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Spatially explicit simulation of long-term boreal forest landscape dynamics: incorporating quantitative stand attributes

Juho Pennanen[a,*], David F. Greene[b], Marie-Josée Fortin[c], Christian Messier[d]

[a] *Department of Forest Ecology, University of Helsinki, P.O. Box 27, FIN-00014, Finland*
[b] *Department of Geography, Concordia University, 1455 de Maisonneuve W., Montréal, Qué., Canada H3G 1M8*
[c] *Department of Zoology, University of Toronto, 25 Harbord St., Toronto, Ont., Canada M5S 3G5*
[d] *Département des Sciences Biologiques, Université du Québec à Montréal, Case Postale 8888,*
Succursale Centre-ville, Montréal, Qué., Canada H3C 3P8

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. We propose a new approach to bridge the forest stand and landscape processes. Hence, while interested in the boreal forest dynamics at the landscape level, we develop a submodel of stand-level forest dynamics that responds to the landscape-level processes in a spatially explicit landscape model. Compared to the LANDIS model that we used as a starting point, our approach incorporates, in a spatially explicit and quantitative manner: (1) stand-level prediction of basal area and tree volume, and (2) seed dispersal, and sexual and asexual regeneration. Stand development is partly based on growth tables given as model input which means that stand submodel behavior is constrained within a reasonable range. We tested the approach in simulating the development of mixed boreal forests of Quebec, Canada. The simulations demonstrate that stand dynamics can be calibrated to match specific targets and that responses to changes in the initial conditions are realistic. This new modeling approach should allow addressing various theoretical questions and developing, as well as testing, alternative silvicultural and forest management scenarios.
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1. Introduction

The boreal forests are influenced by both natural (e.g., insect epidemics, wildfires) and anthropogenic (logging activities) disturbances. These disturbances operate at multiple spatial and temporal scales, generating a complex forested landscape mosaic (Levin et al., 1997) and influencing forest regeneration (Greene et al., 1999).

The only way to evaluate the long-term impacts of different disturbance regimes on forest regeneration and development at the landscape scale is by means

* Corresponding author. Tel.: +1 358 9 191 58144;
fax: +1 358 9 191 58100.
E-mail address: juho.pennanen@helsinki.fi (J. Pennanen).

of model simulations (Shugart, 1998; Mladenoff and Baker, 1999; Messier et al., 2003). Simulation modeling can be used to evaluate the economic and ecological consequences of different management and harvesting regimes (Messier et al., 2003; Fall et al., 2004). Models can also be used to explore the historical or natural variability of the forest landscapes, under which the current biological diversity has evolved (Kuuluvainen, 2002; Pennanen, 2002; Wimberly, 2002).

Spatially explicit simulation models of forest landscape dynamics need to incorporate processes functioning on two levels of spatial hierarchy: landscape level processes (e.g., fire, insect outbreaks, harvesting, seed dispersal) affect several patches or mediate interactions among the patches, and patch-level processes affect individual forest patches, responding to the structures created by the landscape-level processes.

Our goal was to develop a model which incorporates forest stand processes in enough detail to estimate ecological and economic values, as well as simulates the landscape-level processes of disturbance and dispersal. In terms of model scope, the specific targets for this paper were that the model: (1) tracks the basal area and volume of each tree species in each forest patch, (2) simulates quantitatively seed dispersal and tree regeneration in a spatially explicit manner, (3) simulates stand-replacing and non-stand-replacing disturbances, and (4) is suitable for long-term (100–10 000 years) and large-scale (103–106 ha) simulations.

Then, in terms of model applicability, the model: (5) should be useful for exploratory and theoretical studies even when parameterization data are limited, (6) should be amenable to calibration and parameterization using empirical data on stand development or the output of detailed stand-level models, and (7) should produce accurate estimates when sufficient parameterization data are available.

The basic challenge tackled in this paper is therefore to design and integrate a submodel of stand development with a landscape simulator. Simulating the change in cohort volume or basal area requires a certain level of detail in the description of stand dynamics. The stand submodel also needs to be mechanistic enough to react reasonably to different types of disturbance events and to changes in seed input from the surroundings. However, the submodel should be simple enough that it can be parameterized with reasonable effort. We also wanted the computing requirements to be low enough

for operation on standard PCs when simulating landscapes with 10 000–1 000 000 grid cells.

One possibility would be to use or modify an existing model of stand development in a landscape simulator. There are numerous simulation models of stand and landscape level forest dynamics, but we are not aware of models that directly or after small adjustment would be suitable for our purpose (Bossel, 1991; Botkin, 1993; Pacala et al., 1993; Shugart, 1998; Mladenoff and Baker, 1999; Urban et al. 1999; Barrett, 2001; Bugmann, 2001; Bugmann et al., 2001; Hynynen et al., 2002; Messier et al. 2003).

This paper describes an approach to landscape level forest simulation, focusing on the sub-model for stand-level forest dynamics, and shows that it meets the above goals to a large extent. Our model development builds from recent developments of the LANDIS (Mladenoff et al., 1996; He and Mladenoff, 1999) and FIN-LANDIS models (Pennanen and Kuuluvainen, 2002). The starting point in developing the new model, Q-LAND, is the addition of quantitative attributes to tree cohorts, which are used to describe the tree layer in LANDIS. The possibility of adding quantitative cohort data was already suggested by He et al. (1999). We test the Q-LAND model by simulating dynamics of boreal mixedwood forests in Quebec, Canada.

2. Model structure and processes

2.1. General approach

The dynamics of our Q-LAND landscape model consists of landscape-level processes of disturbance and seed dispersal, as well as stand-level processes of regeneration, growth, mortality and seed production (Fig. 1). Q-LAND adds to the FIN-LANDIS design (Pennanen and Kuuluvainen, 2002) quantitative cohort attributes and quantitative calculation of seed production and dispersal. The FIN-LANDIS model was designed by modifying and expanding the LANDIS model (Mladenoff et al., 1996; He and Mladenoff, 1999), through adding detail to the simulation of tree regeneration, stand structure and fire behavior (Pennanen and Kuuluvainen, 2002).

