Development of Q-LAND, a spatial model of forest landscape dynamics incorporating prediction of tree volume and seedling recruitment

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Abstract
Spatial simulation models of long-term dynamics of forest landscapes are needed for investigating how different actual or potential disturbance regimes determine the structure and dynamics of forest landscapes. This report presents the work done so far in modifying LANDIS and FIN-LANDIS models to develop a new model of spatial forest landscape dynamics that incorporates (1) prediction of basal area and tree volume at the cell level and (2) seed dispersal and sexual and asexual regeneration in a spatially explicit, quantitative manner. This new landscape model developed for the region of Abitibi, Québec, called Q-LAND, should allow us to address various theoretical questions and develop and test alternative silvicultural and forest management scenarios inspired by natural disturbance dynamics in boreal forests. We first present the model FIN-LANDIS that was developed and modified from LANDIS. Then we explain in more detailed how we are planning to incorporate prediction of basal area and tree volume at the cell level and seed dispersal and sexual and asexual regeneration in a more spatially explicit way. A preliminary test of the model is presented for one stand-type in Abitibi, Québec.
1. Introduction
Spatial simulation models of long-term dynamics of forest landscapes are needed for investigating how different actual or potential disturbance regimes determine the structure and dynamics of forest landscapes. Such disturbance regimes may be natural or based on forest management. Simulation modeling can be used to predict the economic and ecological consequences of different timber harvesting regimes, and to increase knowledge about the natural variability of the forest landscapes, under which the current biological diversity has evolved.

The goal of this work is to develop a simulation approach to forest landscape dynamics, which
- is suitable for long-term (100 – 10 000 years) and large-scale (10^3 – 10^6 ha) investigations,
- predicts the basal area and volume of each tree species for each forest stand,
- may be flexibly calibrated and parametrized using a stand-level model such as SORTIE (Pacala et al.1996) and empirical data on stand development
- incorporates seed dispersal and sexual and asexual regeneration in a spatially explicit, quantitative manner,
- can be flexibly linked with separate models representing fire, harvesting, and other landscape disturbance events,
- can produce realistic predictions in practical applications when sufficient empirical data is available, and
- is useful for exploratory work even when there is little empirical data for parameterization.

Our work follows the developmental line from the LANDIS model (Mladenoff et al. 1996, He and Mladenoff 1999), through FIN-LANDIS (Pennanen and Kuuluvainen 2001). These models do not track the quantitative attributes of forest stands and therefore they fulfil the above requirements only partially.

In our approaches, following Mladenoff et al. (1996), a landscape is represented by a raster map of 10^2 - 10^6 square cells, which represent individual forest stands, with size of 1 to 10 hectares. Smaller cell size would require incorporating tree competition (shading) between cells and larger cells would make assumption of homogeneous cells unrealistic. The simulation proceeds in time steps of fixed length, e.g. 5 or 10 years. Trees in a forest stand are represented by cohorts. Each cohort contains the trees of certain species that established during the same time step. This cohort-based data structure is inherited from VAFS / STANDSIM of Roberts (1996).

FIN-LANDIS model was tailored for simulating boreal forest landscapes by modifying and expanding the LANDIS model, through adding mechanistic detail to the simulation of stand dynamics
and fire behavior (Pennanen and Kuuluvainen 2001). We used FIN-LANDIS as a basis for a new Q-LAND model design, incorporating the quantitative attributes of tree cohorts and capable of meeting the other requirements mentioned above. Q-LAND aims to include as little stand-level processes as possible. However, the forest stands have to react to the landscape level events realistically, i.e. the seed dispersal from outside the stand, and exogenous disturbance events, such as fire and harvesting.

