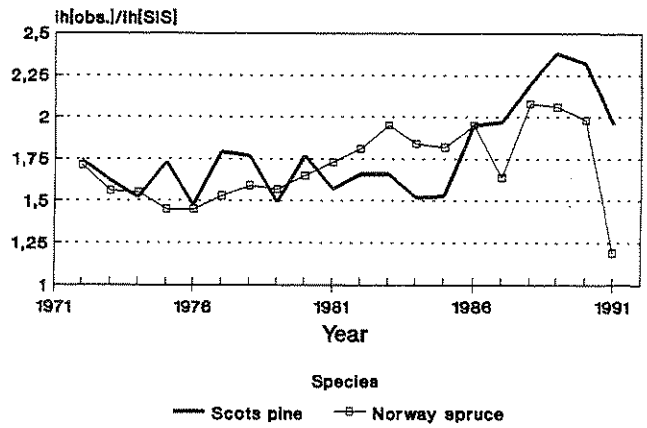

Figure 2: The average ratios between observed (ih_{obs}) and from Guttenberg's site index system projected height increments (ih_{SIS}) for Norway spruce and Scots pine.

Spiecker (1987 and 1990) pointed out that due to the influence of different weather conditions growth might show deviations from the expectations of yield tables and age trends. In our case we found significant relationships between precipitation, temperature and the ratio, q. The equations found by regression analysis were

$$q_{Spruce} = 85.4 + 0.456 \cdot q_{Spruce_{-1}} - 0.297 \cdot P_{spring} - 0.0704 \cdot P_{autumn_{-1}} + 0.189 \cdot P_{summer} \quad (1)$$

and

$$q_{pine} = 102.1 + 0.595 \cdot q_{pine_{-1}} + 0.538 \cdot P_{spring} - 26.6 \cdot H_{spring} - 4.02 \cdot T_{autumn_{-1}} \quad (2)$$

with q, the ratio between observed and projected height increment with an index pointing out the species. The second index used with q, namely, *-1*, means the ratio of the year before which was used as an auto-regressive variable. P means the precipitation in spring and summer of the current year and in the autumn of the year before respectively, T the mean temperature and H, the humidity sensu Kublin et al.(1988) who defined

$$H = \frac{Precipitation[mm]}{Mean\ temperature[^oC] + 10}$$

The partial coefficients of determination (Table 1) show that the contribution of the climatic variables to the explanation of the variance of the ratio, q, is only small. When omitting the auto-regressive variable from the equations, several climatic variables of the preceding year will become significant without decreasing the total coefficients of determination as they are shown in Table 1.

Table 1: Partial coefficients of determination, R^2., for the regressions of the ratio between the observed and the expected height increments of Norway spruce and Scots pine.

	Norway spruce		Scots pine	
dependent variable	R^2.	$\sum R^2$.	R^2.	$\sum R^2$.
q_{-1}	0.2315	0.2315	0.5758	0.5758
all sign. climatic variables	0.0427	0.2742	0.0329	0.6088

From this we conclude that the increments of the preceding year are able to describe the weather conditions of this year better than the precipitation and temperature data only. This point of view gains support from the fact that Eckmüllner (1990a) found that the tree ring widths at the base of the crown of the preceding year were higher correlated with the height increments of the current year than the tree ring widths of the current year. The two species react differently to different weather conditions. While Norway spruce gains from high summer precipitation, Scots pine seems to prefer humid and wet springs. Nevertheless Table 1 shows that the effect of the weather conditions of the preceding year are more important for height growth than those of the current year.

With these regressions (equ. **(1)** and **(2)**) the potential height growth of future periods could have been simulated assuming different weather conditions. Because it is difficult to make reasonable assumptions on climatic development we chose the way not to assume a certain climate in detail but to make assumptions on the average ratios, *q*, which result at least partly from these weather conditions. These average *q*s and the associate climatic measures are given in Table 2 for two different periods in comparison to the average of the "normal year", i.e. the period from 1901 until 1960.

Table 2: Average ratios (q) between observed and expected height increment, precipitation (P) in spring, summer and preceding autumn, mean temperature (T) in the preceding autumn and mean humidity (H) according to Kublin et al. (1988) in spring for the normal year and the two periods 1971-1985 and 1986-1991.

period	P_{spring}	P_{summer}	$P_{autumn,-1}$	H_{spring}	$T_{autumn,-1}$	*q*	
1901-1960	169	281	116	3.44	7.49	Spruce	Pine
1971-1985	165	264	148	3.47	6.67	1.68	1.65
1986-1991	211	250	148	3.34	6.97	1.79	2.16

The simulation runs

The above mentioned periods were taken as typical examples for possible height increment deviations as they may occur due to changing climatic conditions. Using the initial data of the 30 years old mixed species stand of Norway spruce and Scots pine six scenarios were simulated. These scenarios are described in Figure 3 by means of the values of q which were assumed for different periods.

The ratio, *q*, serves as a measure of height growth acceleration. In the scenario 0 there is no height growth acceleration assumed, this scenario serves as a "control". Scenario 1 assumes that from age 30 until age 80 the height growth acceleration is the same as it had been observed from the stem analysis data between 1971 and 1986. There the height increments of both, Norway spruce and Scots pine were about 65 % higher than from the stem analyses of Guttenberg would have been expected. In scenarios 2 to 6 the height growth acceleration was higher for Scots pine than for Norway spruce. The values of 2.16 and 1.79 respectively were taken from the stem analysis data in the period from 1986 to 1991. In scenario 2 these conditions are

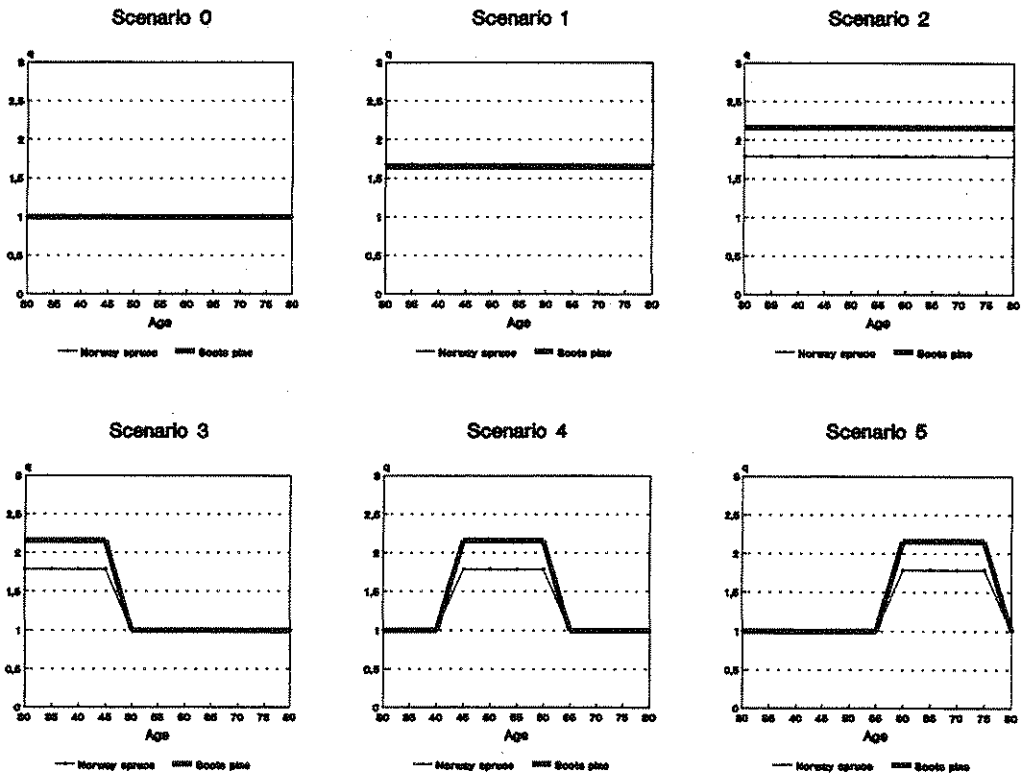

Figure 3: Simulated scenarios with respect to the "height growth acceleration ratios", q, acting during different periods of the stand's age.

assumed to last from age 30 to age 80, in scenario 3 from age 30 to age 45 only. In scenario 4 this height growth acceleration starts at age 45 and lasts until age 60, while in scenario 5 it lasts only from age 60 to age 75.

The overall assumption of these simulation runs was that no thinning was done during the whole period from age 30 to age 80. Only natural mortality sensu Assmann (1956) occurred.

The results of these runs are given in Tables 3 and 4. As it was to be expected, height growth acceleration results in higher final volumes. The longer and the later in the life time of the stand it occurs the higher is the effect in final total volume. On the other hand height growth acceleration increases mortality especially for Scots pine (Table 3), thus reducing final stem number and increasing the average stem volume. Except in the scenarios 1 and 2 where the height growth acceleration lasts from age 30 to age 80 the mean volume of Norway spruce in the final stand will be less enlarged than that of Scots pine. The earlier the period of 15 years height growth acceleration starts the more the mean volume of the remaining Scots pine will be favored compared with that of Norway spruce (Table 4).

Table 3: Main results of the simulation runs by scenarios, Sc, for Norway spruce (Spruce) and Scots pine (Pine).

Sc	Stem number per hectare in age 80			Total volume in age 80 [m^3/ha]				Average yearly mortality in % of stem number		
	Spruce	Pine	Σ	Spruce	Pine	Σ	% Pine	Spruce	Pine	Σ
0	750	150	900	575	88	663	13	3.7	1.4	3.3
1	600	75	675	949	61	1010	6	4.0	2.7	3.9
2	575	100	675	954	91	1045	9	3.1	2.4	3.9
3	600	150	750	688	111	799	14	4.0	1.4	3.7
4	700	75	775	794	68	862	8	3.7	2.7	3.6
5	750	100	850	784	79	863	9	3.6	2.2	3.5

Table 4: The ratio between the average stem volumes of Norway spruce and Scots pine (v_{Spruce}/v_{Pine}) by scenarios.

