Designing Mixedwood Experiments

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Multi-species Competition: Studies at the University of Minnesota

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ABSTRACT

This paper provides a brief summary of two mixed species competition studies under way at the University of Minnesota, USA.

MULTI-SPECIES COMPETITION STUDIES

Competitive pressure is perhaps the strongest non-disturbance phenomenon that determines plant growth and survival and thus affects productivity of crop plants in agricultural and forest ecosystems. Competition can be separated into two components: the usurpation or pre-emption of resources, and the tolerance or response to a reduced availability of resources due to pre-emption by competitors.

In managed forest and agricultural ecosystems the outcome of competition is evaluated at several stages (e.g., thinning operations) and is most important at the time of harvest. Under most conditions, light and nutrient availability to *individual plants* is greatest soon after disturbance (harvest, fire, wind) during the regeneration phase. On moderate to fertile sites, species that can pre-empt resources and utilize them will dominate during this early phase. Species tolerant of low resources will persist until resource levels decrease to a point below which the growth of fast-growing species is reduced. While the combination of species and resource availability determines the potential competitiveness of a species, the competitive conditions and performance of individual plants are also determined by neighbouring plants.

To investigate the physiological basis of multi-species competition and to provide a framework for other long-term studies, we established two related studies: 1) a 3-species addition series; and, 2) a 10-species random mix.

The studies are located on the Cloquet Forestry Center (CFC) of the University of Minnesota in northern Minnesota, located approximately 32 km southwest of Duluth. The climate is cold-temperate, continental; the boralfisol soils are Omega and Cloquet series.

Experiment 1 is an addition series of three species (tamarack, white pine, and black spruce) and was planted in 1992 in monoculture and in row mixtures of two species combinations (tamarack/white pine, tamarack/black spruce, white pine/black spruce) at each of five planting densities (12.5, 25, 50, 100, and 200 cm between seedlings). Plots with spacing less than 2 m were replicated three times and plots with 2 m spacing were replicated twice. This design will examine the response of these species with respect to growth and resource depletion.

Experiment 2 is also a long-term experiment using a random-mix design with three replicates of 10 species (white spruce, black spruce, white pine, jack pine, balsam fir, tamarack, yellow birch, red oak, sugar maple, aspen) at four planting densities (25, 50, 100, and 200 cm between seedlings). This study is located adjacent to Experiment 1 on both field sites and on the St. Paul campus. In this study we will examine the response of individual trees to a range of competitive conditions, provided by the different neighbourhood species compositions. Both experiments utilize approximately 25 000 saplings in 127 plots, all of which are mapped, allowing measurements to be linked to specific individual plants (and plant neighbourhoods).

A subsample of trees will be destructively harvested and allometric relationships determined to enable us to estimate total plant Relative Growth Rate. Portable infrared gas exchange systems will be used to measure rates of net photosynthesis and dark respiration under average growth conditions, *in situ*, on a subset of seedlings from each of the studies. Within the random mix plots, height and stem diameter of all seedlings were measured while a stratified subsample of 15% was used in the addition series experiment. Baseline height and diameters were measured in the fall of 1993 and re-growth measurements were done in the fall of 1994. Baseline foliar nutrient samples were collected in July 1994. Baseline soil nutrient status was determined in a full year cycle of three sampling dates (fall, spring, and mid-summer) in all plots. Results to date show no measurable effect of spacing or species composition on sapling growth. However, the trees in the highest density were just reaching canopy closure at the end of the 1994 field season.

Future work on both of these studies will include examining the physiological traits that lead to competitive advantages within the multi-species framework. We will focus initially on the ability to capture resources and the efficiency of resource utilization by using techniques such as nutrient labelling, residence time and nutrient use efficiency, allometry, and carbon allocation. This study also provides a long-term framework for additional research by graduate students, visiting faculty, and post-doctoral fellows.

Problems in Modelling Growth of Mixtures Using Data from Temporary Sample Plots

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ABSTRACT

Since the 1920s, the forests of Finland have been inventoried eight times. The tens of thousands of sample trees provide an excellent basis for both growth modelling and calibration of the models. Even with the best growth models, non-biased results are only possible for those stands for which real data exist. Growth models can be divided into three categories: stand models, single-tree models, and process models. Each of these modelling categories has its own uses and limitations. Finnish growth and yield modellers are attempting to model even-aged mixed stands of Scots pine and birch and Norway spruce and silver birch; and uneven-aged stands using both growth and mortality, and regeneration models.

INTRODUCTION

The sustainable use of forest resources pre-supposes non-biased estimates of the wood production of forests within large regions. The growth models applied must be capable of predicting the future yield of young and old, pure and mixed stands growing on all kinds of sites.