Q-LAND and FIN-LANDIS are implemented directly in object-oriented manner using C++ programming language. A low-level language like C++ provides the most flexibility in the model design and the fastest execution of simulations. However, modification of the model and understanding its functioning are easier if a specialized language for spacial simulation modeling is used. Such language is provided by the SELES simulation environment (Fall and Fall 2001), which also has tools for debugging, visualization and linkage with GIS. Because of these advantages of SELES, a linkage between Q-LAND and SELES models was designed. This allows executing parts of the simulation, e.g. fire and other landscape disturbance events using the SELES environment, as well as using SELES for input and output of GIS-format maps and viewing landscape change during the simulation. Through this linkage, the work done using SELES to simulate forest management (Fall et al., 2001) can be directly used with the more detailed simulation of forest dynamics provided by the Q-LAND model.

This report provides first a short description of the FIN-LANDIS model and then a more detailed account of the Q-LAND design. Parameterization of the Q-LAND model is discussed in the end of the report.

2. FIN-LANDIS

2.1 General structure

FIN-LANDIS expands the LANDIS representation of stand structure (He et al. 1999) using two binary arrays for each site. The first array represents the presence/absence of each species in 10-year age classes. The other one determines whether each cohort present is classified as dense or thin. (Pennanen and Kuuluvainen 2001). Thin and dense cohorts have different effects on regeneration of new cohorts under them and on seed availability. This makes it possible to predict the presence of non-dominating age classes and model the development of the multi-layered stands which are typical of many pine-dominated ecosystems (Agee 1998, Kuuluvainen et al. 2001). The thin/dense characterization of cohorts is not an ad hoc substitute for quantitative data but an application of rule-based modeling approach.
A FIN-LANDIS iteration consists of the following steps: 1) Fire events are simulated in the landscape, resulting in removal or thinning of tree cohorts. 2) Species regeneration is simulated for each cell and species. Seed availability and the possibility of vegetative reproduction is checked first. Regeneration also depends on species, site properties and competition. 3) Stochastic thinning and death of old cohorts is simulated for each cell.

2.2 Stand dynamics

For each species and site, the regeneration routine first checks whether the competitive environment allows regeneration. A species of a certain shade tolerance class may regenerate only when shading (dense) cohorts of species with the same or higher shade tolerance class are not present (Roberts 1996). The presence of seeds is assessed in a spatially explicit, but non-quantitative manner, i.e. presence of seed only depends on the distance of the nearest seed source. When the availability of seeds and light allow regeneration, the establishment still depends on the species, land type, and time-since-disturbance. Of the two establishment parameters for each land type and species, the first gives the establishment probability immediately after a disturbance and the second after the ground vegetation and organic soil layer have recovered from the disturbance. Vegetative reproduction may occur when one or more cohorts of the species have been removed from the site during the same model iteration. The actual probability of vegetative sprouting is given as a parameter.

When the probability of the establishment of a new cohort is $p$, the probability of getting a dense cohort is $p^c$, and the corresponding probability of a thin cohort is $p - p^c$. The exponent $c$ is related to the spatial aggregation of the regeneration. If there are not enough seeds for the establishment of a dense cohort, new cohorts are always thin.

In the absence of large-scale disturbance, trees die from senescence. After the age of a dense cohort reaches 50% of the longevity of the species, it may turn into a thin cohort, corresponding to the death of individual old trees or small groups of trees. After the cohort age reaches 80% (or a user-defined proportion) of longevity, the cohorts start dying completely. Fires kill cohorts depending on the fire intensity, cohort age and species-specific fire resistance.

2.3 Fire events

The number of ignition attempts during each model iteration follows a time-homogenous Poisson distribution and the spatial pattern of ignitions attempts is random. Whether an ignition leads to a fire and whether a fire is able to spread depends on the vegetation structure and weather. Weather conditions at the time of the fire determine the set of sites that are flammable during a fire event. The
design implements the idea that when weather conditions are not especially favorable for fires, fire ignition and spread are restricted by the landscape structure. Under favorable (dry and warm) conditions, however, the fire spread is only constrained by the duration of favorable weather. The maximum duration of each fire is exponentially distributed with the mean duration given as a parameter. Another random variable represents the weather conditions during the fire. Fires spread through the flammable sites until the maximum duration is reached or the landscape structure causes fire extinction. Different rates-of-spread, depending on the site properties or the direction of fire spread, are also implemented. Fire intensity, i.e. tree mortality, is determined based on the weather variable and the stand structure.