Following Mladenoff et al. (1996), a landscape is represented by a raster map of 102–106 square cells, where each cell represents a forest stand. Reasonable cell size is 1–10 hectares, as between-cell tree
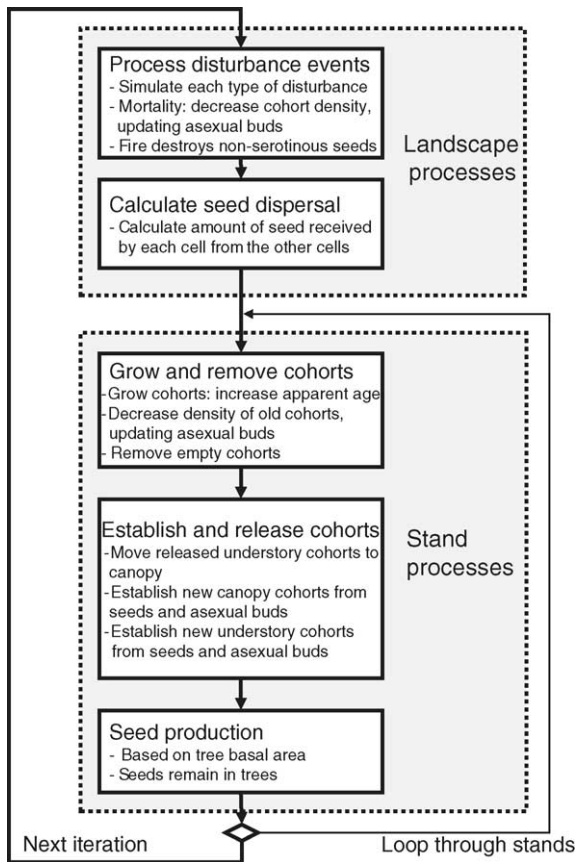
Fig. 1. Flow chart of Q-LAND. During one model iteration, landscape processes are first simulated, then the stand processes for each raster cell are simulated.

Table 1
A growth table used for trembling aspen (*Populus tremuloides* Michx.)

Age (years)	Density	Basal area (m²/ha)	Volume (m³/ha)
0	1	0	0
10	0.992	3.6	4.8
20	0.984	10.8	43
30	0.976	21.3	107
40	0.966	27.9	165
50	0.942	31.3	210
60	0.908	32.8	243
70	0.869	33.3	266
80	0.828	33.3	283
90	0.790	33.1	295
100	0.749	32.3	301
110	0.661	28.4	278
120	0.490	20.8	220
130	0.187	8.9	111
140	0	0	0

Data by Pothier and Savard (1998) for high density aspen stands in Quebec with site quality index 21. See Section 3 for the derivation of cohort density values.

competition is not simulated and vegetation and seed input are assumed to be spatially uniform within cells. 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 comprises the trees of a species that established during the same time step. This cohort-based data structure is inherited from VAFS/STANDSIM of Roberts (1996).

Our solution to the problem of decoupling the details of tree growth from landscape dynamics is based on the simple idea that simulated tree cohorts follow growth tables that are given as model input. The growth tables give quantitative attributes of the tree cohorts, such as basal area, volume and tree dimensions as a function of cohort age, tree species and site quality (Table 1). The growth tables may be based on empirical models or produced by stand-level simulation models.

Most empirical growth tables describe the development of even-aged, single-species stands. However, realistic stands have multiple tree species and age classes in varying proportions and spatial arrangements. While there is no perfect way to use the simple growth tables in such complex situations, the growth tables obviously contain information that is useful for estimating cohort and tree growth in heterogeneous stands.

The formulation of the stand submodel is based on a conceptual model where each grid cell consist of *territories*, each capable of lodging one full-grown tree. A cohort *occupies* a territory if the dominating canopy tree of the territory (the tree that will eventually be the sole occupant of the territory) belongs to the cohort. The territories are not explicitly simulated in the landscape model. Instead, we track the proportion of the territories occupied by each cohort with the cohort variable called *density*. The sum of the densities of all canopy cohorts is 1 or less. Cohort-level quantitative attributes such as basal area are derived by multiplying the values obtained from the growth table by cohort density, while tree level variables such as diameter are obtained directly from the growth tables.

The initial density of a cohort is determined based on the number of seedlings and asexual sprouts present, taking into account competition with other cohorts in the stand. Over time, a cohort's density may only

decrease, when some territories no longer have trees that belong to the cohort.

With the above assumptions, a territory can be occupied by only one shade intolerant species at a time. However, shade tolerant trees may survive in the same territories as understory trees through the lifespan of the canopy trees. Therefore, in addition to the canopy cohorts, the simulation model has a separate set of understory cohorts for each cell. The density of understory cohorts also adds up to 1 or less. When the density of a canopy cohort decreases or a cohort is eliminated, the understory cohorts may occupy the released space in the canopy layer.

Growth and mortality of trees depend on the competitive environment. This is implemented by controlling the rate of cohort development along the path defined by the growth table. For this purpose, each cohort has an attribute called *apparent age*, which may increase at a slower rate than actual age. Apparent age is used to index cohort attributes from the growth table.

2.2. Implementation and data structure

We implemented Q-LAND in an object-oriented manner using the C++ programming language. Most of the input–output routines, landscape level data framework and landscape level events were inherited from the LANDIS (Mladenoff et al., 1996) and FIN-LANDIS (Pennanen and Kuuluvainen, 2002) models.

Cohorts on each landscape cell are contained in linked lists. There are two lists per tree species per cell, one for canopy and one for understory cohorts. Each cohort has two numerical attributes, apparent age and density. In addition, the cohort has a pointer to the assigned growth table.

The permanent site properties of the landscape are defined as a static site type map together with a corresponding attribute file, which are given as model input, similar to LANDIS model (He and Mladenoff, 1999).