Scenario	0	1	2	3	4	5
v_{Spruce}/v_{Pine}	1.72	1.94	1.82	1.55	1.25	1.32

DISCUSSION

Relationships between radial- and volume increment on the one hand and precipitation on the other hand have been reported for Norway spruce many times (Schweingruber et al. 1986; Weihe, 1959; Spiecker, 1987, Spiecker 1990). From the stem analysis data we could proof this for height increment of Norway spruce and Scots pine as well. We also found differences in the height growth reaction to precipitation between Norway spruce and Scots pine resulting in two different equations (**1**) and (**2**). While the increment of Norway spruce seemed to depend more on summer precipitation, Scots pine height growth was more influenced by spring precipitation and humidity. These findings get support from the observations of Burger (1926) who found that height growth of Scots pine starts earlier in the year than that of Norway spruce, and the maximum height increment of Spruce occurred nearly one month later (end of June) than of that of Scots pine.

But although the observed deviations from the predicted height growth from Guttenberg's (1896) stem analysis data can be partly explained by climatic changes during the years 1971 to 1991, there are still deviations left unexplained by precipitation and temperature. The remaining deviations are not only random ones. Inserting the precipitation- and temperature data of the "normal year", i.e. the period from 1901 - 1960, into equations (**1**) and (**2**) results in growth acceleration ratios, q, which are distinctly smaller than those for later periods but still significantly higher than 1 (1.26 for Norway spruce and 1.31 for Scots pine). The expectations of height increment have been developed from the original Guttenberg's (1896) stem analysis data which had been won on very nearby sites. So the reason for the observed deviations cannot only be sought in the application of a simply wrong site index system. The fact that this site index system suits well to the new stem analysis data until 1960 gives support to the hypothesis that there are changing site factors since then additionally to the change of the weather records. Similar facts of increasing increments of Norway spruce - not only being due to weather conditions - have been found by Kenk and Fischer (1988) who interpreted this as an effect of nitrogen fertilization by increasing nitrogen deposition. Similar findings for the current volume increment of Scots pine were reported by Pretzsch (1985). He relates these unexpectedly high increments to "improved site conditions after reduced forest litter removal, growth accelerating weather conditions between 1965 and 1970, fertilizing effects of nitrogen deposition and increased atmospheric carbon dioxide concentrations". The combined effect of stopping litter collection and favorable weather conditions on the height growth of Scots pine has been proved already by Schmidt (1969).

So the assumed height growth accelerations in the 6 scenarios may describe some reasonable effects of "site amelioration" and favorable weather conditions. The resulting final volumes had not been unexpected. When the growth acceleration lasted from age 30 to 80 (Scenarios 1 and 2) the increase in final volume was about 55 % compared to an increase in height increment of about 75 % as an average. From those scenarios where only a 15 years period of accelerated height growth was assumed, expectedly the scenario where the growth acceleration started and ended earlier had the smallest increase in final volume.

More unexpected - but reasonable - was the effect of growth acceleration on mortality. As an average the mortality increased by 18 % (3.9 % mortality against 3.3 % of the "control"-scenario 0) in the scenarios with increased height growth from age 30 to 80. In the other scenarios the increase of mortality was the smaller the later in the life time of the stand the period of increased height increment was situated. For all scenarios the increase in mortality was higher for Scots pine than for Norway spruce. Even in the scenarios where the height growth acceleration of Scots pine was distinctly higher than for Norway spruce the mortality of Scots pine increased more than that of Norway spruce. This is sure the effect of the difference in light tolerance of Scots pine which is very light intolerant compared with Norway spruce.

These results suit well to the report on the mortality observed by he national Austrian forest inventory (permanent plots on a grid of 2.75 km x 2.75 km each of them comprising 4 angle counts with a basal area factor of 4 m^2/ha which are revised every 5 years) and the Austrian "Forest-Condition-Inventory" which determines crown transparency classes on 2200 plots with a total of 70,000 trees every year (Neumann and Stemberger, 1990). Table 5 shows the results from the national forest inventory. Since 1970 the total mortality of conifers has increased steadily. And the mortality of Scots pine increased much faster than that of Norway spruce. Note that the absolute figures of mortality cannot be compared between the forest inventory and the projections of the simulator because in Austria the forest owners are obliged by law to remove dead trees from their forests. So the observed mortality observed by

Table 5: Mortality in percent of stem number of a 5-inventory period from the national forest inventory according to Neumann and Stemberger (1990).

	1961-64	1971-75	1976-80	1981-85
mortality of conifers	1.04	1.21	1.26	1.78
Scots pine / Norway spruce mortality	.74	1.04	1.39	1.97

Austrian forest inventory is only a part of real mortality because usually the trees will have been the removed before they died. Nevertheless the tendency supports the results from our simulation runs. Since 1971 the mortality increases and while between 1961 and 1964 the mortality of Scots pine is only 74 % of Norway spruce mortality, in the last period (1981-85) Scots pine mortality is already 1.78 times higher than Norway spruce mortality. The same is true for the yearly observations of the Forest - Condition -Inventory between 1985 and 1989 (Neumann and Stemberger 1990) where the overall mortality increased by a factor of 1.57 and the ratio between pine- and spruce-mortality increased from 1.8 to 4.5 between 1985 and 1989.

Comparing the results of increasing mortality with the observation of an increasing total volume increment in both, our simulations and in the national forest inventory (Schieler and Schadauer, 1993), the interpretations show that both, increasing volume increment and increasing mortality is possible simultaneously. Higher increments may increase competition and thus lead to higher mortality. Scots pine as a light intolerant species may show this effect to a larger extent than Norway spruce.

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PROJECTING GROWTH OF A PROVENANCE TRIAL WITH A DISTANCE-INDEPENDENT INDIVIDUAL TREE MODEL

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ABSTRACT

Eucalypts were introduced in Portugal ca. 150 years ago, at first for mere ornamental purposes. The high productivity exhibited by the genus, in particular by the species *Eucalyptus globulus*, led to its expansion, being the plantation area at present ca. 500,000 ha. The establishment of provenance trials is essential when exotic species become important as plantation forests. Accordingly a set of provenance trials of *Eucalyptus globulus* were established in several sites in Portugal. A randomized complete block design with 37 provenances, 7-9 replications and 5 trees per plot was used in each site. The use of small plots (with one to ten trees) is very common in provenance trials as a consequence of the great number of provenances under test and the need for homogeneous conditions inside each block. These plots are usually considered adequate to provide efficient estimates of means to rank the provenances. Since none of these trials has already reached harvest age provenances must be evaluated on the basis of early height and dbh measurements or future height and dbh predicted with growth and yield models. However the small number of trees per plot brings some problems to the use of growth and yield models. A distance-independent individual tree model for eucalypt plantations was selected to project 2 years height and dbh measurements in one of the above mentioned provenance trials through the rotation age. Several assumptions had to be made in order to allow for the use of the growth model to this type of data: i) mean height and quadratic mean dbh of 5 trees efficiently estimate the corresponding values of a stand; ii) dominant height and quadratic mean dbh of dominant trees can be estimated from mean height and quadratic mean dbh, respectively; iii) provenance affects site index level but not the shape of dominant height growth curves; iv) the same is true in what concerns individual tree growth in dbh. Diameter projections to the age of 4 years were validated against diameter measurements available at 4 years of age and the results did not evidence significant differences between real and estimated values suggesting the likelihood of the assumptions and the adequacy of the growth model to project data from provenance trials.

INTRODUCTION

Eucalyptus spp., exotic trees originally from Australia, were first introduced in Portugal by the end of the last century as ornamental near farmhouses, in roadside plantations or as windbreak. After its introduction it was soon recognized as an interesting species as a consequence of the good environmental conditions for its growth under

intensive cultivation and the high quality of its wood as raw material for pulp. The area of plantations extended slowly until de 1950s but, after that, the area of plantations and the pulp industry grew in parallel, being the plantation area at present ca. 500,000 ha. One of the problems that must be considered when exotic species become important as plantation forests is the establishment of provenance trials. We must guarantee that the genetic quality of the population available for a tree improvement program will give a maximum gain by unit time and also that this population has a gene base broad enough to avoid unwanted inbreedings that may reduce the gain as tree improvement programs move into advanced generations. Accordingly a set of provenance trials to evaluate *Eucalyptus globulus* genetic variation in the portuguese population, to compare it with provenances from the natural and exotic areas, and to evaluate genotype X environment interaction, through observation of survival, growth and cold tolerance, were established in 6 sites in Portugal, from North to South and from coast to inland in the spring of 1985. This paper describes the research that was made in order to investigate if it is possible to use a distance-independent growth and yield model available for the species to get reliable predictions for future tree and stand characteristics from early height and dbh measurements.

METHODS

Data

A provenance trial established in the spring of 1985 at Óbidos, near the coast in central Portugal, was selected in order to investigate the reliability of future tree and stand characteristics predicted with a growth and yield model from early height and dbh measurements. The trial was set up as a randomized complete block design with 37 provenances, 7 replications and 5 trees per plot, in a total of 1295 trees and ca. 1.2 ha (spacing is 3X3 m). The borderline for the trial consists of at least three plantation lines. Replanting was undertaken 2 and 11 months after planting in order to avoid different competition between trees that could affect growth. Height measurements were made with a telescopic pole at 4, 15 and 26 months of age and dbh measurements with a caliper at 26 and 51 months. Table 1 briefly characterizes the trial at the age of 26 months.