2.4. Model testing

As part of the evaluation of FIN-LANDIS it was tested, whether the model was able to reproduce the current forest composition of the Ulvinsalo nature reserve, eastern Finland, based on a GIS map of ecological site types and the fire history of the area. Current GIS data by the Forest and Park Service (FPS) was used as reference conditions. The errors in the predicted area of cover types based on species composition, and in the predicted occurrence of spruce and pine, were all less than 20%, both in relation to the FPS values or in relation to total landscape area (Pennanen and Kuuluvainen 2001). The qualitative pattern of the tree age distribution was also similar in both the simulated and the empirical data sets. The accuracy was considered satisfactory.
Figure 1. The mapped distribution of stand types in the Ulvinsalo area according to the presence of coniferous trees, based on the field data by the Forest and Park Service and the output of FIN-LANDIS simulation. Species name in parenthesis represents sparse presence (for more details, see Pennanen and Kuuluvainen 2001).

3. Q-LAND model

3.1 General structure

The dynamics of the Q-LAND model consist of the landscape-level processes of disturbance and seed dispersal, and the stand-level processes of seed regeneration, growth, mortality and seed production (Fig. 2). The essential changes in the Q-LAND as compared to FIN-LANDIS, are the addition of quantitative cohort attributes, and the quantitative calculation of seed dispersal. The basic idea is to use empirical or simulated growth curves for deriving the basal area or volume of the cohorts. The difficulty is that there are usually several cohorts in a stand, and the growth space has to be allocated
between the cohorts. To solve this as simply as possibly, the actual quantitative attribute of the cohorts
is its density, meaning the proportion of the stand area occupied by it. The initial cohort density is
determined by the regeneration process and competition between trees. During the cohort lifespan, its
densities may only decrease due to disturbance events or old age.

Figure 2. Flow chart of a Q-LAND iteration. The landscape processes are first simulated, and then the
stand processes for each raster cell.
Stands (raster cells) are conceptually divided into smaller spatial elements, territories (Fig. 3). The territories are just large enough to accommodate one big canopy tree each (10-100 m²). A territory is said to be occupied by a specific cohort, if the dominating canopy tree in the territory belongs to the cohort, or if there is currently no such tree in the territory but the next large canopy tree will belong to the cohort in question. A cohort’s density is the proportion of the territories it occupies in a cell (Fig. 4). The sum of cohort densities in a cell is by our assumptions 1 or less. Individual territories are not explicitly modelled, but the stand dynamics is based on this conceptual notion.

![Diagram](image)

**Figure 3.** The spatial framework in the simulation model. Landscape is divided into 1-hectare cells in a spatially explicit way. Conceptually, cells consist of territories, but territories are not explicitly simulated.
Figure 4. An example of a stand, divided into 25 territories. (The actual number of territories in a cell is higher.) Trees are divided into 4 cohorts. Cohort 1 is 80 years old, and its density is $10/25=0.4$. Cohort 2 is also 80 years old, but belongs to a different species, and its density is $11/25=0.44$. Cohort 3 belongs to the same species as cohort 2, but is only 20 years old, and its density is $4/25=0.16$. Cohorts 1 – 3 form the canopy layer, and the sum of their densities is 1. Understory cohort 4 has a density $9/25=0.36$.

The quantitative attributes of a cohort are estimated using empirical yield tables or simulated growth curves (using SORTIE or any other model), which give e.g. the basal area of a cohort based on age and species. The basal area or volume curves for fully-stocked single-species stands are scaled by the cohort density to get the actual cohort attributes. The basal area $B_i$ of cohort $i$, is

$$B_i(a) = D_i \cdot B_0(a),$$  \hspace{1cm} (1)

where $a$ is cohort age, $D_i$ is density of the cohort, and $B_0$ is the potential growth curve used.