2.3. Seed production and dispersal

Seed production is based on the basal area of the source tree. We model the mean number of seeds produced annually (Q_0) by

$$Q_0 = 3067 B m^{-0.58}, \tag{1}$$

where B is the basal area of the source tree (m^2) and m the average mass (g) of one seed. The equation is applicable to a range of tree species (Greene and Johnson, 1994). Seed production is calculated during each simulation step for each cell before the fire events are simulated. For the serotinous tree species seeds remain in the trees over fires, but otherwise seeds are killed along with the trees.

We model seed dispersal by empirically fitted equations (Greene and Johnson, 1989, 1996 and unpublished data). Seed number received per m^2 of land area at the distance of x meters from a source tree is

$$Q(x) = Q_0 (2\pi)^{-1.5} \sigma^{-1} x^{-2}$$
$$\times \exp\left(-0.5 \sigma^{-2} \left(\ln\left(\frac{x}{x_0}\right)\right)^2\right), \tag{2}$$

where Q_0 is the seed production of the tree, σ the standard deviation of the logarithms of distance traveled by the seeds, and x_0 the median distance traveled. Moreover,

$$\sigma = \left(\left(\frac{0.6}{f}\right)^2 + 0.55^2\right)^{0.5}, \tag{3}$$

and

$$x_0 = \frac{uz}{f}, \tag{4}$$

where f is the terminal velocity of the seeds (m/s), u the median horizontal wind speed (m/s), and z the seed release height (m). The model is for wind-dispersed seeds, and applicable to all boreal tree species.

We simplified the seed dispersal in the current model implementation by assuming that all the seeds produced in a cell that do not land in the source cell or its eight neighbors are evenly distributed over the whole landscape. This was done to decrease the computational load, to avoid edge effects, and to avoid the effects of possible underestimation of long-range dispersal due to rare weather events. The proportion of the seeds that remains in the source cell and the proportion of the seeds that lands within the eight neighbors were calculated from Eq. (2) through numerical integration. A mean seed release height of 15 m and mean horizontal wind speed of 1 m/s were assumed (Greene and Johnson, 1996). Table 2 shows the seed parameters and calculated dispersal parameters for five tree species.

Table 2
Seed mass and terminal velocity for the simulated species and the corresponding dispersal parameters for the simulation model

Species	Seed mass	Terminal velocity	Seed_local	Seed_near	Seed_far
Aspen	0.0004	0.35	0.463	0.303	0.233
Paper birch	0.0005	0.55	0.575	0.353	0.0721
White cedar	0.002	1	0.762	0.234	0.00378
White spruce	0.0022	0.66	0.635	0.331	0.0337
Balsam fir	0.0065	0.86	0.721	0.269	0.00969

Note: Seed_local, seed_near, seed_far are proportions of seeds that are deposited within the source cell, on the eight neighboring cells, and on the rest of the landscape, respectively. The tree species are trembling aspen, paper birch (*Betula papyrifera* Marsh.), eastern white cedar (*Thuja occidentalis* L.), white spruce (*Picea Glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill).

2.4. Regeneration density

The density of seedlings contributing to cohort establishment depends on seedling survival. Based on Greene and Johnson (1998), seedling survival on good seedbeds (mineral soil and decomposed logs) is

$$s_g = 0.43(1 - \exp(-1.83\,m^{0.43})), \qquad (5)$$

and on other ('poor') seedbeds

$$s_p = 0.43(1 - \exp(-0.33\,m^{0.76})), \qquad (6)$$

where m is the average seed mass (g) of the tree species. The total seedling survival is

$$s_t = ps_g + (1 - p)s_p,$$

where p is the proportion of good seedbeds of the cell area.

We did not find empirical data on the survival of aspen seedlings. We suspect that Eqs. (3) and (4) greatly over-estimate the survival of the tiny aspen germinants. Therefore, we lowered the estimates from Eqs. (3) and (4) by a factor of 100 for this species.

Asexual reproduction may occur following the death of canopy trees. The density of asexual sprouts per m^2 is

$$n_a = vB, \qquad (7)$$

where B is the basal area (m^2) per hectare of the dead stems and v a species-specific parameter (Table 3). Sprouts appear in the same cell as their parent trees.

From the above, the total number of regenerating sexual and asexual seedlings per m^2 is

$$N = n_a + 10s_t Q, \qquad (8)$$

where Q is the number of seeds available per m^2 per year, which is subsequently scaled to a 10-year time step.

2.5. Cohort establishment and release

During a model iteration (Fig. 1), the establishment and release of cohorts begins by simulating the release of understory cohorts, followed by creation of new canopy and understory cohorts from seedlings if growth space remains available. Competition between

Table 3
Species specific parameters for the simulations, apart from ones affecting seed dispersal

Species	Grow	Shade	Veg	S_tot	B_bed	Curve	Gap_reg	S_bckgr
Paper birch	6	1	0.01	72900	0.015	betu.cur	0.90	26282
White spruce	2	2	0	56600	0.026	pice.cur	0.06	95401
Balsam fir	3	3	0	46300	0.038	abie.cur	0.46	2242
White cedar	1	3	0	57600	0.025	thuj.cur	0.14	1088
Aspen	7	1	0.1	7600	0.014	popu.cur	0.50	8810

Note: Grow = juvenile growth rate ranking (1 = low, 7 = high); shade = shade tolerance (1 = low, 3 = high); veg = number of vegetative sprouts per 1 m^2 of parent basal area; S_tot = number of seedlings produced by 1 m^2 of source tree basal area, assuming all seedbeds are good; B_bed = seedling survival on poor seedbeds relative to survival on good seedbeds; curve = filename for the default growth table; gap_reg = late successional establishment coefficient; S_bckgr = background seeding that every cell receives, determined similarly to S_tot. Gap_reg values are given after the calibration. S-bckgr varied between simulations.

species is controlled by two ordinal scale parameters, specific to species and land type. These are juvenile growth rate and shade tolerance.