Description of the growth model

Two models were available to predict eucalypt plantations growth and yield in Portugal, a whole stand model (Carvalho and Tomé, presented to this meeting) and a distance-independent individual tree model (Tomé, 1988, 1989, 1990; Tomé, 1990). The use of an whole stand model for this purpose was completely out of question, so the individual tree model was selected. This model consists of growth functions, for dominant height growth (site index curves) and individual tree growth in dbh, and prediction equations, for individual tree height and volume estimation (table 2).

Using the growth model to project the growth of the provenance trial

As can be seen in table 2, dominant height, quadratic mean dbh of dominant trees and site index are independent variables in the growth functions and in the individual tree height prediction model. In a plot (block) made up of several sets of 5 trees of different provenances the concepts of dominant height, site index and quadratic mean dbh of

Table 1. Observed mean heights for each provenance at the age of 26 months.

		Block						
Provenance[1]	label	1	2	3	4	5	6	7
P. Bogalheira [P]	1	5.90	6.73	8.85	6.75	6.56	5.87	3.36
NE Mansfield [V]	4	5.51	5.00	4.17	6.27	5.52	4.10	4.40
St. Helens [T]	5	5.86	5.74	6.90	6.98	5.76	6.51	4.82
Rheban [T]	6	4.95	6.09	7.60	6.73	5.37	5.44	4.28
Flinders Is. [N]	7	4.22	4.72	6.59	6.70	4.77	6.84	4.86
Felgueiras [P]	9	4.13	5.10	7.44	6.79	6.36	5.15	4.60
Pepper Hill [T]	10	5.15	6.00	7.93	6.67	6.53	5.23	4.59
Henty River [T]	11	5.62	4.94	7.26	7.74	6.45	5.56	4.68
Swansea [T]	12	5.02	3.86	4.41	5.04	6.03	4.59	3.95
Campus Berkeley [C]	13	5.46	6.84	5.71	7.64	6.28	4.61	4.62
The Barnback [T]	15	5.19	6.17	5.84	6.00	6.00	5.10	4.83
Royal George [T]	16	4.68	5.95	7.29	5.19	5.51	5.55	4.40
Pelverata [T]	17	4.60	6.32	7.34	7.12	6.90	7.04	4.56
DGF [P]	19	4.48	4.54	4.88	7.40	5.55	5.71	7.19
Pontevedra [E]	20	5.18	6.13	8.19	5.51	5.46	4.73	4.63
Seymour [T]	21	6.13	5.04	7.42	5.81	4.93	6.92	4.82
SW Nelligan [N]	22	5.47	5.03	5.93	5.20	5.37	4.91	3.88
Geeveston [T]	23	5.46	7.14	7.44	9.28	6.65	7.04	7.88
Channel [T]	24	5.88	5.78	8.76	7.61	6.40	5.60	5.57
WEE Jasper [N]	25	5.70	4.71	6.16	6.32	5.42	4.26	3.19
Mt. Dromedary [N]	26	5.47	4.61	7.16	5.34	5.36	4.83	3.70
Toombullup	27	5.40	4.48	6.15	5.73	4.66	3.13	3.32
Bruny Isl. [T]	28	4.88	5.27	7.68	5.12	5.80	5.91	4.65
W Batemans Bay [N]	29	4.44	3.58	6.49	4.05	5.65	4.05	3.00
Vila do Conde [P]	31	5.16	6.81	5.26	7.27	6.53	5.95	7.04
Taranna [T]	33	5.29	5.49	6.59	6.91	5.04	5.77	4.76
Myrtle Mtn. [N]	35	3.32	4.47	5.93	2.93	2.25	4.52	4.14
Huelva [E]	36	6.26	6.58	7.41	6.57	5.01	4.89	5.21
S. Traralgon [V]	37	5.71	5.08	5.49	8.71	4.43	4.87	3.84
King Isl. [T]	40	5.33	7.45	4.96	7.69	6.15	5.46	4.59
H. Agolada [P]	41	4.64	5.71	6.84	6.81	6.48	6.53	4.61
Cann Valley [V]	42	5.02	6.20	4.44	6.91	5.84	4.66	3.99
Leprena [T]	43	5.03	4.18	7.14	7.21	5.52	6.02	5.32
Coruña [E]	44	5.36	6.44	7.39	6.62	4.72	5.09	4.38
Calligne Forest [V]	45	7.10	6.12	8.97	6.87	5.75	5.87	4.92
Monte das Flores [P]	48	4.25	6.80	7.46	6.94	5.63	5.18	4.32
Tantawanglo Mt.[N]	49	5.19	5.80	7.58	6.99	4.71	4.26	4.04

[1]More information about the provenances can be seen in Almeida (1993)

[P] Portugal; [E] Espanha; [C] Califórnia; [T] Tasmânia; [N] New South Wales; [V] Victoria

Table 2. Individual tree model used to predict growth of the provenance trial.

1. Growth functions

a) Dominant height growth model or site index curves (Tomé, 1990)

$$hdom_2 = A^{1-(t_1/t_2)^n} hdom_1^{(t_1/t_2)^n}$$

with

$$A = 140.3822$$
$$n = 0.2555$$

b) Individual tree dbh growth model (Tomé, 1989)

Dominant trees:

$$d_2 = A^{1-((t_1-t_0)/(t_2-t_0))^n} d_1^{((t_1-t_0)/(t_2-t_0))^n}$$

Other trees:

$$d_2 = d_1 + ipot.e^{b_0((ddom_1-d_1)^{b_1}/d_1^{b_2}}$$
$$ipot = ddom_2 - ddom_1$$
$$ddom_2 = A^{1-((t_1-t_0)/(t_2-t_0))^n} ddom_1^{((t_1-t_0)/(t_2-t_0))^n}$$

with

$$A = 32.2708 + 0.6926si$$
$$n = 0.5945$$
$$t_0 = 4.8304/si$$
$$b_0 = -0.6442 - 0.0473Bha$$
$$b_1 = 1.3819$$
$$b_2 = 1.1938$$

2. Prediction equations

a) Individual tree height prediction equation (Tomé, 1988)

$$h = hdom(1 + b_1 e^{b_2 hdom})(1 - e^{b_3 d/hdom})$$

with

$$b_1 = 0.1287$$
$$b_2 = 0.0211$$
$$b_3 = -1.7701$$

b) Individual tree volume equation (Tomé, 1990a)

$$v = kd^{b_1} h^{b_2}$$

with

$$k = 0.3104E\text{-}4$$
$$b_1 = 1.7313$$
$$b_2 = 1.2242$$

where $hdom_i$,$ddom_i$ and d_i are respectively dominant height, quadratic mean dbh of dominants and dbh at age t_i; $hdom$, d, h and v are dominant height, dbh, tree height and volume at the present age

dominant trees do not have exactly the usual meaning because they may be (and most probably are) different for different provenances. To solve this problem we assumed the hypothesis that 5 trees provide efficient estimates of the stand mean parameters. For instance the mean height for the 5 trees of a provenance would be a good estimator for the mean height of a stand made up of trees of the same provenance as well as the quadratic mean dbh of the 5 trees in relation to the corresponding measure for such an hypothetical stand. Dominant height and quadratic mean dbh of dominant trees for each provenance were then estimated through linear regressions fitted with data from permanent plots available for central Portugal and previously used to fit the individual tree growth model. These linear models were selected from the output of a all possible regressions algorithm based on the values of several fitting and prediction ability statistics and in the inexistence of multicolinearity. In a final step models that produced less significant differences when predicting individual tree heights at 26 months of age or individual tree dbh at 51 months were preferred to other models with similar characteristics. Basal area per ha was computed on a block basis summing up the sectional areas for each tree inside the block, regardless of the provenance.

The simultaneous measurements of dbh and height at the age of 26 months were used to initiate the projections. Dominant height, site index and quadratic mean dbh of dominant trees for each provenance in each block were estimated from the mean height and quadratic mean dbh computed for the corresponding 5 trees. Height and dbh of every tree in the trial were then updated through the rotation and used to rank the provenances at the end of the rotation as well as to estimate genetic gain. The use of the selected growth model to predict growth in the provenance trial assumes that the basic growth relationships are similar for all the provenances. Particularly it assumes that provenance affects site index level but not the shape of dominant height growth curves and that the individual tree growth in dbh is different but with a similar growth pattern. This type of relationships have been found by some authors. For instance, Buford and Burkhart (1987), using a simple logarithm of height to the inverse of age equation to model dominant height growth of open-pollinated families of loblolly pine established in a progeny test, could find significant differences in level (site index) but not in the shape (slope). Sprinz *et al.* (1989) reported differences in shape as well as level when a more flexible nonlinear height-age model was fit to data from a seed source study for the same species in Arkansas. However Nance and Bay (1979) simulated site index curve shape differences by having early dominant height gains of loblolly pine diminish to zero by age 25 and level differences by having early dominant height gains constant through base age. They found out that, depending on the site index, volume gains were minimal with shape differences, but substantial with level differences.

Validation

Several procedures were used to validate the assumptions implied by the above described methodology. Individual tree height predictions were compared with the corresponding tree heights measured at the age of 26 months, while the dbh's registered at the last remeasurement (51 months) were used to validate the dbh growth predictions Validation was made at the individual tree level both for height and dbh predictions and also at the provenance level (estimated basal area per ha for each provenance in each

block) for dbh growth predictions. The evaluation of predictions at the provenance level is very important because one of the analysis of interest in a provenance trial is the ranking of the provenances according to some variables of interest.