The shape of the cohort growth curves depends on the conditions under which the cohort grows. Cohorts established on an open site grow at different rate than cohorts established in the gaps of late-successional stand, or after a partial disturbance. Therefore, a suitable growth curve is assigned to a cohort when it is created. This means that the stand structure at cohort creation is used as a proxy for the growth conditions that the cohort will face.

The density of a cohort will start decreasing at old age, to implement stand disintegration due to single-tree and small-scale disturbance events. A cohort basal area curve is in fact the product of an
increasing curve depicting relative basal area and a decreasing density curve (Fig. 5). Relative basal area means here the basal area of the cohort divided by the number of territories it occupies. The basal area grows first, because the basal area grows in each occupied territory. Later, the basal area decreases when old trees die and the number of occupied territories decreases. The death of old trees typically creates small, expanding gaps in the late-successional stands. These small-scale disturbances are implicitly included through the cohort density curves. Large-scale disturbance events, which affect whole stands or wider areas are simulated separately. They remove cohorts, decrease cohort densities and change the quality of seedbeds. Self-Thinning is not explicitly simulated, because it does not affect the proportion of territories occupied by a cohort, but it is implicitly accounted for in the shape of the growth curves.

**Figure 5.** A basal area curve of a cohort is a product of a decreasing density curve and the increasing relative basal area.

### 3.2 Establishment of cohorts

The establishment of new cohorts is the most essential point of stand dynamics in Q-LAND, as the future of each cohort (apart from the disturbance events) is determined at that point. At the level of a territory, there are two ways of establishment to be considered. In the first case, all the trees in the territory have died, and the territory is empty. The sexual and asexual regeneration of seedlings have to be considered, and the species that will occupy the territory chosen from among the regenerating species. The second case is that there are understory trees already present below a succumbed canopy tree. To implement this, a separate layer of understory cohorts is also included in the model. The
densities of the understory cohorts also sum up to 1 or less for a single cell. When canopy trees die, the released understory trees get established as new canopy cohorts.

Consider first the cohort establishment at an open site, i.e. in a cell with no cohorts present. The availability of seeds, vegetative propagules, and the quality of seedbeds will determine the numbers of new seedlings per square meter, \( N_k \), for each species \( k \), in the cell. A rule is needed to determine the densities of the new cohorts, i.e. which species will occupy each territory. An option for such a rule is that the tree, which will prevail in the end, is randomly chosen from the seedlings available in the territory. Then, the probability that species \( j \) will occupy a territory is

\[
p_j = \frac{N_j}{\sum_k N_k}.
\]  

(Note that \( N_j \) are in fact numbers of seedlings in the whole cell, but if seedlings in a territory form an unbiased sample of the cell population, eq. 2 yields the correct probabilities). When seedling density is low, there are territories with no seedlings at all. The proportion of territories of the cell that contain seedlings is

\[
s = 1 - \exp(-b \cdot A \cdot N^c),
\]

where \( N \) is the total number of seedlings per square meter, \( A \) is the territory size in square meters and \( b \) and \( c \) are empirically fitted parameters describing the spatial patterns of regeneration (D. Greene, unpublished data). Combining the previous, the densities of the new establishing cohorts of each species \( j \) are

\[
D_j = p_j \cdot s.
\]

Note that only one new cohort for each tree species can be established during one time step.

Another option for implementing the establishment is that there is a strict competitive hierarchy of tree species. When there are seedlings of several species in a territory, the most competitive species will occupy it, regardless of numbers of seedlings. Analogously to eq. 3, the proportion of territories with species \( j \) present is \( s_j = 1 - \exp(-b \cdot A \cdot N_j^c) \). If species are ordered so that competitiveness decreases when \( j \) increases, we now get \( D_1 = s_1, D_2 = s_2 \cdot (1-s_1), D_3 = s_3 \cdot (1-s_1-s_2), \) and so forth.

