# Stand Dynamics Modelling Approaches for Multicohort Management of Eastern Canadian Boreal Forests

Arthur Groot, Sylvie Gauthier and Yves Bergeron

**Groot, A., Gauthier, S. & Bergeron, Y.** 2004. Stand dynamics modelling approaches for multicohort management of eastern Canadian boreal forests. Silva Fennica 38(4): 437–448.

The objective of this paper is to discuss approaches and issues related to modelling stand dynamics for multi-cohort forest management in eastern Canadian boreal forests. In these forests, the interval between wildfires can be rather long, and the development of natural forest stands may include the establishment, growth and mortality of several cohorts of trees. Later cohorts are characterised by increasing structural complexity, including spatial heterogeneity and irregular tree size distribution. A multi-cohort forest management framework has been proposed to maintain this complexity, and associated biodiversity, on the landscape. Multi-cohort forest management planning requires forecasts of the development of stands with complex structure in response to silvicultural treatment and to natural disturbance, but current stand dynamics models in the region are applicable mainly to even-aged mono-specific stands. Possible modelling approaches for complex stands include i) the adaptation of current whole-stand growth and yield models, ii) distance-independent, empirically-derived individual-tree models, such as the USDA Forest Service Forest Vegetation Simulator, and iii) distance-dependent, empirically-derived or process-oriented individual-tree models. We conclude that individual-tree models are needed because observational data for fitting whole-stand models are not available for the full array of silvicultural treatments and natural disturbances encompassed by multi-cohort forest management. Predictive accuracy is a concern with individual-tree models, and the incorporation of coarse-scale constraints into these models is a promising means to control error.

**Keywords** boreal forests, Canada, dynamic models, multi-cohort forest management,
**Authors´ addresses** *Groot:* Great Lakes Forestry Centre, Canadian Forest Service, 1219 Queen St. E., Sault Ste. Marie, ON, P6A 2E5, Canada; *Gauthier:* Laurentian Forestry Centre, Canadian Forest Service, 1055 du P.E.P.S., P.O. Box 3800, Sainte-Foy, QC, G1V 4C7, Canada; *Bergeron:* University of Quebec at Abitibi-Temiscamingue, 445 Boul de l'Université, Rouyn-Noranda, QC, J9X 5E4, Canada
**E-mail** agroot@nrcan.gc.ca; sgauthier@cfl.forestry.ca; yves.bergeron@uqat.ca
**Received** 2 September 2003 **Revised** 19 March 2004 **Accepted** 9 July 2004

# 1 Introduction

Multi-cohort forest management, a natural disturbance based approach to maintaining biodiversity, is being developed and implemented in the eastern Canadian boreal forest. Complex stands, which are characterised by mixed species composition, spatial heterogeneity, or irregular size distribution, are an integral part of this management approach. The implementation of multi-cohort forest management requires long-term forecasts of stand dynamics, but satisfactory forecasts of the dynamics of complex stands in the eastern Canadian boreal forest cannot be made at present. Such stands represent a modelling challenge, and the objective of this paper is to discuss approaches to and issues around developing or adapting stand dynamics models that are applicable to complex stands.

To address this objective, we first provide a background to multi-cohort management and discuss the interaction of stand-level and forest-level modelling. We then examine the requirements for stand dynamics models in multi-cohort management, and summarise possible modelling approaches. We discuss model accuracy in detail, since making accurate forecasts for a wide range of stand structures is a central challenge in modelling complex stand dynamics.

Although this paper focuses on approaches for modelling the dynamics of complex stands in the eastern Canadian boreal forest under multicohort forest management, the conclusions are relevant to other forest regions, to other silvicultural treatments and to other natural disturbance regimes. Because multicohort management involves a wide range of stand structures and dynamics, modelling approaches that are applicable to this type of management are also applicable to complex stands in general.

# 2 Background to the Multi-Cohort Approach

## 2.1 Natural Disturbance as a Basis for Forest Management

Forest ecosystem management based on the understanding of natural disturbance regimes has been suggested as a means to maintain biological diversity and productivity in forest systems (Attiwill 1994, Bergeron and Harvey 1997, Angelstam 1998, Hunter 1999, Bergeron et al. 1999, 2002). At the landscape level (areas in the order of 1 million ha), it implies maintaining structural and compositional patterns that are characteristic of the regional mosaic produced under the natural disturbance regime (Gauthier et al. 1996, Hunter 1999). At the stand level (areas in the order of 10 to 100 ha), it also provides a conceptual framework for silvicultural systems that are inspired by natural stand dynamics and that maintain structural attributes or legacies of natural stands (Franklin 1993, Seymour and Hunter 1999).