The validation was mainly based on the analysis of the prediction residuals or errors, the differences between the real and the predicted values, and of the percent errors, the prediction residuals expressed as percent of the corresponding observed values. Several statistics were computed with the prediction residuals and with their percent counterparts such as mean, mean of absolute values, minimum, maximum, standard deviation, standard error or some quantiles of the cumulative distribution of the errors. The first two are measures of accuracy while the others can be used for precision evaluation. Maximum anticipated or critical errors, proposed by Bell and Groman (1971) and Ek and Monserud (1979) as alternative to the Freese (1960)'s accuracy test, were also used as measures of model accuracy. Some statistical tests, both parametric and non-parametric were also used to give some more information for the evaluation of the procedure selected to predict the growth of the provenance trial: the paired t-test, the non-parametric sign test and Wilcoxon's signed rank test as well as the simple linear regression of real on predicted values (constant equal to zero and slope equal to one).

Correlation between the prediction residuals and the provenance was also evaluated at the individual tree level through qualitative regression. The model used considered both the block effect as the effect of provenances inside the block. Finally at the provenance level the least squares means estimated during the analysis of variance of the observed basal areas were ranked as well as the least squares means estimated during the same analysis carried on with their predicted values and both rankings were compared

RESULTS AND DISCUSSION

Prediction equations for dominant height and quadratic mean dbh of dominants

The equation selected to predict dominant height was obtained with all the data available (n=1103) even those plots with spacings different from 3X3 m or with different ages. It includes both the stand mean height and the number of trees at planting as independent variables. However quadratic mean dbh of dominant trees was more accurately predicted with equations fitted with a restricted data set excluding the plots with other spacings (n=442). Independent variables selected were dominant height, quadratic mean dbh and age. Both models can be seen in table 3.

Validation

The summary statistics as well as the critical errors for all the variables included in the validation procedure, both at the individual tree level and at the provenance level are shown in table 4. As can be seen all the predictions can be considered unbiased. Although the maximum and minimum observed errors can be considered too large, as well as the mean of the abolute percent errors, the critical errors can be considered acceptable. After a carefull inspection of each one of the large errors it was found that most of the times they correspond to trees with a broken top, forked trees or trees with unexpected observed values (measurement errors?). Aditionally, most of the statistical tests show that the small bias associated with the simulation procedure is not significant from a statistical standpoint.

Table 3. Prediction equations for dominant height and quadratic mean dbh of dominants.

Model	Model quality evaluation
Prediction of dominant height:	
$hdom = b_0 + b_1 hmed + b_2 Npl$	
with	$R^2 = 0.978$
$b_0 = -1.8480$	$rms = 1.112$
$b_1 = 1.1336$	$mapress = 0.790$
$b_2 = 0.0019$	$fiv = 1.003$
	$cond.number = 1.125$
Prediction of quad. mean dbh of dom.:	
$ddom = b_0 + b_1 hdom + b_2 dmed + b_3 t$	
with	$R^2 = 0.978$
$b_0 = 1.0533$	$rms = 0.975$
$b_1 = 0.1773$	$mapress = 0.806$
$b_3 = 0.9808$	$fiv = 13.592$
$b_3 = 0.1437$	$cond.number = 67.685$

where *hdom* is dominant height; *hmed* is stand mean height; N_{pl} is number of trees at planting; *ddom* is quadratic mean dbh of dominants; *dmed* is quadratic mean dbh; *t* is stand age; and R^2 is the coefficient of determination; *rms* is residual mean square; *mapress* is the mean of the absolute values of the press residuals; *vif* is the largest variance inflation factor; *cond.number* is the condition number of the $(X'X)^{-1}$ matrix with the data centered and scaled.

The qualitative regression analysis of the prediction residuals on the provenance (table 6) showed that the predition residuals on individual tree height are not associated with the provenance. However, prediction residuals of predicted individual tree dbh showed a slightly significant (α=0.05) correlation between the model errors and the provenance, meaning that at least for some provenance the assumptions envolved in the procedure used to predict dbh tree growth in the provenance trial are not correct. The application of the Duncan (1955)´s test for multiple comparision of the least squares means estimated through the analysis of variance of the prediction residuals of provenance mean dbh selected the groups of provenances with higher positive differences - 4, 6, 9, 25, 44 - and with higher negative differences - 19, 29, 42, 49.

The comparision of the 10 ´best´provenances according to the ranking of the least squares means estimated through the analysis of variance both of the observed and predicted basal areas at 51 months is presented in table 7. As can be seen the growth model predicted reasonably well the ´best´ provenances. Only one provenance with an observed ranking higher than 10 (provenance 5, with an observed ranking of 12) was included in the provenances ranked with the predicted basal areas. However, according to the Duncan´s test for multiple comparisions this provenance did not differ significantly from the third group included in table 7. From the provenances included in table 7 provenance 49 is the only one pertaining to the groupd with higher predition residuals.

Table 4. Summary statistics of the prediction residuals.

Summary statistics	Individual tree level (n=1211/1201)[1] height (26 mth.) (m)	dbh (51 mth.) (cm)	Provenance level (n=259) mean dbh (51 months) (cm)	basal area (51 months) (m^2ha^{-1})
		Accuracy		
Mean Rp	-0.02	0.042 9A	-0.05	-0.05
Mean Rp%	-1.88	0.63	-0.88	-4.42
		Precision		
Mean ARp	0.47	1.18	0.80	0.52
Mean ARp%	8.83	13.77	8.70	15.78
Min Rp	-2.00	-5.25	-2.80	-1.46
Max Rp	2.33	7.69	1.78	1.83
Stand. dev.	0.60	1.52	0.97	0.64
Stand. error	0.02	0.04	0.06	0.04
		Critical errors ($\alpha=\alpha'=0.05$)		
ε_c	1.14	2.89	1.78	1.17

[1] n=1211 at 26 months and 1201 at 51 months

Table 5. Statistical tests for the prediction residuals.

Variable	Stud. t-test	Regression a	Regression b	Sign test N^+	Wilco. z
		individual tree level (n=1211/1201)[1]			
Height	-0.94	-0.34 **	1.06 **	542 **	-1.87
Dbh	0.82	2.26 **	0.77 **	564 *	-1.04
		provenance level (n=259)			
Mean dbh	-0.78	2.03 **	0.79 **	129	-0.27
Basal area	-1.27	0.10	0.96	118	-1.48

[1] n=1211 at 26 months and n=1201 at 51 months

* significant at the 0.05 level; significant at the 0.01 level

CONCLUSIONS

The objective of this study was to assess the reliability of future predictions made with a distance-independent individual tree model in eucalypt provenance trials. From all the previous analysis we may conclud that foresters can feel reasonably confortable in making decisions based on the analysis of projections obtained with the available growth

Table 6. Acumulated analysis of variance for the qualitative regressions.

Change	d.freed.	s.squares	m.square	seq.F-test	
	individual tree height at 26 months (n=1211)				
+block	6	6.9358	1.1560	3.20	
+block.provenance	252	75.3404	0.2990	0.83	
Residual	952	344.1427	0.3615		
Total	1210	426.4189	0.3524		
	individual tree dbh at 51months (n=1201)				
+block	6	555.104	92.517	51.80	
+block.provenance	252	548.934	2.178	1.22	*
Residual	942	1682.333	1.786		
Total	1200	2786.370	2.322		

* significant at the 0.05 level

model. Of course this study respects only to projections to the age of 4 years, but rotation age in eucalypt plantations is around 12 years of age. More validation of the procedure is needed as long as data from remeasurements at older ages become available. Namely no validation could be made on future heights or volumes beacause no data were available on height for measurements after the age of 26 months. Perhaps a distance-dependent growth model would give better results but at the moment there is no model of this type available for eucalypt plantations.

Table 7. Observed and predicted basal areas[1] (cm^2) at 51 months for the 10 best ranked provenances, ranked in ascending order

Observed basal areas			Predicted basal areas		
Provenance	M.bas.area	Dunc. test	Provenance	M.bas.area	Obs. rank
24	419.7		5	424.3	12
21	422.0		36	428.1	7
10	427.6		24	429.2	10
36	428.1		21	438.4	9
49	431.8		45	448.5	3
1	448.4		10	453.0	8
17	455.1		1	457.5	5
45	459.5		31	462.4	2
31	494.0		17	470.3	4
23	532.0		23	548.5	1

[1] Least squares means estimated through analysis of variance

Some more research on the inclusion of genetic information on growth models would be very useful in order to allow for shape variation in the growth functions due to provenance. However data for this type of models willonly be available after the existing

trials get the rotation age. Anyway the type of trial is not the more convenient for growth model building!

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EMPIRICAL PREDICTION MODELS FOR DOUGLAS-FIR RESPONSE TO NITROGEN FERTILIZATION

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ABSTRACT. A stand nitrogen-response prediction model was developed for interior Douglas-fir in northern Idaho. The percent gross volume response was expressed as a function of two rates of nitrogen treatments, stand characteristics, and interaction between site index and stand density. Higher response occurs at low density and/or low site index. Douglas-fir vegetation series has the largest percent response, followed by grand fir series and redcedar or hemlock series, for the same level of treatment. For stands with the same vegetation series, 400 lb N/acre treatment produces higher response than 200 lb N/acre treatment.

INTRODUCTION

Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn) Franco) is an important tree species in northern Idaho due to its large existing volumes, growth potential, and commercial value. Recent studies conducted by the Intermountain Forest Tree Nutrition Cooperative (IFTNC) have shown that interior Douglas-fir significantly responds to two rates of nitrogen fertilizer (Mika and Vander Ploeg 1991, Moore et al. 1991). Across the area, 6-year gross volume growth was increased by 15.8% and 22.7% on plots fertilized with 200 lb N/acre and 400 lb N/acre, respectively, over unfertilized plots. In addition, trees on 400 lb N/acre treated plots grew significantly more than those on 200 lb N/acre treated plots. Shafii et al. (1989) found that fertilization (200 lb N/acre) increased mean tree cubic volume by 14% for unthinned stands over a 14-year period without significant reduction in total cubic volume per acre. In another study, individual-tree diameter growth models were developed for nitrogen-fertilized Douglas-fir stands in northern Idaho (Shafii et al. 1990). They found that initial tree size and initial stand density produce significant interactions on an individual tree's response to fertilization. However, there are no published whole-stand

nitrogen-response models in this area. Therefore the primary objective of this study was to quantify nitrogen fertilization response at whole-stand level for even-aged, managed interior Douglas-fir in northern Idaho.