In actual forest succession, the probability of a certain species to occupy a territory would depend in a complicated way on the numbers of seedlings of different species. There are no detailed models of this process available. We will use a combination of the above two models, where species are classified according to their juvenile growth rates (Table 1). When able to regenerate, the faster growing species will always occupy a territory were they are present. Species in the same tolerance group are assumed equally competitive, and eq. 2 is used to divide the territories between them.
However, the slower growing species are generally the more shade-tolerant ones, and may regenerate as understories.

Next consider tree establishment in small gaps or under canopies thinned by a partial disturbance. The proportion of the territories available for establishment is $e = 1 - \Sigma D_i$, where the sum is over the densities $D_i$ of all canopy cohorts $i$ in the cell. The densities of the regenerating cohorts need to be multiplied by $e$, so that e.g. eq. 4 becomes $D_j = e \cdot p_j \cdot s$. In addition, shade tolerance varies between species. Therefore establishment coefficients will be used to determine the proportion of empty territories that are actually available for establishment of each species. The establishment coefficients depend on the species and the successional state of the stand. As an example, if only 10% of the gap area of late-successional stands actually has enough light for aspen regeneration, the corresponding establishment coefficient is 0.1. The actual density of a regenerating aspen cohort is then $D_j = 0.1 \cdot e \cdot s \cdot p_j$.

The dynamics of the separate understory layer is simpler than the canopy dynamics. The density of the understory cohorts decreases only through establishment to the canopy layer and in the disturbance events. The regeneration of the understory cohorts is calculated in a similar way as above. However, a species is only allowed to recruit to the understory in the territories occupied by canopy trees with a lower shade tolerance (Roberts 1996). Thus, for the understory regeneration, $e$ above is replaced by $d = \Sigma D_i$, where the sum is over all cohorts $i$ that belong to the species that are less shade-tolerant than the regenerating species.

When canopy cohorts die (partially or entirely), the released understory cohorts are first used to fill the new available space. After that, if there is still unused space left, the establishment will proceed directly from new seedlings. As an example, let the total density of the cohorts of species A be $D^A_1=1$ before the disturbance, and $D^A_2=0.3$ after the disturbance. Assume that the density of an understory cohort of species B is $D^B=0.4$ both before and after the disturbance. The understory trees released in the disturbance will cover the proportion $D^B(D^A_1-D^A_2) = 0.28$ of the territories. This leaves the proportion $1-D^A_2-0.28 = 0.42$ of the stand area available for new regeneration from seedlings.

3.3 Seed availability and regeneration

Seed production can be modelled as proportional to the basal area of the source tree. Mean number of seeds produced annually is for boreal tree species

$$ Q = 3067 \cdot B \cdot m^{-0.58}, $$

(5)
where $B$ is the basal area of the source trees and $m$ is the average mass of one seed (Greene and Johnson 1994).

We will use a cell size of 1 hectare, and empirically fitted equations for seed dispersal (D. Greene, unpublished data). The number of seeds arriving from the source cell on a square meter of land at the distance of $x$ meters from the center of the source ($x>50$) is

$$Q(x) = B \cdot c \cdot \exp(-0.22 \cdot f^{0.75} \cdot x^{0.59}),$$  \hspace{1cm} (6)

where $f$ is the terminal velocity of the seeds, $B$ is the basal area of the source trees. Coefficient $c$ is calculated from $f$ and seed mass $m$ to ensure that the integral of $Q(x)$ over the landscape sums up to $Q$ of eq. 5.

In practice, the seed availability will only be calculated for the whole cells of one hectare. We also assume that all the seeds that travel further than the 9 nearest cells from the source cell are uniformly distributed over the landscape. The amounts of seeds traveling between cells can be calculated using the eqs. 5 and 6.