Although even-aged management has been considered well adapted to fire driven systems, it has recently become clear that it is not universally well suited to the Canadian boreal forest. The eastern Canadian boreal forest (occurring in the Provinces of Newfoundland, Québec and Ontario) is a vast region of forests dominated by black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*), with significant representation of white spruce (*Picea glauca*), white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), balsam poplar (*Populus balsamifera*) and eastern white cedar (*Thuja occidentalis*) (Rowe 1972). Recent fire history studies in this region indicate that a significant portion of the forest originates from fires dating from over 100 years B.P. and even to over 200 years B.P. (Bergeron et al. 2001, Kneeshaw and Gauthier 2004). This implies that in many stands, the post-fire cohort will have time to start dying and to be replaced in the canopy by successive cohorts of trees. Furthermore, even within areas burned by wildfire, groups of residual surviving trees introduce irregularity into regenerating stands (Bergeron et al. 1999). Alternatives to the exclusive use of even-aged management

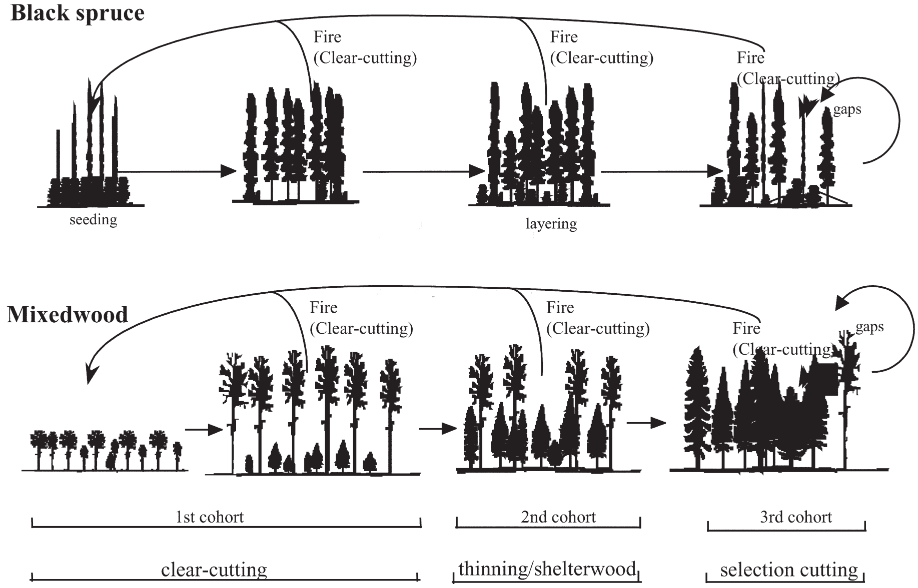


**Fig. 1.** Progression of cohorts under long fire intervals.

are needed to maintain the variety of age classes, stand structures and compositions found in natural eastern Canadian boreal forests.

## 2.2 Multi-Cohort Forest Management

Multi-cohort forest management has been proposed as a means to maintain a forest mosaic similar to that characteristic of natural forests. This strategy focuses on three stages of stand development following wildfire, each characterized by different composition and structure (Bergeron et al. 1999).When fire intervals are shorter than the lifespan of pioneer species, a cyclic succession would be observed, as it is the case in many boreal regions (Johnson 1992). The post-fire cohort is defined as cohort 1. Given that the fire cycle can be relatively long in eastern Canada, at many sites the interval between successive fires is longer than the normal longevity of individual trees of the post-fire cohort, allowing these sites to enter into the old growth forest stage (Kneeshaw and Gauthier 2004). Under a long fire interval, a change in species composition or in stand structure is observed to occur (De Grandpré et al. 2000, Gauthier et al. 2000, Lesieur et al. 2002, Boucher et al. 2003) (Fig. 1). These changes reflect the replacement of individuals immediately established following a stand initiating fire and initially constituting the stand canopy ($1^{st}$ cohort) by individuals previously occupying the understory ($2^{nd}$ cohort). Moreover, in the continued absence of fire, gap dynamics perpetuates the replacement of individuals from these two cohorts by individuals from later cohorts (collectively called $3^{rd}$ cohort as individual cohorts gradually become harder to distinguish).

In multi-cohort management, silvicultural practices are diversified to maintain and promote compositional and structural forest diversity while keeping rotation ages similar to current values (Bergeron et al. 1999, 2002) (Fig. 1). The first cohort, originating from fire, is replaced by clear-cutting and planting or seeding, the second cohort by thinning and shelterwoood management that emulates natural succession, and the third cohort by selection cutting that mimics the natural gap dynamics of old growth stands. The proportion of stands that should be treated by each of these silvicultural practices should vary in relation to the natural disturbance cycle and the maximum harvest age (Fig. 2). Just as in natural landscapes where not all stands survive to a mature or old growth stage before being burned and recommencing succession, not all stands pass through the three cohorts. Reinitiation of the first cohort may be generated by clear-cutting and planting or seeding of stands of any of the three cohorts. Implementation of this management framework has started in some regions of Ontario and Québec (Harvey et al. 2002, Gauthier et al. 2002, 2004), and has called attention to the central role of modelling in multicohort forest management.