DATA AND METHODS

The data were obtained from 19 installations in northern Idaho established by IFTNC from 1980 to 1982, representing second-growth, even-aged, managed Douglas-fir stands. Each installation consisted of six square plots (0.1 acre) selected to minimize among-plot variation. Three fertilization treatments, 0, 200, and 400 lb N/acre (1 lb = 454 g, 1 acre = 0.405 ha), were randomly applied to two plots, respectively. Fertilized plots were surrounded by a treated buffer strip to reduce edge effects. All live trees were measured for diameters for a 6-year growth period. Heights were measured for all trees at the time of treatment. At year six, heights were measured on a stratified random sample of plot trees. Six-year heights for unmeasured trees were estimated using plot-specific regression equations. Tree volumes were estimated using individual tree volume equations in the Stand Prognosis Model (Wykoff et al. 1982). Most of these stands had been thinned 5-12 years prior to fertilizer treatments; other stands were unthinned, but naturally well-spaced. Pretreatment stand characteristics for the 19 Douglas-fir installations are provided in Table 1.

Six-year gross volume increment was estimated using a covariance model in which the initial basal area was the covariate variable (Mika and Vander Ploeg 1991). Percent gross volume response (RESPONSE %) was calculated as follows:

$$\text{RESPONSE \%} = 100*[GVI_{treat} - GVI_{control}] \ / \ GVI_{control} \qquad (1)$$

where GVI_{treat} is 6-year gross volume increments for the treated plots (either 200 lb N/acre or 400 lb N/acre), and $GVI_{control}$ is 6-year gross volume increments for the control plots.

A prediction model was developed to model percent gross volume response to two rates of nitrogen fertilization for Douglas-fir in northern Idaho. The percent gross volume response (RESPONSE %) was expressed as a function of nitrogen treatments and other stand characteristics. The resulting model was as follows:

$$\text{RESPONSE \%} = F\ (\text{TREAT, SERIES, DFSI, TOPH, TPA, GFCOMP, DFSI*TPA}) \qquad (2)$$

Table 1. Averages and ranges of stand characteristics at the beginning of a 6-year growth period for 19 Douglas-fir installations in northern Idaho.

Characteristic	Mean	STD	Min	Max
Site index (ft @ 50 year)	83	9	66	96
Stand total age (year)	49	17	27	88
Trees per acre	351	138	150	702
Top height (ft)	75	15	49	102
Basal area (ft^2/acre)	165	45	92	256
Total volume (ft^3/acre)	4432	1792	1625	7987
Grand fir composition (BA%)	8.5	7.8	0	23.3

where:

TREAT = fertilization treatments, 1 if 200 lb N/acre, 2 if 400 lb N/acre.
SERIES = vegetation series, 1 if Douglas-fir series, 2 if grand fir series, 3 if redcedar or hemlock series.
DFSI = Douglas-fir site index (ft).
TOPH = stand top height at the beginning of the 6-year growth period (ft).
TPA = trees per acre at the beginning of the 6-year growth period.
GFCOMP = grand fir composition in percent basal area.

Ordinary least-squares was used to estimate the parameters of the model. Residual analysis was conducted to examine the adequacy of the model and to test for violations of statistical assumptions.

RESULTS AND DISCUSSION

Response Prediction Model

The model statistics and parameter estimates of the response prediction model (Equation (2)) are provided in Table 2. Residual analysis indicated that there was no detectable pattern for residuals versus predicted percent gross volume response. The results showed that Douglas-fir vegetation series has the largest percent gross volume response, followed by grand fir series and redcedar or hemlock series, for the same level of treatment. If stand top height increases, percent response decreases. Within a stand, response increases as grand fir composition (in percent basal area) increases because grand fir shows larger

Table 2. Model statistics and parameter estimates of the nitrogen-response prediction model for Douglas-fir in northern Idaho.

SOURCE	DF	SS	MSE	F	PR > F
MODEL	8	5139.05	642.38	4.86	0.0007
ERROR	29	3832.69	132.16		
C TOTAL	37	8971.75			

R^2=0.5728 C.V.=55.35 RMSE=11.49 RESPONSE% MEAN=20.77

PARAMETER		ESTIMATE	T	PR >|T|	STD
INTERCEPT		-50.8354	-0.78	0.4410	65.07
TREAT	1	-6.1153	-1.64	0.1119	3.73
	2	0.0000	.	.	.
SERIES	1	10.9345	1.97	0.0583	5.55
	2	6.8691	0.93	0.3616	7.41
	3	0.0000	.	.	.
DFSI		1.3401	1.82	0.0798	0.74
TOPH		-0.4218	-2.62	0.0138	0.16
TPA		0.4511	2.59	0.0148	0.17
GFCOMP		1.1272	3.36	0.0022	0.34
DFSI*TPA		-0.0060	-2.92	0.0067	0.002

relative response than Douglas-fir. In general, increasing site index and stand density has a negative effect on percent gross volume response. In order to investigate the effects of site quality and stand density interaction on percent gross volume response, simulations were conducted as follows.

Simulations of the Response Prediction Model

The prediction model of percent gross volume response for Douglas-fir in northern Idaho had six predictor variables and an interaction term of site index and stand density. To evaluate the trends of percent gross volume response across site productivities and stand densities, simulations were conducted under the following stand conditions: two nitrogen treatment levels (200 lb N/acre and 400 lb N/acre); two vegetation series (Douglas-fir series and grand fir series); grand fir composition in percent basal area and stand top height were set at the averages in this area; Douglas-fir site index ranged from 75 to 95 ft, and trees per acre varied from 200 to 600 trees per acre. The simulation results were plotted on response surface graphics for the combinations of the two treatment levels and two vegetation series (Figure 1). The simulations are described and interpreted as follows:

Higher response occurs at low stand density and/or low site index. Lowest percent response will be obtained if both site index and stand density are high. For high site index, stand density should be less than 300 trees per acre for 200 lb N/acre treatment and Douglas-fir series if 30% gross response is expected (Figure 1(a)). For poorer site quality (e.g. site index equals 75), 30% gross volume response can be achieved across a wider range of stand densities. Similar trends of response were observed for two rates of nitrogen treatments and two vegetation series. However, Douglas-fir series has larger response than grand fir series for the same level of the treatment (Figure 1(a) vs. 1(b), and Figure 1(c) vs. 1(d)). For stands with the same vegetation series, 400 lb N/acre treatment produces higher response than 200 lb N/acre treatment. Also higher level of nitrogen treatment (400 lb N/acre) allows wider ranges of site indices and stand densities than 200 lb N/acre for the same predicted response (Figure 1(a) vs. 1(c), and Figure 1(b) vs. 1(d)).

The discussion above was based on percent gross volume response to nitrogen fertilization. If the percent response is translated to absolute response, total volume gain due to fertilization should be considered. For example, although poorer sites may have higher percent response to nitrogen fertilizer, the absolute volume response may be smaller than good sites since growth rates will be greater on better sites. Incorporating these response models into a simulation model will provide a convenient way to evaluate relative versus absolute fertilization response.

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ACKNOWLEDGMENTS

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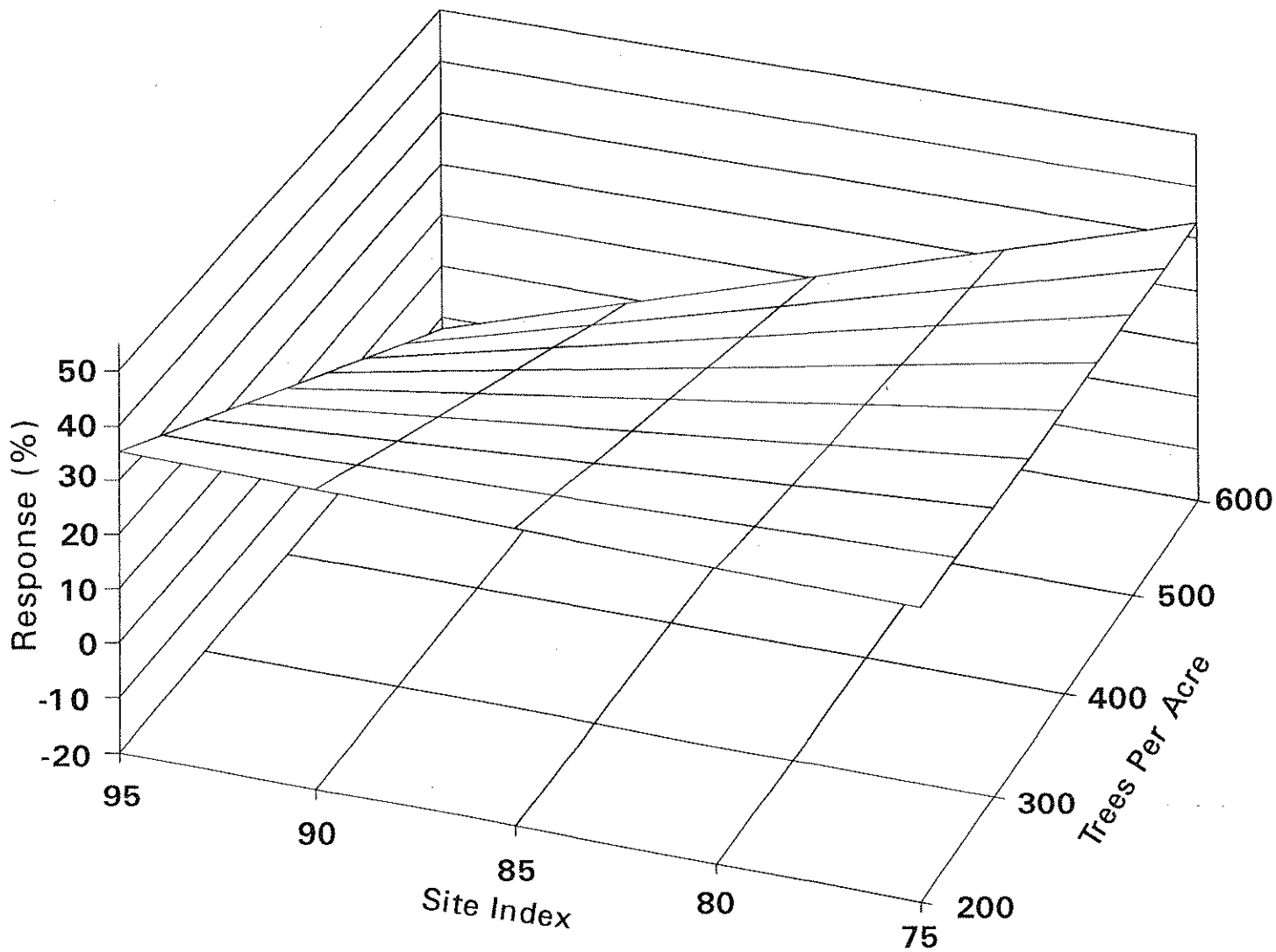