The release of understory cohorts proceeds as follows. The proportion of territories with no canopy layer trees is calculated as

$$D = 1 - \sum_k d_k, \tag{9}$$

where d_k is the density of cohort k, and k goes through the indexes of all canopy cohorts on the cell. Tree species are then considered one at a time, in the order of decreasing juvenile growth rates. For each species, proportion D of its understory cohorts will be released; i.e., the density d_k of each understory cohort k will change by

$$\Delta d_k = -d_k D, \tag{10}$$

where D is obtained from Eq. (9). Then, a new canopy cohort of the same species is created, with density $d_j = \Delta d_k$, and having the same apparent age as the released understory cohort.

Establishment of cohorts is based on the density of seedlings and asexual sprouts, and competition with other species. In terms of the conceptual model, we will assume that if several species are present in a territory, the species with the highest juvenile growth rate will occupy it.

The proportion of territories of the cell that contain seedlings of a species is

$$q = r(1 - \exp(-bAN^c)), \tag{11}$$

where N is the number of seedlings of the species per square meter, A the territory size in square meters and b and c are empirically fitted parameters describing the spatial patterns of regeneration (D. Greene, unpublished data). A gap establishment coefficient, r, modifies the seedling density when the stand has not recently experienced a stand-replacing disturbance. The establishment coefficients are required to regulate stand dynamics, because within-cell spatial variation in light levels and other factors affecting tree establishment are not explicitly considered.

Tree species are again considered in the order of decreasing juvenile growth rate. The density of the new

canopy cohort of species i is

$$d_i = q \left(1 - \sum_k d_k \right), \tag{12}$$

where q is obtained from Eq. (6), and d_k is the density of cohort k, and k goes through the indexes of all the canopy cohorts on the cell. Values of d_k are updated between species, to account for new cohorts created.

New understory cohorts are created in a similar process, but space available for the understory cohorts of each species depends on the shade tolerance ranking of the species. The density for the new understory cohort of species i is

$$d_i = q \left(1 - \sum_m d_m \right) \sum_k d_k, \tag{13}$$

where q is obtained from Eq. (6), and d_m the density of cohort m, and m goes through the indexes of already existing understory cohorts, and k goes through the indexes of the canopy cohorts of the species that have lower shade tolerance than species i. In terms of the conceptual model, this corresponds to the idea that a species can occupy an understory position only in territories lacking trees with the same or higher shade tolerance. Such 'competitive hierarchy' was proposed by Roberts and Betz (1999).

2.6. Cohort growth and mortality

Tree growth occurs as an increase in the apparent age of a cohort, which is used to look up the quantitative properties from the growth tables. A freely growing cohort not shaded from above grows at the maximum rate 1; i.e., its apparent age changes by one each simulated year. Suppressed cohorts grow slower, so that apparent age v changes during a time step by

$$\Delta v = gT, \tag{14}$$

where T is the time step length and g the growth rate modifier that depends on the stand structure.

In our simulations, the growth rate modifier for cohort j is

$$g_j = 1 - h \sum_k d_k, \tag{15}$$

where h is a parameter, d_k the density of cohort k, and k goes through the indices of the canopy cohorts whose apparent age is higher than that of cohort j. In the simulations below, we use a value of $h = 0.8$ for all species.

Tree mortality is manifested as a decrease in cohort density. Cohort density may only decrease during its lifetime. When the density reaches zero, the cohort is removed. A deterministic decrease of density corresponds to tree death due to small scale disturbance and old age. Stochastic disturbance events initiated at landscape level may also affect cohort density.

Growth tables given as model input give the cohort densities as a function of age. Because growth tables are for fully stocked cohorts, the density starts at 1.0, and ends at 0. According to the growth table, the relative change $m(t)$ in cohort density at cohort age t, during a 10-year time step, is

$$m(t) = \frac{(d(t+10) - d(t))}{d(t)}, \tag{16}$$

where $d(t)$ is the density given by the growth table at the age of t years. In the simulation, the deterministic change in cohort k's density d_k during a model iteration is

$$\Delta d_k = d_k m(v), \tag{17}$$

where v is the apparent age of the cohort.

The model derives the quantitative cohort attributes from the cohort's density, apparent age and the growth table. Attributes V such as basal area or volume are proportional to cohort density and are calculated as

$$V = \frac{V(v)d}{d(v)}, \tag{18}$$

where d is cohort density, v apparent age, $V(v)$ the value of the attribute given in the growth table at age v and $d(v)$ the density given by the growth table at v. An attribute A that is not directly related to cohort density, such as average tree height or diameter, is looked up directly from the growth table.

2.7. Minimum cohort density

The number of tree cohorts tends to increase in a simulated stand during forest succession. When growing space is released in small amounts, cohorts with a very low density will be created. Cohorts also split when understory cohorts are partially released to the canopy cohort layer. Over time, a cell may contain hundreds of cohorts. This is problematic because computer memory requirement increases linearly with the number of cohorts.

To solve this problem we defined a minimum density, $d_{\min}$ for new tree cohorts. If a new tree cohort, according to the description above, would have density $d < d_{\min}$, the cohort is actually created only with probability $d/d_{\min}$, and the density of a new cohort is set at $d_{\min}$. Increasing the minimum cohort density parameter will lead to a smaller number of cohorts, but on average should not affect stand composition and structure.

2.8. Disturbance events

Models to simulate fire (He and Mladenoff, 1999; Pennanen and Kuuluvainen, 2002) and harvesting (Gustafson et al., 2000; Fall et al., 2004) have been developed earlier, and can be used with Q-LAND. 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 run-time interface.

Landscape disturbance events are initiated stochastically, but their occurrence may depend on site type, forest stand structure and, in the case of harvesting, management zoning. Disturbance events affect individual stands by killing trees, killing seeds in the trees and changing the seedbeds. Tree mortality is implemented by decreasing the density of cohorts, which changes the cohort basal areas proportionally. The proportion of good seedbeds on a cell is determined by the time since a stand-replacing disturbance.

3. Parameterization

Q-LAND has three types of parameters: (1) parameters specific to site type, successional stage, and tree species, (2) parameters specific to species and site type, and (3) parameters specific for site type and successional stage. In addition, model input includes the growth tables specific to tree species (e.g., Pothier and Savard, 1998, as used in this study) and site type. Site types are defined for model simulations in an input raster map and a corresponding attribute file. We discuss here only parameters that influence the simulations presented in this study.