The density of surviving seedlings depends further on the quality of seedbeds. Seedling survival on mineral soils and some other good seedbeds is

$$s_g = 0.43 \cdot (1 - \exp(-1.83 \cdot m^{0.43})),$$

and on other (‘poor’) seedbeds

$$s_p = 0.43 \cdot (1 - \exp(-0.33 \cdot m^{0.76})),$$

where $m$ is the average seed mass (Greene and Johnson 1998). When $p$ is the proportion of good seedbeds of the cell area, the total seedling survival is $s_t = ps_g + (1-p) s_p$.

Two further aspects of regeneration are the serotiny and asexual propagation. To take care of serotiny, the number of seeds produced in the trees needs to be calculated before simulating fire disturbance. Depending on the degree of serotiny, fire may kill all, some, or none of the seeds in the trees. Seed dispersal is simulated after the fire events during the model iteration. Asexually propagated seedlings are simply added to the numbers of sexual seedlings, and they stay in the same cell as their parent tree. The number of asexual sprouts produced is $s_a = vB$, where $B$ is the basal area of dead parent trees in the cell and $v$ is a species-specific parameter describing the strength of asexual propagation. From the above, the total number of regenerating sexual and asexual seedlings per square meter is

$$s = T \cdot s_t \cdot Q(x) + 10^{-4} \cdot s_a,$$

where $T$ is the timestep length in years, and cell size is one hectare.
3.4 Disturbance events

Models to simulate fire and harvesting have been developed earlier, and can be used with Q-LAND. Such fire submodels have been described by Pennanen and Kuuluvainen (2001), and He and Mladenoff (1999). Models of forest harvesting have been developed by Gustafson et al. (2000) and by Fall et al. (2001). SELES modeling environment (Fall and Fall 2001) provides a generic platform for simulating landscape disturbance processes (among others) and can be linked to Q-LAND simulations with a runtime interface.

Disturbance events change the stand by killing trees, killing seeds in the trees and changing the seedbeds. Tree mortality is implemented by decreasing the density of canopy or understory cohorts, which changes the cohort basal areas proportionally and releases growth space for new regeneration and establishment. Seedbed quality is given for each successional stage as a parameter, where successional stage depends on the disturbance history. The maximum fire intensity tolerate by seeds in the trees is given as a parameter, and is positive for species with serotinous cones.

3.5 Parameterization

Q-LAND has three types of parameters: (1) parameters specific to site type and tree species, (2) parameters specific to species, site type and successional stage, and (3) parameters specific for site type and successional stage. Site type and successional stage are used to stratify especially the cohort growth curves, establishment coefficients and area of good seedbeds. For practical reasons, only a limited number of different combinations can be used. To begin with, we only used two successional stages: open stage after stand-replacing disturbance, and wooded stage covering all other conditions. In addition to the parameters listed below, other parameters are needed to define the disturbance occurrence.
Figure 6. The development of a forest stand through time in a simulated forest landscape. Simulation begins with only seedlings present. A fire occurs at year 900. Output is from the prototype model which has not been rigorously parameterized. Fir = Abies balsamea, w. spruce = Picea glauca, birch = Betula papyrifera, aspen = Populus tremula.

The parameters specific to species and site type are shade tolerance class, juvenile growth rate, fire resistance, serotiny, seed mass, seed terminal velocity, and the strength of asexual propagation (Table 1). Shade tolerance is an ordinal classification, used to determine which species may grow as understory cohorts. Fire resistance class is used to determine fire mortality, but is not considered here in more detail. Juvenile growth rates are used to determine the outcome of competition between seedlings. Serotiny is so far implemented as a binary variable determining whether seeds survive fires or not. Seed mass is used as a proxy for seedling survival on good and poor seedbeds separately and for parametrizing the seed production equation. The vertical terminal velocity of he seeds determines the seed dispersal. Strength of asexual propagation measures the average number of sprouts created per square meter of parent basal area. Values for all these parameters can be found in the literature for the most important tree species of the boreal region. Of these parameters, only the juvenile growth rate depends necessarily on the site type, and it is in the beginning only needed on an ordinal scale. Therefore growth rates can be estimated from the available data for typical sites and the general habitat requirements of the species.
Table 1. Species attributes. Growth rates (competitive ability at early succession) for mesic sites.