On a regional basis, the best material for the formulation of non-biased growth models is provided by inventory plots based on objective sampling. Since the 1920s, the forests of Finland have been inventoried eight times. The tens of thousands of sample trees provide an excellent basis for both growth modelling and calibration of the models.

Even the best growth models give non-biased results only for the population from which the data are collected. The only way to determine the impact of new forest treatment systems (e.g., thinning, fertilizer application, drainage) and environmental changes on increment growth is through establishing experiments.

Permanent purpose-designed experiments have one shortcoming: they are longterm. By the time these experiments begin to yield results, the operational treatments are usually obsolete (old-fashioned). The lack of inventory data and the time required for permanent experiments have led to a situation in which most growth models are based on subjectively selected temporary sample plots.

CATEGORIES OF GROWTH MODELS

Models available for predicting growing stock increment may be divided into three categories: stand models, single-tree models, and process models.

The simplicity of stand models is both their advantage and disadvantage. The predicted development of stand characteristics can be presented either in table form or calculated using a pocket calculator. Stand models fail to provide us with a complete picture of stand structure.

The advantage of single-tree models is that they automatically provide us with an estimate of the future development of every tree in the stand as well as the yields of different timber assortments. Spatial single-tree growth models are able to take into account the competition from the rest of the ecosystem. However, instead of depicting growth processes, competition indexes are "artificial" and data-specific.

The purpose of using process models is to gain more in-depth knowledge of the growth processes in trees than can be provided by either of the other two model types. The biomass produced in photosynthesis is divided among the different tree components, which enables us to examine the growth of the various tree dimensions, too. At present, process models are too complicated, in terms of both the data required and model programming, to be applied in forest management planning.

MODELLING GROWTH OF EVEN-AGED MIXED STANDS

Scots Pine and Birch

In Finland, Scots pine and birch, both shade-intolerant species, form single-storied stands following forest fires, storms, and clear felling. The growth of mid-rotation and mature mixed stands of pine and birch is the easiest of all mixed stands to model.

The growth conditions in mixed stands differ in many ways from those in pure stands. Differences in the growth rhythm of tree species, in their root systems, and in their demands for light, temperature, and nutrients mean that the tree-to-tree competition in mixed stands differs from that in pure stands. The wood production and monetary returns from a mixed stand do not correspond to those of pure stands.

The most difficult mixed-stand factor to be taken into account in modelling is the possible long-term impact of different tree species on soil productivity. Some studies report improved wood production in terms of faster height development of conifers due to the presence of broadleaved species. If site classification is based on the dominant height development in mixed stands, this will lead to overestimations of the long-term yield of pure stands compared to that of mixed stands. This is a difficult problem to solve when predicting the growth of mixed stands using data from temporary sample plots.

The influence of a mixture of broadleaved species on the height development of Scots pine (i.e., influence on the site productivity) was examined by measuring three temporary sample plots in each stand (Mielikäinen 1980). The height development of pine was similar in both the pine-dominated and the mixed-species subplots. There was no evidence of the mixed-stand effect on the height of dominant pine trees (see Hägglund 1975). This may be a result of the possible influence of birch on soil in all the adjacent subplots.

Single-tree analyses indicated that the abundance of silver birch in the mixed stand reduced the diameter growth of both pine and birch. The same phenomenon was subsequently observed in the Norway spruce-birch studies (Mielikäinen 1985). Both studies demonstrated that both conifers and silver birch grew best in conifer-dominated mixed stands. Downy birch (*Betula pubescens*) did not have the same effect.

Norway Spruce and Silver Birch

In Finland, Norway spruce and birch form both single-storied and two-storied stands. Spruce is a shade-tolerant species that readily regenerates underneath a birch overstorey. The growth modelling of the spruce-birch mixtures was based on single-tree, distance-independent models (Mielikäinen 1985). In addition to tree and stand mean parameters, competition indexes based on the location of trees did not result in marked improvements in the models. Tree diameter and relative tree height were the best variables in the cross-sectional area growth models.

The biggest problems encountered in the formulation of tree growth models were the intercorrelations between predictor variables and the systematic error in the height increment measured using binoculars. In extreme cases, the intercorrelations (multicollinearity) between predictor variables resulted in a negative regression coefficient for site index. In other words, an improvement in the site index resulted in reduced growth. To make the intercorrelations between predictor variables weaker, ridge regression analysis was used (Hoerl and Kennard 1971). Ridge regression analysis resulted in weaker intercorrelations, reduction of the standard error of regression coefficients and a biased model. A ridge-regression model thus is a compromise between the degree of explanation of single predictor variables and the bias of the model.