Species, site type and successional stage are used to stratify the establishment coefficients. Our simulations use two successional stages: open stage after stand-replacing disturbance, and wooded stage covering all other conditions.

Parameters specific to species and (optionally) site type are shade tolerance class, juvenile growth ranking, efficiency of asexual reproduction, and parameters defining seed production, and seedling survival. The values used in the simulations are given in Tables 2 and 3. Shade tolerance and juvenile growth rate are ordinal scale parameter. Of these parameters, only the juvenile growth rate is specific to site type.

The parameters specific to site type and successional stage are the proportion of good seedbeds, and the parameters *a* and *b* describing the spatial pattern of regeneration, used in Eq. (3). We assumed the proportion of good seedbeds to be 10% for stands that burned during the same time step and 1% otherwise. The empirical figure of 15–20% (Greene and Johnson 1998)
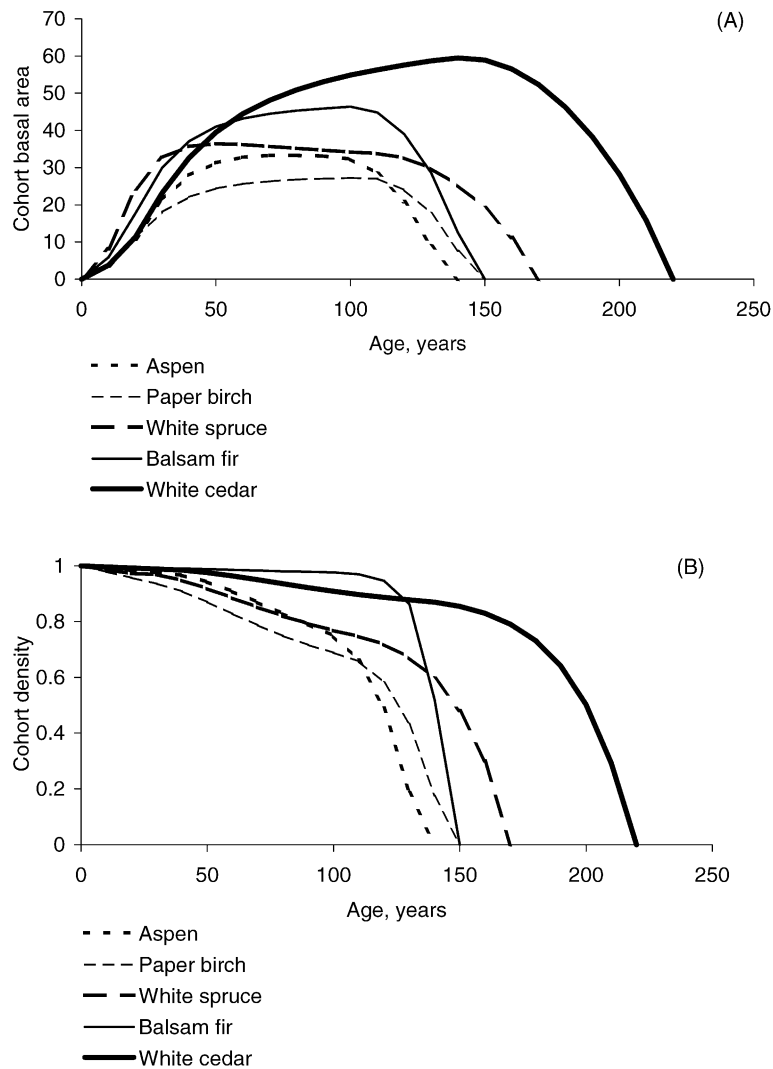

Fig. 2. Density curves and basal area curves given by growth tables used for the simulations in the study. Based on data from Pothier and Savard (1998). See text for details.

for burned areas was modified because seedbed quality would decrease during the 10-year model time step.

We used growth tables from Pothier and Savard (1998), choosing the tables for high-density stands with site quality indices 18 (coniferous species) and 21 (broadleaved species). Table 1 shows an example of a growth table used as model input. Basal areas against cohort age are shown in Fig. 2A.

We defined cohort density as the proportion of 25 m^2 plots that it occupies (corresponding to a territory size of 25 m^2 in the conceptual model). Assuming a random spatial pattern, cohort density

$$d = 1 - \exp(-0.0025M), \qquad (19)$$

where M is the number of trees per hectare. As the growth tables only give the number of trees with dbh >9 cm, the density curve was adjusted by setting it to start at 1.0 and by assuming a linear decrease in density between age 0 and the age of maximum tree density in the tables by Pothier and Savard (1998). After that, Eq. (10) is used to model density. The resulting density curves are shown in Fig. 2B.

4. Simulations

Model behavior with regard to stand-level forest dynamics was calibrated and tested using a 'landscape' with just one 1 ha cell. Simulation time-step was 10 years and simulation duration was 1500 years. We controlled the initial conditions, disturbance occurrence, and seed input from outside the stand, to study the simulated stand response. Seed input from outside the cell was controlled with background seeding parameters (Table 3). After the four single-stand scenarios, we tested the model on a landscape level to assess practicality in terms of computer requirements.

4.1. Scenario 1

The first simulation scenario describes stand succession initiated by a stand-replacing fire, and proceeding without other disturbance events. Seed input and initial seedbed quality were defined to correspond to a situation of a stand in the middle of a large burned area. This was done by first setting background dispersal to long-range dispersal on an average landscape. The dispersal

parameter 's_loc' (Table 3) for each species was set to 'seed_local' + 'seed_near' (see Table 2). This mimics the situation where the stand's neighbors are identical successional stands.

Scenario 1 was used to calibrate the gap establishment coefficients, which regulate tree regeneration under shaded conditions. The calibration target was defined by a specified steady state composition of old-growth stands. The target proportions of tree species, based on Kneeshaw and Bergeron (1998), were 61% (balsam fir), 22% (eastern white cedar), 7% (paper birch), 5% (white spruce), and 5% (aspen). We ran the simulation for a hypothetical 1500-year period with no landscape-level disturbance. The steady state composition of the simulated stands was defined as the average basal area proportions of the tree species during the last 300 years of the simulation. Gap establishment coefficients for all species were initially set at 1.0, and then adjusted until the steady state species proportions were within one percentage point from the target.