<table>
<thead>
<tr>
<th>Species</th>
<th>Pinus banksiana</th>
<th>Picea glauca</th>
<th>Thuja occidentalis</th>
<th>Betula papyrifera</th>
<th>Abies balsamea</th>
<th>Populus tremuloides</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shade tolerance</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Fire resistance</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Juvenile growth rate (ordinal scale)</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>5</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Serotiny (on/off)</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Strength of asexual propagation</td>
<td>0</td>
<td>0</td>
<td>50</td>
<td>100</td>
<td>0</td>
<td>1000</td>
</tr>
<tr>
<td>Seed terminal velocity (m/sec)</td>
<td>0.75</td>
<td>0.66</td>
<td>1.0</td>
<td>0.55</td>
<td>0.86</td>
<td>0.35</td>
</tr>
<tr>
<td>Seed mass (g)</td>
<td>0.0035</td>
<td>0.0022</td>
<td>0.002</td>
<td>0.0005</td>
<td>0.0065</td>
<td>0.0004</td>
</tr>
</tbody>
</table>

Parameters specific to species, site type, and successional stage are the growth curves for the quantitative attributes and the establishment coefficients. The growth curves after a stand-replacing disturbance can be derived from the yield tables for single-species stands or from a validated stand-level simulation model such as SORTIE (Pacala et al. 1996). The curves that apply for other successional stages (i.e. for cohorts grown under shading in old-growth conditions or after partial disturbances) can be estimated using a stand model. Curves can be determined also using empirical age-size relationships, with some simplifying auxiliary assumptions.

The establishment coefficients, which correspond to the survival of young trees, are only used to adjust the regeneration under shaded conditions, to take into account the differences between species in shade tolerance. The establishment coefficients must be estimated by calibration, i.e. through adjusting them until the model output is satisfactory. The reference data can be derived from a stand-level model or from empirical data. E.g. the steady-state (climax) stand composition (BA proportions of species) can be used to estimate the establishment coefficients for some species.

Fig. 6 shows a simulated development of one stand in a landscape. The tree parameters, especially the establishment coefficients, can be calibrated by comparing such model output to empirical data on forest composition and to the output of stand-level models.
The parameters specific to site type and successional stage are the proportion of good seedbeds, and the parameter $a$ and $b$ describing the spatial pattern of regeneration in eq. 3. There are empirical data for each of these for boreal landscapes with fire disturbance (Greene and Johnson 1998).

4. Conclusions

The development, calibration and implementation of our new Q-LAND landscape model for the region of Abitibi, Québec are being conducted with the long-term goal of being able to address various theoretical questions and develop and test alternative sylvicultural and forest management scenarios inspired by an understanding of natural disturbance dynamics in boreal forests. We will work closely with the natural disturbance group of the SFMN for the implementation phase of this project. Because of the diversity of species and disturbance types in the boreal forest, we need to understand how different disturbance regimes interact to shape the forests of this large biome. Our modeling approach will permit the testing of different scenarios at multiple scales. We can then more appropriately choose management scenarios to implement in the field based on the needs of our various partners.

Some theoretical and practical questions and applications to be addressed with this model are:

(1) What are the impacts of interactions between disturbance types (insect outbreaks, gaps and fires) on structure and composition at stand and landscape levels; this work will include the evaluation of changes in different disturbance regimes;

(2) What are the ecological and silvicultural implications of the multiple cohort approach suggested by Bergeron et al. 1999 for black spruce and mixed-wood forest of north-western Québec;

(3) Evaluating the ecological and silvicultural implications of the various alternative silvicultural scenarios suggested by Greene et al. (2000) to naturally regenerate the boreal mixed-wood forest of Canada;

(4) Use of Q-LAND to help TEMBEC select the best ecological and silvicultural scenarios for the implementation of its natural-based forestry operation in the Temiskaming. Simulations and disturbance history reconstructions will be used to develop field tests.

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