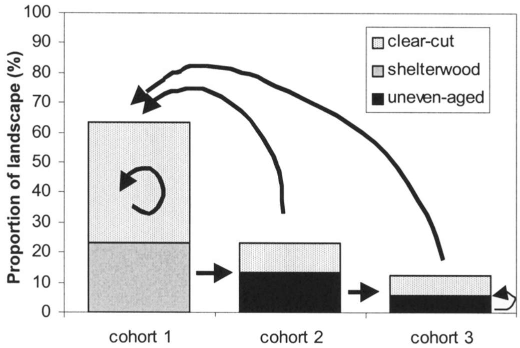


**Fig. 2.** Maintaining the structure associated with different stand age classes by using variable silvicultural treatments.

## 2.3 Role of Modelling in Multi-Cohort Forest Management

Multi-cohort forest management involves the maintenance of wood supply and forest structure over large spatial and time scales. As a result, planning for multi-cohort forest management requires long-term forecasts of stand and landscape structure and dynamics. This requirement places strong emphasis on modelling at the forest and stand levels. Stand level models forecast the dynamics of individual forest stands, whereas forest level models forecast wood and habitat supply for entire forest management units, which may comprise thousands of stands.

Forest level models are central to forest management planning in eastern Canada, which is carried out on management units with areas in the order of 1 000 000 ha. The forest level models are used to develop and examine forest management strategies, particularly the timing of forest harvesting and silvicultural treatments on different forest strata (aggregations of similar stands) within the management unit. Ontario uses a linear programming-based optimisation model called the Strategic Forest Management Model (SFMM) (Davis 1993), whereas Québec uses a simulation model called SYLVA. Despite the different approaches, both models are used to determine forest management strategies that will achieve wood supply and forest structure objectives subject to a variety of constraints. Forest sustainability is addressed by analysing the modelled results of management strategies over very long time periods (e.g., 300 years).

The forest-level models require two main sources of information: current forest inventory and models of stand dynamics. Forest inventories in eastern Canada consist of forest stands mapped from aerial photographs. Stand attributes including age, dominant height, canopy tree species proportion, productivity (3 or 4 classes) and site occupancy (0 to 1) are interpreted from photographs supplemented by ground inventory plots and records of forest disturbance (such as fire history). The inventory does not provide any explicit information on stand structure, stem sizes, or understory vegetation. To reduce the size of the forest-level modelling task, stands with similar attributes (species composition, site quality) may be grouped into forest strata.

The models of stand dynamics that are used in the forest-level models are essentially stand-level yield curves that specify the stand volume by tree species as a function of stand age. The yield curves are based on normal yield curves (e.g., Plonski 1974), but adjusted to account for site occupancy. These adjustments are derived from temporary and permanent sample plots, from the mapped forest inventory and from local experience. Similar to the forest inventory, the yield curves do not provide any explicit information on stand structure, stem sizes, or understory vegetation.

Planning for multi-cohort forest management will be carried out, at least for the foreseeable future, using these stand and landscape level tools. The lack of explicit information on stand structure in inventory data and yield curves is an impediment to planning multi-cohort forest management, but this lack is compensated for by the fact that forest structural characteristics can be correlated to attributes such as stand age, species composition and site quality. A more fundamental problem is that although the dynamics of younger (first cohort), even-aged, single-species stands are reasonably well-described by empirical yield curves, information is lacking about the dynamics of older, mixed, and structurally irregular stands and about the long-term response of stands to silvicultural manipulations designed to create particular structures. Consequently, it is necessary to use models to provide this information.

# 3 Modelling

### 3.1 Model Requirements

Stand dynamics models for multi-cohort forest management must be able to provide robust long-term forecasts of stand growth, yield, structure and composition for complex stands. The models also should be applicable to even-aged, single-species stands, since many stands will pass through such a stage before or after complex structure stages. The models should be able to represent the effects of silvicultural treatments, particularly partial cutting treatments designed to create or maintain desired structural characteristics, but also even-aged silvicultural systems. Additionally, the models should be able represent responses to non-stand replacing natural disturbances such as windthrow, insects and disease.

### 3.2 Possible Modelling Approaches

Modelling approaches for uneven-aged stands (Peng 2000) and for mixed stands (Porté and Bartelink 2002) have been reviewed recently. Although approaches can be classified in a number of ways (Porté and Bartelink 2002), the broad categories originally proposed by Munro (1974) remain the basis for most classifications: whole-stand distance-independent models, single-tree distance-independent model, and single-tree distance-dependent models. At the time these categories were proposed, nearly all models were empirical (or statistical). More recently, considerable effort has been devoted to developing process-based (or mechanistic) models (e.g., Mäkelä et al. 2000, Johnsen et al. 2001). As a consequence, each of the categories proposed by Munro (1974) now includes both empirical and process-based models.

Although a large number of forest dynamics models have been developed world-wide (Peng 2000, Porté and Bartelink 2002), relatively few models relevant to the eastern Canadian boreal forest have been developed, are being developed or are being adapted. Nevertheless, each of the three main model categories contains one or more relevant models.