Calibration of gap establishment coefficients required about 20 simulations. The final coefficients produced a steady state stand composition according to the specified target conditions (Fig. 3A). The calibrated gap establishment coefficients were 0.5 (trembling aspen), 0.9 (paper birch), 0.06 (white spruce), 0.46 (balsam fir), and 0.14 (eastern white cedar). The corresponding steady state basal area percentages were 61% (balsam fir), 21% (white cedar), 6% (aspen), 6% (birch) and 5% (white spruce). The stand reaches its steady state composition at about year 500, with little change thereafter.

The stand is initially dominated by broadleaved trees. White spruce and balsam fir exceed the basal area of birch and aspen in 100 years. Balsam fir stabilizes at 60% of stand basal area while the abundance of broadleaved trees and white spruce drops before reaching their steady state values. Basal area of white cedar starts increasing after 100 years and stabilizes at about year 500.

4.2. Scenario 2

In scenario 2, the initial stand structure corresponded to a situation after a stand-replacing wind disturbance. Seed input from outside was set to mimic the situation in a stand surrounded by old-growth stands with the species composition of the steady state in the
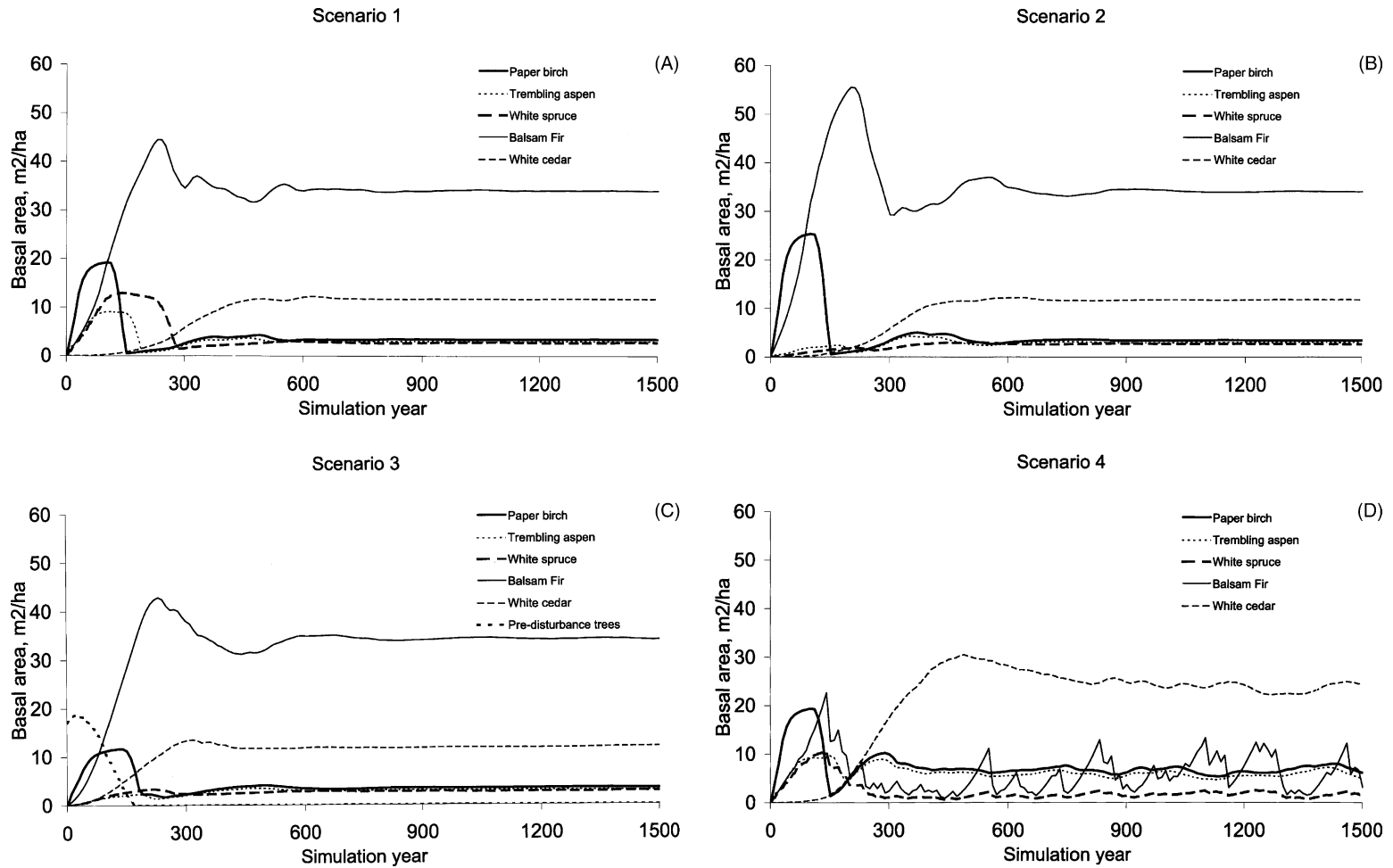
Fig. 3. (A–D) Simulated development of stand composition after a disturbance in four different scenarios (see text for description of scenarios).

first scenario. The calibrated gap regeneration coefficients generated in scenario 1 were used in scenario 2 simulations. Simulation duration was 1500 years.

Compared to scenario 1, aspen and white spruce are never abundant in the early part of stand development (Fig. 3B). Birch dominates the stand initially, and is later replaced by balsam fir. Differences from scenario 1 are caused by relative changes in seed input and seedling survival. Aspen seedlings survive poorly on undisturbed ground. Seed input of balsam fir is high enough for it to increase quickly, outcompeting white spruce. Eventually, the stand composition stabilizes to the same steady state composition as in scenario 1.