Fig. 1(a). Gross percent volume response to N fertilization for north Idaho: 200 lb N/acre and Douglas-fir series.

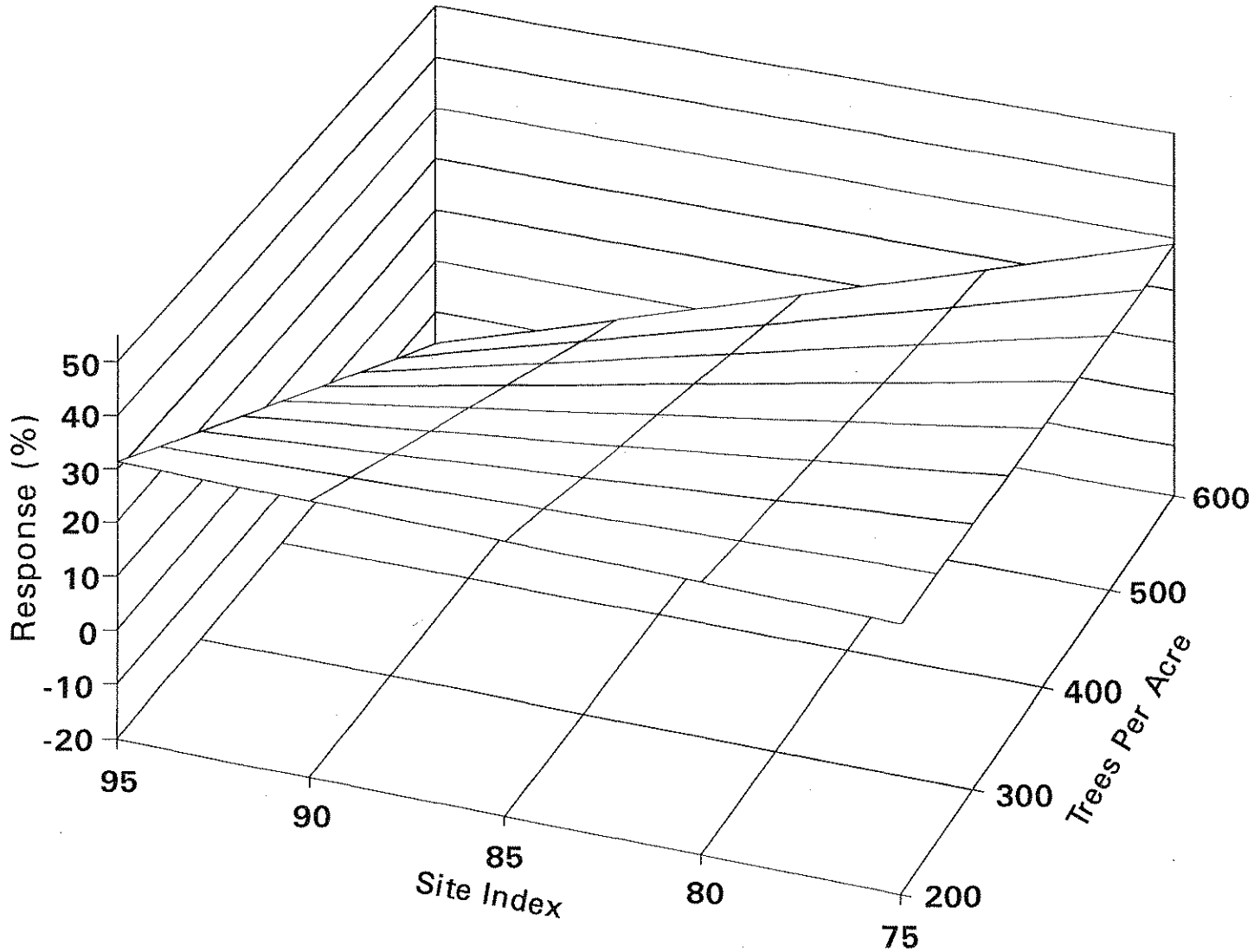

Fig. 1(b). Gross percent volume response to N fertilization for north Idaho: 200 lb N/acre and Grand fir series.

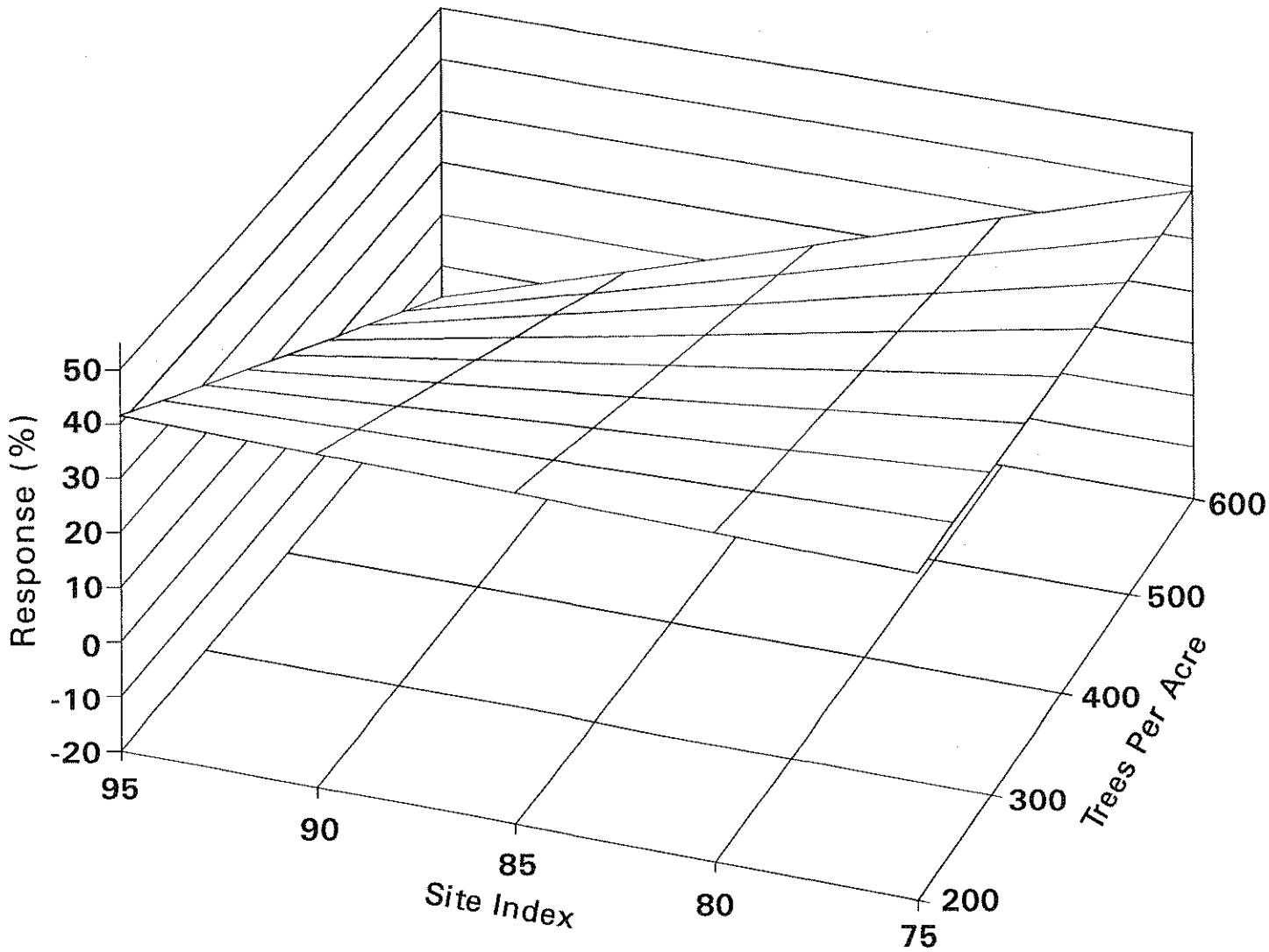

Fig. 1(c). Gross percent volume response to N fertilization for north Idaho: 400 lb N/acre and Douglas-fir series.