#### *3.2.1 Whole-stand Distance-independent Models*

Current forest management planning in this region uses empirical stand level models almost exclusively. As noted earlier, these models are based on normal yield tables (e.g., Plonski 1974), but adjusted to take into account local site occupancy patterns. The adjustments are often local to management units and are generally not available in published form. The normal yield tables (and consequently the empirical models that are based on them) are applicable mainly to monospecific, even-aged stands, with maximum age from 90 to 150 years depending on species.

Some work is underway in adapting the 3-PG model (Landsberg and Waring 1997), a process-based whole-stand model, to central Canadian forests (Fournier et al. 2000). This work is aimed more at productivity estimation than at modelling growth and yield or succession, however.

#### *3.2.2 Single-tree Distance-independent Models*

Empirical single-tree distance-independent models have been developed for a variety of species in a number of locations. These models estimate the growth of individual trees from tree, stand and site characteristics. Regular mortality is estimated in many models, usually as a function of tree and stand characteristics. Less commonly, components such as regeneration, understory vegetation, and susceptibility to insect and disease attack are also modelled.

Empirical single-tree distance-independent models form the core of the USDA Forest Service Forest Vegetation Simulator (FVS), which is used across the US and parts of Canada to simulate forest growth and yield (Teck et al. 1996). The FVS comprises a number of regional variants, and the variant most applicable to the eastern Canadian boreal forest is derived from the TWIGS/STEMS model developed in the Lakes States (Miner et al. 1988). Some efforts were made to calibrate TWIGS for Ontario boreal species (Payandeh and Papadopol 1994), but these calibrations are not being applied at present. Further calibration efforts for Ontario species are currently underway (pers. comm., M. Woods, Ontario Ministry of Natural Resources). The TWIGS variant does not include a regeneration component.

The FVS can provide forecasts for stands with complex structure, although it is not clear that highly irregular spatial structures are simulated well. Evaluations with independent data sets indicate that, despite large calibration data sets, TWIGS/STEMS produced biased or anomalous results for certain forest structures (Brand and Holdaway 1989, Leary 1997). Predictions of stand characteristics were reasonable over short periods (5 to 10 years), but errors increased with time, leading to warnings about making long-term forecasts with such models (Holdaway and Brand 1986) It is notable that long-term errors tended to be greater for stand-level variables (e.g., stand basal area) than for tree-level variables (e.g., DBH).

An empirical single-tree distance-independent model for peatland black spruce was developed by Hökkä and Groot (1999). This model predicts basal area growth as a function of tree diameter, stand basal area, basal of trees larger than the target tree, and organic matter depth. An evaluation of stand level estimates of basal area growth indicated accurate predictions over 40 years. The ability of this model to forecast the development of highly clumped spatial distributions was not evaluated, and Hökkä and Groot (1999) concluded that spatial models might be necessary to characterise competition more exactly.

#### *3.2.3 Single-tree Distance-dependent Models*

Empirical single-tree distance-dependent models use information on tree position to calculate a competition index for each tree (Peng 2000). Mailly et al. (2003) have recently tested such models for black spruce in eastern Canada, and found that distance-dependent competition indices provided more precise estimates of individual-tree basal area growth than distance-independent indices. However, the accuracy of these models in predicting stand level or long-term growth was not examined.

Considerable effort has been expended recently to adapt the partly process-based model SORTIE (Pacala et al. 1993, 1996) to forests in in Canada (Coates et al. 2003). SORTIE was originally developed to estimate growth rates of understory trees and recruitment in eastern North American mixed deciduous forests. In these circumstances, stem radial growth rates were related to light level and not to other environmental conditions (e.g., moisture and nutrients), and the light-growth relationship is at the core of SORTIE. Because light is the only resource considered, SORTIE currently does not represent the effect of site quality on growth rates.

Work is ongoing by A. Groot to develop a model that relates stem volume growth of black spruce to crown light interception, taking advantage of the functional relationship between growth and light capture (Bartelink et al. 1997).The recently developed model CORONA (Groot 2004) can be applied to compute the amount of light intercepted by individual tree crowns during the photosynthetic season, using information about tree positions, crown dimensions, crown transmissivity and latitude. The determination of light interception by tree crowns is a conceptually straightforward alternative to the use of statistically based competition indices in individual-tree growth models.

### 3.3 Is Stand Level Modelling Sufficient?

At first glance, it would appear that a whole-stand level approach is suitable for modelling forest dynamics, since this scale is consistent with the inventory and with the input required for the forest level models. Stand level models are generally considered to be realistic over long periods of time because they are highly constrained by the data used to fit them.

Stand level modelling would be fully sufficient to carry out forest management planning for the multi-cohort approach, if accurate stand level models could be constructed for the entire range of possible silvicultural treatments. Such models have been constructed for specific treatments in other jurisdictions (Pienaar and Rheney 1995, Snowdon 2002), but it is not feasible to fit models to data for a wide range of treatments, sites and stand conditions, particularly when many of the treatments have a very short history of implementation.