4.3. Scenario 3

Scenario 3 was similar to scenario 2, except that the initial stand represented a partial disturbance (e.g., variable retention cut), which had left 30% of stems of the steady state stand determined in scenario 1.

Stand development differs from scenario 2 mostly in that the new cohorts grew slower as long as the pre-disturbance trees remain (Fig. 3C). White cedar increases quickly, due to its competitive advantage in shaded environments. Pre-disturbance cohorts disappear from the stand in 160 years.

4.4. Scenario 4

Scenario 4 added a chronic spruce budworm disturbance to scenario 1. The average mortality due to

spruce budworm was set at 20% per 10-year iteration for balsam fir, corresponding roughly to the budworm induced mortality in northwestern Quebec during the last 100 years (Bergeron et al., 1995). Average white spruce mortality rate was assumed to be 50% of balsam fir mortality rate (Blais, 1983). The decadal mortality was chosen from a uniform distribution $U(0, 2x)$, where x is the average mortality.

Spruce budworm disturbance decreases balsam fir and white spruce abundance compared to scenario 1 (Fig. 3D). White cedar takes the dominant position in the steady-state stand. Aspen and birch also have clearly higher basal areas in the late-successional stage, compared to scenario 1.

4.5. Scenario 5

In scenario 5, we examined model performance by simulating fire-mediated dynamics of a large landscape. We simulated 1500 years of fire disturbance on a 50 000 ha landscape using a cell size of 1 ha. The mean fire rotation was ca. 100 years.

We initially applied a range of minimum cohort density values to evaluate changes in model predictions with execution speed. Increasing the minimum density value increased temporal variation in stand composition, but systematic bias was not apparent (Figs. 4 and 5). In general, a value of 0.02 produced the best balance between execution speed and realistic dynamics. Using this minimum cohort density value, a 1500-year simulation of the 50 000 ha landscape took a
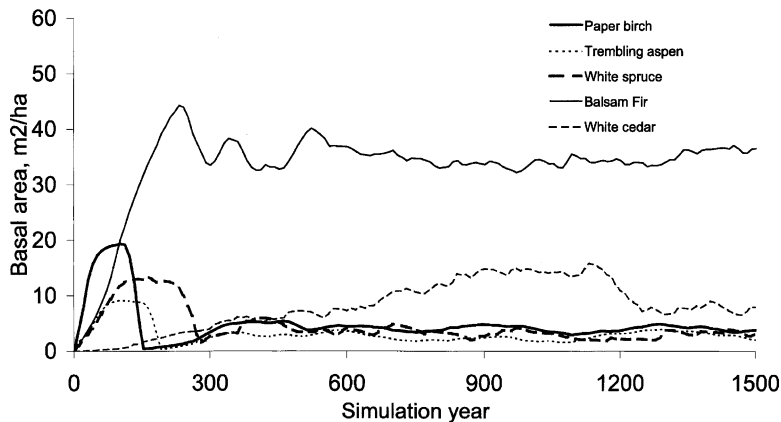

Fig. 4. Simulated development of stand composition after a stand-replacing disturbance, when minimum density of new cohorts is set at 0.02. Compare to scenario 1 (Fig. 3A) where minimum density value was 0.
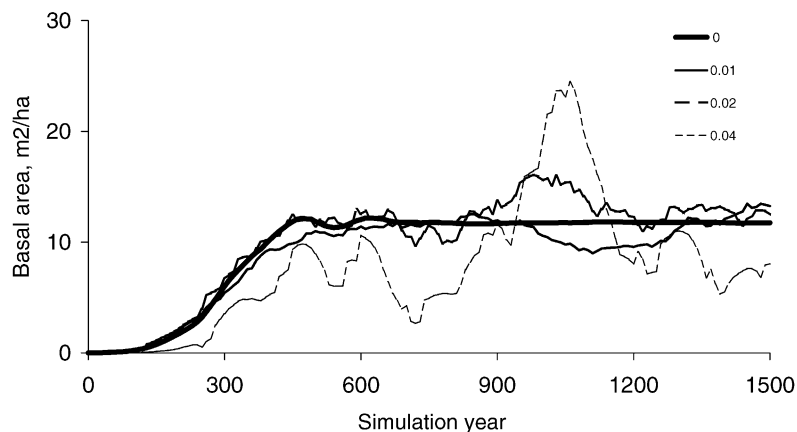
Fig. 5. Simulated trends in basal area of white cedar. Curves correspond to different values of minimum initial density of new tree cohorts. Stochastic temporal variation increases with increasing minimum cohort density.

30 min of CPU time on a 2.4 GHz Pentium PC. Memory requirements were relatively constant at 140 Mb of RAM.

5. Discussion

5.1. Simulation experiments

The modeling approach was flexible enough that it could be calibrated to reach the target of steady-state stand composition in scenario 1. It should be noted that the target steady state composition was an estimate based on species replacement rates (Kneeshaw and Bergeron, 1998), and not a direct observation.

Simulated stand-level trends in species composition were in general agreement with empirical chronosequences for mixed boreal forests of Quebec (Bergeron and Dubuc, 1989; Bergeron, 2000). However, in the simulations aspen is less abundant than birch during early succession, in contrast to some empirical observations (Bergeron, 2000). This is because the initial number of asexual sprouts at stand initiation, so that the first generation of aspen and birch is regenerated from seed only. Hence, the simulated scenarios correspond to the somewhat unrealistic assumption that there was no aspen or birch in the stands before the initial disturbance.

Establishment coefficients are basically a means to fine-tune cohort regeneration after shade tolerance is first taken into account. Therefore it only makes sense to compare the calibrated coefficients between species within a same shade tolerance class. White cedar and balsam fir are two species in the shade tolerance class 3. The gap establishment coefficient for white cedar had to be set much lower (0.35) than that of balsam fir (1.0), in order to reach the pre-defined steady-state composition. However, there is no evidence that white cedar is more light-demanding than fir, rather the opposite. We see several alternative explanations for the low value required by white cedar: first, Kneeshaw and Bergeron (1998) did not study stands older than 234 years, and thus their data may not reflect the actual steady state abundance of cedar that would be reached in later succession. On the other hand, it may be that other factors than light are important for establishment, and then, establishment coefficients actually aggregate several different effects. It is also possible, that the Greene and Johnson (1998) model we used for seedling survival may need refinement.