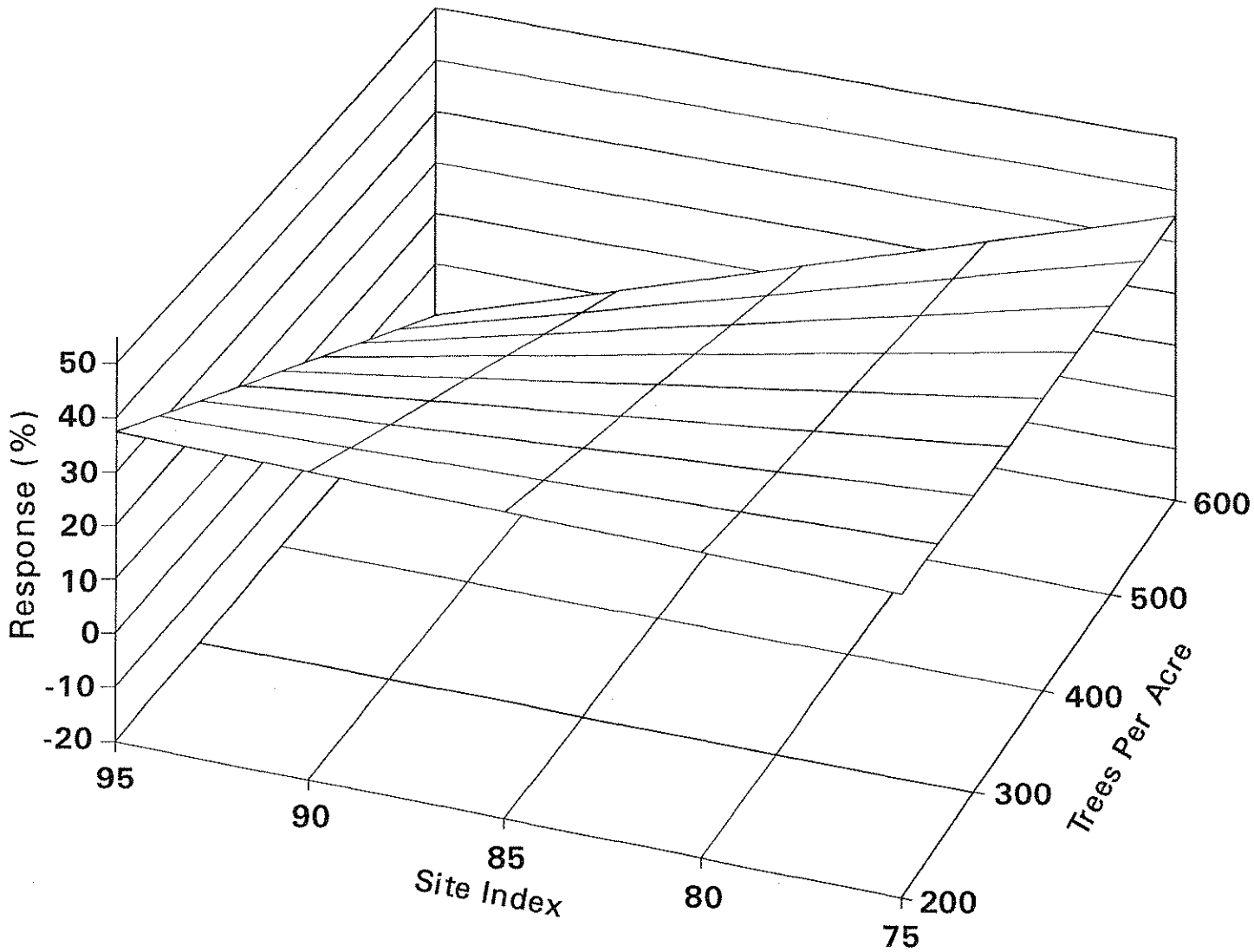

Fig. 1(d). Gross percent volume response to N fertilization for north Idaho: 400 lb N/acre and Grand fir series.

SIMULATION OF EFFECTS OF THINNING ON LIGHT AVAILABILITY

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Thinning is a powerful tool for forest managers to influence forest development. After thinning, the trees in the remaining stand will benefit from the increased resource availability. However, this increase is difficult to quantify. Evaluation of thinnings is usually based on the effects of the increased resource availability (e.g. volume increments). Aim of the present study was to quantify the effects of low and crown thinnings and thinning intensity on light availability and interception.

A spatial model, FORFLUX, was developed that simulates light interception by individual trees in a stand. For reasons of convenience here diffuse light conditions were assumed. Two regularly spaced Scots pine stands were simulated to examine thinning influences on the light availability of single trees, and on the total amount of intercepted light.

Simulation showed that light availability for single trees is not only influenced by the presence of the nearest neighbour trees but also by more remote neighbours. Hence, when selecting future trees, foresters should pay attention to these competitors as well.

Varying the thinning intensity revealed that the decrease of the amount of intercepted light was relatively smaller than the loss of leaf area. Crown and low thinnings differed in total stand amount of intercepted light as well as in light distribution between individual trees.

The study confirmed that thinnings have large impact on forest development, as they strongly influence light competition relationships between trees. To compare management options, simulation models form helpful tools by quantifying effects, in terms of potential stand production as well as of individual tree growth.

A WHOLE STAND GROWTH MODEL FOR EUCALYPT PLANTATIONS

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ABSTRACT

Eucalyptus spp., exotic trees originally from Australia, were first introduced in Portugal by the end of the last century as ornamental near farmhouses, in roadside plantations or as windbreak. After its introduction it was soon recognized as an interesting species as a consequence of the good environmental conditions for its growth under intensive cultivation and the high quality of its wood as raw material for pulp. The area of plantations extended slowly until de 1950s but, after that, the area of plantations and the pulp industry grew in parallel, being the plantation area at present ca. 500,000 ha. The substantial expansion of the pulp industry in the last years, presumably not covered by the annual area of new plantations, suggests that the availability of eucalypt wood for industry supply is becoming increasingly crucial. In order not to be caught in a forthcoming deficit situation, the Association of Pulp Producers in Portugal (ACEL) has been monitoring eucalypt areas and volumes through continuous forest inventories since 1985 in order to obtain updated information of the eucalypt resource which can be used to make long term forecasts of available volumes for the industry. A whole stand growth model is an essential tool if we want to have reliable forecastings of future wood availability, based on forest inventory data. So there is a research project going on in cooperation between ACEL and the Dept. Forestry in Lisboa to develop such a model using available information on eucalypt growth. A preliminary version of this model allowing for the simulation of eucalypt growth under different environmental conditions (coastal or inland) and with different initial spacing is already available. The model includes: i) polymorphic non-disjoint site index curves; ii) a basal area growth model; iii) a total volume prediction equation. A rough description of the three model components as well as of the methodologies and data base used in obtaining them are presented in this poster. Some information is also given on the results of a series of tests that were carried out as model validation. The model can be used as an interactive PC version in QUICK BASIC or implemented as a FORTRAN subroutine used in a computer program to project forest inventory data.

RESPONSE SURFACE APPROACH FOR EXAMINING EFFECTS OF COMPETING VEGETATION ON LOBLOLLY PINE GROWTH

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ABSTRACT

A loblolly pine (Pinus taeda L.) plantation study has been installed across the Southeastern U.S. by members of the Auburn University Silvicultural Herbicide Cooperative. The study is designed to quantify and model the effects of controlling competing vegetation on long-term pine growth. A matrix of initial stand conditions was established encompassing three site index classes, six plantation ages (0-5 years), four hardwood rootstock density classes (class limits vary by age), and absence or presence of herbaceous weed control.

Five 0.13 ha (0.33 ac) treatment plots with 0.06 ha (0.15 ac) measurement plots were established at each location, with variation among plots controlled by sampling and matching of plots on the basis of pre-treatment pine and hardwood tree and stand attributes. Each plot was selected for no treatment (check), total hardwood control for one year, or some level of intermediate hardwood control (one-time treatment by basal spray of herbicide). Herbaceous weed control was combined with hardwood control for selected treatments at selected locations.

The study uses a response surface approach and will be analyzed by developing growth response models for various pine and hardwood tree and stand attributes as a function of the design variables. As of 1993, most of the 56 locations have reached plantation age five. More than half will reach age 8 by 1994. Response to herbaceous weed control has been dramatic, but only weak response trends have developed at age five for levels of hardwood control. Response trends to hardwood control are long-term in nature and expected to become more evident by plantation age 8.

Models developed from this study will allow managing foresters to better evaluate the biological and economic outcome of vegetation control decisions. Submodels will be developed for inclusion into existing growth and yield models. Data can also be shared with participating companies and growth and yield cooperatives in the Southeastern U.S. to allow current and future models to incorporate experimental study-based vegetation control response information into growth and decision models.

INTER PROVENANCES VARIATION IN INDIVIDUAL TREE TAPER AND VOLUME ALLOMETRY

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ABSTRACT

A set of provenance trials to estimate *Eucalyptus globulus* genetic variation in the portuguese population, to compare them with provenances from the natural and other exotic areas, and to evaluate genotypeXenvironment interaction, were established in several sites in Portugal in the spring of 1985. Each trial was designed as a randomized complete block design with 37 provenances, 7-9 replications and 5 trees per plot. Survival, growth and cold tolerance were registered at several ages. Growth of the different provenances was evaluated through direct measurement of individual tree height and dbh. Estimated individual tree volume was also selected as an important variable, because the greater economic values are associated with the higher yields in volume per hectare. The use of a volume equation available for industrial stands is questionable because it assumes that tree taper and allometry is the same for all provenances. To verify this hypothesis some data on taper of individual trees were gathered in one of the provenance trials. Every standing tree from each one from 6 selected provenances, including the faster and the slower growers, was object of mensuration, in a total of 194 trees, ca. 35 per provenance Tree diameter at breast height and at 15 and 50 cm were measured with a caliper. Total height, height to and diameter at the base of live crown as well as one or two diameters at heights between the breast height and the crown were measured with a Bitterlich telerelaskope. Analysis of variance of crown ratio, stability coefficient (dbh to total height ratio) and tree form coefficient evidenced significant differences between provenances. The same conclusion could be drawn through the analysis of multiple allometric relationships between volume and dbh and total height fitted with nonlinear regression techniques to all data and separately to data from each provenance.