Furthermore, the difficulty of constructing stand level models, even for natural stands, in Canada's eastern boreal forest region may be greater than is commonly appreciated. Stand dynamics must be modelled for long periods of time (often >100 years) for a wide range of site and stand conditions, but there is a dearth of long-term permanent plot data. A number of problems have been encountered in developing stand dynamics models for natural stands, particularly when a large proportion of stands are relatively old. Smith (1984) pointed out the problems inherent in yield curve construction from temporary sample plots when age is confounded with site quality. The dynamics of stands with ages greater than 100 to 150 are currently a matter of conjecture, even though Bergeron et al. (2001) have shown that a substantial proportion of stands in the region are older than this.

Because of the difficulties involved in constructing stand-level models directly from observational data, it can be concluded that stand-level modelling alone will not be sufficient to represent stand dynamics in planning multi-cohort forest management. In many cases, it will be necessary to construct stand-level models from single-tree models.

### 3.4 Model Accuracy

The construction of stand-level models from single-tree models leads to the question of model accuracy. Accuracy is a key requirement for stand dynamics models in a multi-cohort forest management framework, because planned strategies for wood harvest, habitat supply and landscape pattern depend on the realisation of predicted future states of forest stands. Forest level planning can likely tolerate imprecision in model forecasts, but minimising bias is important, so that errors in the forecast for one stand will be compensated by opposite errors in the forecast for another stand. The model quality required might be better termed robustness than accuracy, because models must provide low bias forecasts for long periods of time, for a wide variety of stand structures, and for responses to silvicultural treatments and to natural disturbances.

It is clearly unrealistic to expect that models can provide error-free forecasts, and differences between projections and reality can be dealt with through adaptive management methods (Kneeshaw et al. 2000, Tittler et al. 2001). Nevertheless, it is important to control model error, because deviations from planned outcomes are likely to have the effect of reducing the range of options in subsequent planning cycles.

Model robustness has been one of the motivations for the development of process-based models. It has been argued that models incorporating knowledge of underlying mechanisms should prove useful over a wider range of conditions than empirical models (Korzukhin et al. 1996, Battaglia and Sands 1998, Mäkelä et al. 2000, Johnsen et al. 2001). But as Zeide (2003) has noted, the increased scientific understanding embodied in process-based models has not necessarily resulted in greater predictive accuracy of growth and yield. This conclusion is well justified with respect to "bottom-up" ecophysiological models. However, it appears that stand level process-based models such as 3-PG (Landsberg and Waring 1997) can provide useful estimates of stand growth (Landsberg 2003). Stand-level process-based models appear to fulfil the promise of providing robust predictive capability across a wide range of environmental conditions, although dynamic predictive ability is less certain.

As noted in the preceding discussion of TWIGS/STEMS, concerns about model accuracy are not limited to process-based models. This empirical, distance-independent individual tree model may not provide accurate forecasts for longer periods, for certain forest structures, or for stand level variables (Brand and Holdaway 1989, Holdaway and Brand 1986, Leary 1997). Model accuracy may be more closely related to whether a model is top-down or bottom-up in structure than to whether it is process-based or empirical (Zeide 2003). In bottom-up models, results of models of fine-resolution components or processes must be aggregated to obtain predictions at the stand-level scale. Aggregation and propagation of error are problems in bottom-up models, and errors become more serious if interactions between components or processes are strong and if there are no coarse-resolution constraints incorporated in the model structure. This situation is particularly characteristic of fine-resolution process-based models, which likely accounts for the lack of predictive ability for this model type. Individual-tree empirical models have some degree of coarse-resolution constraint by virtue of being fitted to data from stands. The inclusion of stand level variables (typically stand basal area) in individual-tree empirical models provides a further measure of coarse-resolution constraint. These coarse-level constraints are not sufficient to prevent propagation of error with time, however, and the utility of long-term (>30 year) forecasts of growth and yield is questionable.

### *3.4.1 Using Constraints to Control Error*

The preceding discussion seems to indicate an impasse for modelling complex stands: top-down models may be fairly robust, but cannot adequately represent heterogeneity in species composition, spatial structure and size distributions, while the accuracy of bottom-up models decreases with time and possibly with the model resolution. A possible solution to this impasse is to control error aggregation and propagation by constructing models that allow interaction between fine resolution components and coarse-resolution constraints. This concept has been advanced by researchers working with a number of different types of models.

For example, Stage (2003) noted that because of concern about error propagation, he considered structuring the empirical PROGNOSIS model to include a stand-level model operating in parallel with the individual-tree model, with information passing back and forth at each time step. Although it was never incorporated, the stand-level model would have provided a coarse-resolution constraint to the tree-level model. Mäkelä (2003) has similarly highlighted the need to incorporate coarse-resolution constraints into models comprising fine-resolution processes in order to increase the robustness of predictions. Luan et al. (1996) structured the model FORDYN so that higher-level constraints or boundary conditions were placed on lower level (finer-scale) processes.