Height increment models based on measurements using binoculars were calibrated through measurement of felled sample trees. In the case of old Norway spruce, overestimation resulting from the use of binoculars exceeded 50%. Following calibration, height development of dominant spruce followed the site index curves of pure spruce stands.

Modelling the development of two-storied mixed stands of spruce and birch in Finland has up to recently received little attention. However, models based on temporary research plots have provided some knowledge about the further development of spruce when released from the influence of birch overstorey.

MODELLING THE DEVELOPMENT OF UNEVEN-AGED STANDS

Modelling the growth of uneven-aged mixed stands is among the greatest challenges facing yield researchers because the researcher is required to formulate models for tree recruitment, increment, and eventual death. The treatment rules applied during the simulation are also far more difficult to take into account than when dealing with even-aged stands (Haight 1987).

The first major problem is to find suitable research material. In Central Europe, the proportion of forest stands grown as uneven-aged stands is no more than a few percent of the region's total forested area; in northern Europe, it is even less. The transformation of even-aged stands into uneven-aged stands, and the scientifically sound comparison of stand yields by means of permanent long-term experiments, require decades. In order to reduce the time period required to obtain results, the Finnish Forest Research Institute has launched a research project with the aim of developing a stand simulator for predicting the yields of both even- and uneven-aged stands. The project uses growth models largely based on temporary study plots (Mielikäinen et al. 1992). Data are being sought from stands in which the transformation of even-aged to uneven-aged structure (or uneven-sized structure) began at least 5–10 years ago.

Growth and Mortality Models

The growth models used in uneven-aged stands must be able to depict the development of both even-aged and uneven-aged stands, as well as the transitional stages required when shifting over from even-aged to uneven-aged. The stand measurements must also be of sufficient detail for the regeneration model. Furthermore, the model must permit consideration of different harvesting methods and their associated costs. All the aforementioned models require the measurement of tree locations (i.e., the use of single-tree distance-dependent models).

Macro-variation in the wood production capacity of a site is usually described in terms of site index. A site index system based on dominant height cannot be applied in uneven-aged stands. The variation in growth caused by the site is dealt with in the model formulation stage as random variation between sample plots. Later on, the increment level can be linked to selected site variables by modelling the random parameter b_k as their function.

Predicting stand development from tree mortality models for bigger trees is dependent on stand density. In order to examine stands approaching self-thinning, it is essential to apply mortality models. Ongoing work will study the applicability of both self-thinning models for stands (Hynynen 1993) and mortality probability models for single trees. Increment models will be formulated on the basis of temporary sample-plot data. In the case of mortality models, existing permanent experiments for even-aged stands will be used.

Regeneration Models

The regeneration model is probably the weakest link in the simulation of stand development at the moment. The essential issue in the development of an uneven-aged stand is regeneration, not tree growth. Regeneration is also the basic factor deciding what kind of a stem diameter distribution can be maintained when treating uneven-aged stands.

The modelling of regeneration in this work is based on the models presented by Pukkala (1987) and Pukkala and Kolström (1992) for even-aged stands. The model will be adapted to uneven-aged stands. The rate of maturation of seed, number of empty seed, and rates of predation and germination will also be taken into account. Methods will also be developed to evaluate the effect of plant cover characteristics on regeneration. In order to introduce the rate of variation into the model through numerous simulations, all the subprocess models will include a random effect with a fixed distribution.

Forest regeneration is a complex process characterized by considerable annual variation. Seed crops vary a great deal, as do weather conditions. This is why the regeneration model cannot be based on single measurements carried out during a particular year. The model's mortality part, on the other hand, requires seedling inventories repeated every autumn and spring over a period of many years.

The regeneration models included in the ongoing research work are based on measurements carried out on permanent experiments. Seed crop volumes and their spatial distribution, seed germination, seasonal seedling mortality, and the development of the ground vegetation are receiving the highest emphasis. A prototype of the whole simulator is due to be available by the end of 1995.

CONCLUSIONS

Yield, vegetation, and soil studies carried out in different parts of Europe indicate that the forest ecosystem is undergoing continuous change (Falkengren-Grerup and Tyler 1991). Part of the change is due to natural development, another part is the result of man's activities. Recently, these changes have been so rapid that yield models and tables published a couple of decades ago are no longer valid in predicting the current forest growth.

The biggest challenge facing growth modellers in the future will probably no longer be that of how to make growth models behave optimally based on given data, but rather the ability to predict what forests will look like in the future. Temporary reprieve is provided by continuous calibration of existing models with new data. A more permanent solution may be in the form of new environmental variables, which would permit the user to make longer-term assessments with respect to the continuously changing environment.

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