DYNAMICS OF UNEVEN-AGED FORESTS

FROM A VIEW POINT OF BASAL AREA BY DIAMETER CLASS

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ABSTRACT

Stand growth of natural or uneven-aged forests can be described in a variety of ways. The stand structure of Uneven-aged forests is complicated and heterogeneous, and the spatial arrangement varies in age, size and species. Furthermore, two factors make it difficult to understand the law about stand growth of uneven-aged forests ; one is mortality and the other is ingrowth. So further research connected with stand growth of uneven-aged forests has been mainly carried out by means of observational data, some distribution functions and transition probability. In this study, it is assumed that solar energy is first absorbed into upper story trees and next absorbed into middle and lower story trees in turn. Utilization of solar energy produces an increase of basal area in the living trees. If the crown of upper story trees is closed, self-thinning occurs between upper story trees, and if not, it occurs between middle or lower story trees. When the crown isn't quite closed, ingrowth trees are able to grow into lower story which is measurable. The aim of this study is to describe dynamics of uneven-aged forests in terms of basal area by diameter class using a system of liner ordinary differential equations. Data of boreal natural forests of Japan under selective cutting is utilized for deciding some parameters of these equations.

A PERMANENT SAMPLE PLOT DATA BASE FOR MODELLING EFFECTS OF SILVICULTURAL PRACTICES ON THE GROWTH AND YIELD OF NORWAY SPRUCE AND OAK IN DENMARK

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ABSTRACT

Objective

A permanent sample plot data base is currently being established with the main objective of modelling the growth and yield of Norway spruce (*Picea abies* L.) and oak (*Quercus robur* L. and *Quercus petraea* Liebl.) in Denmark. The models will include spacing and thinning regime (type and intensity) as variables, and will provide information on the assortment distribution of growth and yield.

Material

Denmark has a long tradition of monitoring forest growth and yield. The first plots were established over 100 years ago as observation plots with no alternative treatments and no replication. Later, sample plots were established more systematically within an experimental design. They include different spacings or thinning regimes as well as a range of other silvicultural practices. So far, data have been compiled as handwritten notes, and have only been available in that form. Converting and transferring original observations to a computer data base involves reorganizing and evaluating data.

Data base structure

The data base include information at 4 levels:

(1) General information on the sample plot (climate, soil, flora etc.).
(2) Stand level information on each plot (volume factors, current and periodic increments, etc.).
(3) Information on groups of trees (diameter classes, height samples, thinnings, damaged trees (wind, storm and snow damages, attacks by insects and fungi), etc.).
(4) Individual tree level information (breast height diameter, height growth, form factor investigations, stump diameters, bole heights, crown details, stem maps etc.).

Data quality

The data base includes some 80 Norway spruce sample plots (280+ plots) and some 60 oak sample plots (120+ plots) comprising a variety of different thinning treatments ranging from unthinned control plots to extremely heavily thinned shelterbelts, and a variety of spacings. Generally the sample plots have been treated according to specified standards, and have been measured at regular intervals throughout the rotation period. Measurement procedures remain practically unchanged since the 1880's. Vanclay et al. (1993) evaluated the data base for Norway spruce in relation to the national forest estate. They concluded that this part of the material covers most of the growth conditions encountered in Denmark, but that some remedial sampling could be beneficial.

Research potential

The primary objective of this quite comprehensive data base is growth and yield modelling for forest management. Other possible research areas are process oriented growth models, short and long term effects of climate changes on growth and yield (both at the forest level and at the individual tree level), effects of silvicultural practices on crown structure and development, and influence of species as well as silvicultural practices on soil development. International cooperation and data exchange will expand the research potential.

Acknowledgements

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SIMULATING TWO HARVESTING STRATEGIES IN MIXEDWOOD FOREST TYPES ON SPRUCE-FIR HABITAT WITH FIBER 3.0

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Eight spruce-fir stands from permanent growth plots were selected to make four simulations of two cutting practices using FIBER 3.0. When either softwoods or hardwoods, or both, were cut, stands on spruce-fir habitat exhibited a strong tendency to remain or return to softwood stands. Hardwood ingrowth did not exceed 20% of the stand basal area (square feet) over the 140 years.

The objectives were:

- to simulate yields from diameter-limit cutting and thinning from below.
- to compare yields when partial removal of hardwoods was included with the two cutting regimes.

For each simulation, an initial cut created a mixedwood stand with 50% of the residual stand basal area in hardwoods. A 30-year cutting cycle was used. After three harvests, either all trees down to 10 inches d.b.h. (diameter limit) or trees 5 to 8 inches d.b.h. (thin from below) were removed.

Volumes (standing plus harvest) showed that diameter-limit cutting yielded more than twice as much board-foot volume (43977 bf, s.e.=3186) than did the thinning from below (18445 bf, s.e.=1438). The diameter limit, likewise, nearly doubled the cubic-foot volume yield (9692 cf, s.e.=457) over that of the thinning from below (5894 cf, s.e.=256). While not statistically significant, under hardwood management, the average cubic-foot yield increased from 8766 cf (without hardwoods) to 10618 cf and board-foot yield increased form 38233 bf to 49722 bf. This increased volume was accompanied by a shift from mixedwood to softwood forest type.

THE 3/2 POWER LAW IN LIGHT OF SYSTEMS THEORY

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SUMMARY

This paper is intended to discuss some aspects of the self–thinning model which was developed by the author. First, a logarithmic linear system of the simultaneous differential equation is introduced for describing the relationship between stand density and stand characteristics , such as mean DBH, mean height ,mean stem volume,stand volume and stand basal area and so on. The model is compared with the other growth ones in terms of growth modeling. Second, it is examined on the basis of growth data taken from unthinned experimental plots. Then, some considerations of the model are given from the mathematical and ecological point of view. It indicates that the model is a generalization of the GOMPERTZ equation and the 3/2 power law associated with self–thinned stands , and that the "full density curve" concept can be regarded as a kind of eigenspace in terms of linear algebra. Finally, a comparison among many interpretations of the 3/2 power law is made, showing that the model is more synthetic than the other growth ones describing the self–thinning process.

VOLUME GROWTH IN RESPONSE TO STAND STRUCTURE IN CONIFEROUS PLANTATIONS

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SUMMARY

This paper deals with modelling the growth process in response to stand structre in a pure even-aged stand in terms of stand and tree volume growth. First, the following assumptions are made: (1) The maintenance respiration rate in a stem is proportional to 2/3 power of its volume, and the construction respiration rate in a stem is proportional to the growth rate of its volume; (2) In a stand, the net photosynthesis rate in a tree is proportional to the n-th power of its stem volume, and the distribution ratio of surplus production in leaves to stems is constant; (3) In closed stands, the net photosynthesis rate per unit area is constant, and it is dependent only on species and site; (4) In open stands, the net photosynthesis rate per tree is proportional to the β-th power of average stem volume per tree and the proportional coefficient depends on thinning. Next, the growth equations for stand volume V and tree volume v are derived as follows on the basis of these assumptions and analyses of measurements on plantations of sugi(*Cryptomeria japonica*) and hinoki(*Chamaecyparis obtusa*): $dV/dt = A - b\ \Sigma v^{2/3}$, $dv/dt = A\ v\ /\ V - b\ v^{2/3}$ when the canopy is closed and $dV/dt = \alpha A\ V^{\beta} N^{1-\beta} - b\ \Sigma v^{2/3}$, $dv/dt = \alpha A\ V^{\beta} N^{1-\beta}\ v^{n}\ /\ \Sigma v^{n} - b\ v^{2/3}$ when the canopy is open, where N is stocking, A is a constant dependent on species and site, b is a constant dependent on species, and n is a positive number smaller than 1. Moreover, it follows from the assumptions that the equation $\log V + (1 - \beta) / \beta \log N = -\log\alpha / \beta$ holds between stand volume and stocking, when the canopy closes. Assuming that β is a constant dependent on species, α is determined by stand structure before and after thinning.

MANAGEMENT OF NORWAY SPRUCE IN MULTI-COHORT, MIXED STANDS AND SINGLE TREE SELECTION

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ABSTRACT

Norway spruce is widely grown in pure and mixed stands in the Northern Boreal forests. The ecologically flexible climax species allows for a variety of management options.

The emphasis of growth modelling has been on stands with homogenous structures. The need to model regeneration, survival and growth in stands of multi-cohort, mixed structures is obvious. This is the objective of a series of current studies.

Norway spruce tends to form cohorts of advance growth and two-storied structures in admixtures with pioneer species. Single tree growth models and size distribution models are applied to describe the large variety of feasible stand structures. The obvious multitude of treatment options necessitates the application of models with distance dependent competition measures. However, simple stand variables have also been feasible if the tree cohorts are uniform.

Models with distance-dependent competition indices have been applied with promising results in describing growth in selection systems. On the contrary, regeneration and mortality are controlled by very many interactive ecological factors. Their spatial and temporal variations are not readily accounted for in models based on statistical inference from tree and stand attributes. Our knowledge of the ecology of selection forests in order to identify model components and validate model structures seems to be insufficient, and the theoretical formulation for the regulation of structural dynamics deserves further development.