Mäkelä (2003) suggested a number of types of coarse-level constraints, including i) environmental restrictions; ii) emergent properties, such as optimality functioning; and iii) allometric ratios. Resource-based constraints are particularly attractive because they implement the principle of the conservation of matter and energy. Trees compete for light, moisture and nutrients, and resources captured by one tree are not available for the growth of competitors. Modelling light capture is an obvious first step in incorporating resource-based constraints into models of complex stands (Battaglia and Sands 1998): light capture varies strongly among individual trees in heterogeneous stands and computer speed and memory have advanced to make this modelling more feasible. An initial emphasis on light does not diminish the importance of moisture or nutrients for tree growth, and constraints based on these resources are necessary as well. Meinzer (2003) has pointed out that plant anatomical, structural and chemical attributes place constraints on physiological functioning, resulting in functional convergence of plant responses to the environment.

An individual-tree growth model based on light capture, currently under development by A. Groot, is an example of an individual-tree growth model with a resource-based constraint. In this spatially explicit model, light captured by the crowns of all trees within a plot is determined by a ray-tracing algorithm (Groot 2004). This model exhibits conservation of light energy, since any light captured by one crown is not available for capture by another crown. Volume growth is related to light capture by a two parameter empirical function (Table 1). Although volume growth is estimated for individual trees, volume growth at

**Table 1.** Equation for estimating volume growth from light capture computed by CORONA (Groot 2004).

$$\textit{Annual volume growth} = a_1[1 - \exp(a_2 \textit{ Intercepted light})]$$

**Table 2.** TWIGS equations for estimating diameter growth (Miner et al 1988).

$$\textit{Annual Diameter Growth} = \textit{Potential Growth} \times \textit{Competition Modifier} + \textit{Diameter Adjustment Factor}$$

$$\textit{Potential Growth} = b_1 + b_2D^{b3} + b_4SI \cdot CR \cdot D^{b5}$$

$$CR = \frac{a_1}{1 + a_2 RBA} + a_3[1 - \exp(a_4 D)] + CF$$

$$\textit{Competition Modifier} = 1 - \exp\{-f(R) \cdot g(AD) \cdot [(BA_{max} - BA) / BA]^{1/2}\}$$

$$f(R) = d_1[1 - \exp(d_2R)]^{d3} + d_4$$

$$g(AD) = c_1(AD + 1)^{c2}$$

$$\textit{Diameter Adjustment Factor} = k_1D + k_2D^2 + k_3$$

**Table 3.** Modelled effects of an increase in crown ratio using an empirical individual-tree model (TWIGS) and a resource-constrained individual-tree model (CORONA). The characteristics of the modelled *Picea mariana* stand were basal area 31.3 $m^2$ $ha^{-1}$, and mean diameter at breast height 12.5 cm.

| | Site index$_{50}$ (m)[1] | TWIGS<br>Total volume growth ($m^3$ $ha^{-1}$ $yr^{-1}$) | CORONA |
|---|---|---|---|
| Mean crown ratio = 0.57 | 18.3 | 5.11 | 5.10 |
| Mean crown ratio = 0.67 | 18.3 | 6.09 | 5.25 |
| Volume growth increase | | 19% | 3% |

[1] The site index value for TWIGS was chosen to result in a volume growth estimate matching that obtained from CORONA.

the stand level is constrained by the finite quantity of light falling on the stand.

It is interesting to compare this resource-constrained approach to a fully empirical individual-tree growth model. The light capture approach could be considered as being more straightforward conceptually, which is reflected by the fact that the growth equation for this approach has two parameters (Table 1), whereas the growth equation for TWIGS uses up to 19 parameters (Table 2). The influence of a resource constraint can be illustrated by considering the sensitivity of stand growth to crown description in a fully occupied stand. In the light capture model, nearly all of the available light is already captured at the lower crown ratio. Increasing the length of the crown doesn't significantly increase light capture, and there is a minor stand volume growth increase (Table 3). In TWIGS, an increase in the crown ratio of trees results in a substantial increase in stand volume growth (Table 3), and this effect propagates and possibly amplifies with time. The TWIGS result is unrealistic and leads to inaccuracy, whereas the light availability constraint in the light capture model helps to control error.

It should be noted that the inclusion of light (or any other resource) into a model does not necessarily mean that a coarse-level constraint has been incorporated. For example, in SORTIE (Pacala et al. 1996) the radial growth of individual trees is a function of light level at the crown apex. In a real stand, the addition of a neighbour tree would reduce the light captured by a tree, but in SORTIE the addition of a neighbour of equal or shorter height has no effect on crown apex light level. The lack of a conservation constraint for light in SORTIE may account for the rather unrealistic basal area development generated by high initial seedling densities (Pacala et al. 1996). A further peculiarity in the original version of SORTIE was that the radial growth of adult trees was capped by a maximum value of stem basal area growth, so that many canopy trees had the same basal area growth. SORTIE now has been modified through the addition of a distance-dependent individual-tree growth module to estimate growth of canopy trees (Coates et al. 2003).