Model responses to variable assumptions of scenarios 2–4 were realistic. When conifers where dominating the seed sources, broad-leaved trees were less abundant during the early succession, and the late-successional conifers gained abundance faster. After a partial disturbance, shading benefited shade-tolerants at the expense of broad-leaved trees and white spruce. The presence of spruce budworm kept the balsam fir from canopy dominance and increased the compositional diversity of the stands.

Constraining the minimum density of new cohorts improved model performance markedly. It was possible to derive a parameter value which made large-scale simulations possible but did not impair simulation of stand development. Increasing the parameter value increases the temporal variation in stand composition. However, such variation occurs in actual forest stands and the parameter value we used for the landscape simulations does not seem to produce any less realistic results than occurred when not constraining initial cohort density.

A positive minimum density parameter means that the smallest cohorts are aggregated into fewer larger cohorts. The downside is that this could affect some applications requiring detailed description of the internal size and age structure of forest stands. This is one trade-off between the level of detail at stand level and the ability to simulate large landscapes.

5.2. Modeling approach implications

In terms of model scope, Q-LAND meets the goals set in the introduction. It tracks quantitative attributes of tree cohorts and forest stands, and is suitable for long-term and large-scale simulations. The model simulates dispersal and regeneration in a spatially explicit, quantitative manner, and is capable of simulating various stand-replacing and partial disturbance processes.

Dispersal was simplified in the current model implementation by assuming that all seeds that do not fall in the source cell or its eight nearest neighbors are distributed evenly over the landscape. However, the dispersal model given in Section 2.3 contains all the information needed to implement a more detailed version with an explicit calculation of seed transfer between all landscape cells.

Fire and harvesting are simulated using the modified disturbance submodels of LANDIS (He and Mladenoff, 1999) and FIN-LANDIS (Pennanen and 1Kuuluvainen, 2002). We implemented chronic spruce budworm disturbance for this study. The cohort data structure makes it possible to couple the model with detailed disturbance submodels, which remove a specific portion of trees from each size or age class.

The current model implementation is practical for simulating a landscape with 50 000 grid cells over several thousand years with an ordinary desktop computer.

Landscape size could be substantially increased by developing memory management by the simulation software. Forest data could be saved on hard disk so that only part of the data would be fetched to RAM for processing at a time. This should not greatly decrease model performance in relation to landscape size. This is because most of the CPU time is used in the cell level processes, which do not require access to the whole landscape data.

We showed that Q-LAND model can be parameterized by data available from the literature. Exploratory work is possible even with less data than were used in this study. Approximate growth tables including tree volume and basal area can be derived if species longevity, maximum volume and basal area of a cohort, and the age of maximum volume and maximum basal area are known. Greene and Johnson (1994, 1996, 1998) provide approximate models of dispersal and regeneration for all boreal tree species. Spatial seedling pattern could be assumed to be random if no better data are available (Eq. (11)). Species life history parameters are usually well known, and even if they are not, they have ecologically obvious roles, which makes exploration of different assumptions possible without rigorous data.

An advantage of the growth table approach is that the estimates of quantitative stand attributes are automatically constrained to reasonable levels even if some parameters estimates are inaccurate.

The obvious limitation of the growth table approach is that the tables automatically provide accurate growth predictions only for even-aged single-species stands. Model accuracy for stands with a more complex composition and age structure can be improved by refining the growth rate modifier function. The current model implementation has a fixed formulation of the growth rate modifier with one parameter (Eq. (15)). In the next version of the simulation software, the user will be able to define the formulation of the growth modifier and its dependence on stand structure and composition.

In management-related applications of landscape simulations, accuracy of model predictions and quantification of model errors are important. Such applications require further work on model parameterization and testing, and may also need refinement of model processes.

We believe that with a suitable formulation of the growth rate modifier, the growth of understory

cohorts and growth of cohorts established after partial disturbances can be simulated with an accuracy that is sufficient for many management-related model applications. The growth of tree cohorts can be adjusted and model accuracy can be evaluated by comparing simulated development of cohorts and stands with empirical data or the output of stand level simulation models.

Q-LAND tracks in principle all the quantitative cohort attributes that are in the input growth tables. However, the growth table approach assumes a static allometric relationship between the cohort attributes, such as tree basal area and volume, or tree diameter and tree height, which limits the accuracy of model predictions. This problem could be mitigated by using several growth tables per species and site type. For instance, different growth tables could be assigned to cohorts that establish after a stand-replacing disturbance and to cohorts establishing under shaded conditions.

Apart from cohort growth, stand development depends on the allocation of growing space through cohort establishment. Greene et al. (1999) concluded that processes affecting seedling recruitment were not known well enough for modeling regeneration density accurately. This is still true, and the questions of seed dispersal, seedling survival and juvenile competition between species need more study. Our model provides one method for evaluating how the effects of these processes may propagate to landscape level. If improved models of dispersal and recruitment become available, substituting them in the simulation model is straightforward.

Between-species competition within one tree age class is another difficult issue. The current formulation of the establishment submodel is based on the idea that, in a territory of certain size, the seedlings of a species with the highest juvenile growth rate will outcompete the seedlings of all other species. This assumption may not be realistic when the difference in juvenile competitive ability is small.

Forest landscape simulation models are notoriously difficult to test rigorously (Urban et al., 1999). Model validity should be tested in the context of specific applications and research problems. Sensitivity analysis should be used in order to find out the modeling assumptions that any conclusions are sensitive to. One way to assess sensitivity of predictions to model assumptions is to compare the predictions of different simulation models.

The current version of Q-LAND meets the model scope as defined in the introduction, and is already suitable for exploratory applications. We also believe it is feasible to parameterize and refine the model to produce sufficiently accurate predictions of tree volume and harvest yield to make it useful for comparing economic and ecological effects of specific management scenarios. However, confirming this will require further model testing and sensitivity analysis.

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