## 4 Summary

Multi-cohort forest management is a promising approach to reconcile the goals of timber production and the maintenance of biodiversity and ecosystem function. Planning for multi-cohort forest management will place greater demands on modelling at the landscape and stand levels. Current stand dynamics models used in management planning are applicable mainly to younger, even-aged, single-species forest stands, but not to stands with more complex structure. Although whole-stand models of stand dynamics are compatible with forest inventory and with strategic forest-level models, it will be necessary to construct these models using individual-tree models. Prospective individual-tree modelling approaches include process-based and empirical versions of distance-dependent and distance-independent models. Individual-tree models that are based solely on a bottom-up approach are prone to inaccuracy because of error aggregation and propagation. Incorporating coarse-level constraints into individual-tree models can reduce this inaccuracy. Resource-based constraints may be particularly effective.

The Forest Vegetation Simulator and SORTIE can be used to construct stand dynamics models for use in planning, but the resulting models may contain substantial error because of incomplete calibration and because of error propagation. It is important to further develop resource-constrained individual-tree models to construct stand dynamics models for use in planning multi-cohort forest management.

## References

Angelstam, P.K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9: 593–602.

Attiwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63: 247–300.

Bartelink, H., Kramer, K. & Mohren, G.M.J. 1997. Applicability of the radiation-use efficiency concept for simulating growth of forest stands. Agric. For. Meteorol. 88: 169–179.

Battaglia, M. & Sands, P.J. 1998. Process-based forest productivity models and their application in forest management. Forest Ecology and Management 102: 13–32.

Bergeron, Y. & Harvey, B. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwoods of Quebec. Forest Ecology and Management 92: 235–242.

— , Gauthier, S., Kafka, V., Lefort, P. & Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Canadian Journal of Forest Research 31: 384–391.

— , Harvey, B., Leduc, A. & Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: Stand forest level considerations. Forestry Chronicle 75: 49–54.

— , Leduc, A., Harvey, B.D. & Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fennica 36(1): 81–95.

Boucher, D., De Grandpré, L. & Gauthier, S. 2003. Développement d'un outil de classification de la structure des peuplements et comparaison de deux territoires de la pessière à mousses du Québec. Forestry Chronicle 79: 318–328.

Brand, G.J. & Holdaway, M.R. 1989. Assessing the accuracy of TWIGS and STEMS85 volume predictions: a new approach. Northern Journal of Applied Forestry 6: 109–114.

Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L. & Messier, C. 2003. Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. Forest Ecology and Management 186: 297–310.

Davis, R. 1993. Analyzing Ontario's timber supply with the Strategic Forest Management Model. In: Davis, R. (ed.). Analytical approaches to resource management. Queen's Printer for Ontario. p. 52–71.

De Grandpré, L., Morissette, J. & Gauthier, S. 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. Journal of Vegetation Science 11: 791–800.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications 3: 202–205.

Fournier, R.A., Guindon, L., Bernier, P.Y., Ung, C.-H. & Raulier, F. 2000. Spatial implementation of models in forestry. Forestry Chronicle 76: 929–940.

Gauthier, S., Leduc, A. & Bergeron, Y. 1996. Vegetation modelling under natural fire cycles: a tool to define natural mosaic diversity for forest management. Environmental Monitoring and Assessment 39: 417–434.

— , De Grandpré, L. & Bergeron, Y. 2000. Differences in forest composition in two ecoregions of the boreal forest of Québec. Journal of Vegetation Science 11: 781–790.

— , Lefort, P., Bergeron, Y. & Drapeau, P. 2002 . Time since fire map, age-class distribution and forest dynamics in the Lake Abitibi Model Forest. Canadian Forest Service, Ste-Foy, Quebec, Canada. Information Report LAU-X-125.

— , Nguyen, T.-X., Bergeron, Y., Leduc, A. Drapeau, P. & Grondin, P. 2004. Developing forest management strategies based on fire regimes in northwestern Quebec, Canada. Chapter 18. In: Perera, A.H., Buse, L.J. & Weber, M.G. Emulating natural forest landscape disturbances: concepts and applications. Columbia University Press, New York, NY.

Groot, A. 2004. A model to estimate light interception by tree crowns, applied to black spruce (Picea mariana). Canadian Journal of Forest Research 34: 789–799.

Harvey, B.D., Leduc, A., Gauthier, S. & Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecology and Management 155: 369–385.

Holdaway, M.R. & Brand, G.J. 1986. An evaluation of Lake States STEMS85. USDA Forest Service Res. Pap. NC-269. 10 p.

Hökkä, H. & Groot, A. 1999. An individual-tree basal area growth model for second-growth peatland black spruce. Canadian Journal of Forest Research 29: 621–629.

Hunter, M.L., Jr. (ed.). 1999. Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge, UK.

Johnsen, K., Samuelson, L., Teskey, R., McNulty, S. & Fox, T. 2001. Process models as tools in forestry research and management. Forest Science 47: 2–8.

Johnson, E.A. 1992. Fire and vegetation dynamics. Studies from the North American boreal forest. Cambridge University Press, Cambridge, United Kingdom.

Kneeshaw, D.D. & Gauthier, S. 2004. Old growth in the boreal forest: a dynamic perspective at the stand and landscape level. Env. Rev. 11: S99–S114.

— , Leduc, A., Drapeau, P., Gauthier, S., Paré, D., Carignan, R., Doucet, R., Bouthillier, L. & Messier, C. 2000. Development of integrated ecological standards of sustainable forest management at an operational scale. Forestry Chronicle 76: 481–493.

Korzukhin, M.D., Ter-Mikaelian, M.T. & Wagner, R.G. 1996. Process versus empirical models: which approach for forest ecosystem management. Canadian Journal of Forest Research 26: 879–887.

Landsberg, J.J. & Waring, R.H. 1997. A generalised model of forest productivity using simplified concepts of radiation use efficiency, carbon balance and partitioning. Forest Ecology and Management 95: 209–228.

Landsberg, J. 2003. Modelling forest ecosystems: state of the art, challenges, and future directions. Canadian Journal of Forest Research 33: 385–397.

Leary, R.A. 1997. Testing models of unthinned red pine plantation dynamics using a modified Bakuzis matrix of stand properties. Ecological Modelling 98: 35–46.

Lesieur, D., Gauthier, S. & Bergeron, Y. 2002. Fire frequency and vegetation dynamics for the south-central boreal forest of Quebec, Canada. Canadian Journal of Forest Research 32: 1996–2009.

Luan, J., Muetzelfeldt, R.I. & Grace, J. 1996. Hierarchical approach to forest ecosystem simulation. Ecological Modelling 86: 37–50.

Mailly, D., Turbis, S. & Pothier, D. 2003. Predicting basal area increment in a spatially explicit, individual tree model: a test of competition measures with black spruce. Canadian Journal of Forest Research 33: 435–444.

Mäkelä, A. 2003. Process-based modelling of tree and stand growth: towards a hierarchical treatment of multiscale processes. Canadian Journal of Forest Research 33: 398–409.

— , Landsberg, J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ågren, G.I., Oliver, C.D. & Puttonen, P. 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiology 20: 289–298.

Meinzer, F.C. 2003. Functional convergence in plant repsonses to environment. Oecologica 134: 1–11.

Miner, C.L., Walters, N.R. & Belli, M.L. 1988. A guide to the TWIGS program for the North Central States. USDA For. Serv. Gen. Tech. Rep. NC-125. 105 p.

Munro, D.D. 1974. Forest growth models – a prognosis. In: Fries, J. (ed). Growth models for tree and stand simulation. Royal Coll. For., Res. Notes 30, Stockholm. p. 7–22

Pacala, S.W., Canham, C.D. & Silander, J.A., Jr. 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Canadian Journal of Forest Research 23: 1980–1988.

— , Canham, C.D., Saponara, J., Silander, J.A., Jr., Kobe, R.K. & Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecological Monographs 66: 1–43.

Payandeh, B. & Papadopol, P.E. 1994. Partial calibration of “ONTWIGS” for several species of boreal mixedwood in Ontario. Northern Journal of Applied Forestry 11: 41–46.

Peng, C. 2000. Growth and yield models for uneven-aged stands: past, present and future. Forest Ecology and Management 132: 259–279.

Pienaar, L.V. & Rheney, J.W. 1995. Modeling stand level growth and yield response to silvicultural treatments. Forest Science 41: 629–638.

Plonksi, W.L. 1974. Normal yield tables (metric). Ontario Ministry of Natural Resources. 40 p.

Porté, A. & Bartelink, H.H. 2002. Modelling mixed forest growth: a review of models for forest management. Ecological Modelling 150: 141–188.

Rowe, J.S. 1972. Forest regions of Canada. Canada. Dep. Environ., Canadian Forest Service Publ. No. 1300.

Seymour, R.S. & Hunter, M.L., Jr. 1999. Principles of ecological forestry. In: Hunter, M.L. Jr. (ed.). Maintaining biodiversity in forest ecosystems. Cambridge University Press. Cambridge, UK. p. 22–61.

Smith, V.G. 1984. Asymptotic site-index curves, fact or artifact? Forestry Chronicle 60: 150–156.

Snowdon, P. 2002. Modeling Type 1 and Type 2 growth responses in plantations after application of fertilizer or other silvicultural treatments. Forest Ecology and Management 163: 229–244.

Stage, A. 2003. How forest models are connected to reality: evaluation criteria for their use in decision support. Canadian Journal of Forest Research 33: 410–421.

Teck, R., Moeur, M. & Eav, B. 1996. Forecasting ecosystems with the Forest Vegetation Simulator. Journal of Forestry 94: 7–10.

Tittler, R., Messier, C. & Burton, P.J. 2001. Hierarchical forest management planning and sustainable forest management in the boreal forest. Forestry Chronicle 77: 998–1005.

Zeide, B. 2003. The U-approach to forest modeling. Canadian Journal of Forest Research 33: 480–489.

*Total of 55 references*