Synthesizing published knowledge of boreal forest cover change for large-scale landscape dynamics modelling

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We reviewed the published knowledge on forest succession in the North American boreal biome for its applicability in modelling forest cover change over large extents. At broader scales, forest succession can be viewed as forest cover change over time. Quantitative case studies of forest succession in peer-reviewed literature are reliable sources of information about changes in forest canopy composition. We reviewed the following aspects of forest succession in literature: disturbances; pathways of post-disturbance forest cover change; timing of successional steps; probabilities of post-disturbance forest cover change, and effects of geographic location and ecological site conditions on forest cover change. The results from studies in the literature, which were mostly based on sample plot observations, appeared to be sufficient to describe boreal forest cover change as a generalized discrete-state transition process, with the discrete states denoted by tree species dominance. In this paper, we outline an approach for incorporating published knowledge on forest succession into stochastic simulation models of boreal forest cover change in a standardized manner. We found that the lack of details in the literature on long-term forest succession, particularly on the influence of pre-disturbance forest cover composition, may be limiting factors in parameterizing simulation models. We suggest that the simulation models based on published information can provide a good foundation as null models, which can be further calibrated as detailed quantitative information on forest cover change becomes available.

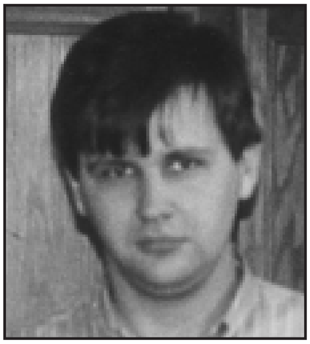
Key words: probabilistic model, transition matrix, boreal biome, landscape ecology

Nous avons révisé les informations publiées sur les successions forestières du biome boréal de l'Amérique du Nord pour leur applicabilité dans la modélisation des changements du couvert forestier sur de grandes superficies. À grande échelle, les successions forestières peuvent être visualisées comme des changements dans le couvert forestier au cours du temps. Les études de cas quantitatives des successions forestières dans la littérature révisée par des spécialistes du milieu représentent des sources fiables d'information sur les changements dans la composition du couvert forestier. Nous avons révisé les aspects suivant des successions forestières dans la littérature : les perturbations; les directions suivies du changement du couvert forestier après perturbation; la chronologie des étapes successives; les probabilités entourant le changement du couvert forestier après perturbation et les effets de la localisation géographique et des conditions écologiques de la station sur le changement du couvert forestier. Les résultats de ces études dans la littérature qui reposaient surtout sur les observations tirées des parcelles-échantillons, semblaient être suffisant pour décrire le changement du couvert forestier boréal comme un processus généralisé de transition par état successif, les états successifs étant marqués par la dominance des espèces d'arbres. Dans cet article, nous soulignons une approche pour incorporer les informations publiées sur les successions forestières dans des modèles stochastiques de simulation du changement du couvert forestier boréal de façon uniformisée. Nous avons constaté que le manque de détail dans la littérature sur les successions forestières à long terme, particulièrement sur l'influence de la composition du couvert forestier avant la perturbation, représentent probablement un facteur limitatif pour établir les paramètres des modèles de simulation. Nous suggérons que les modèles de simulation basés sur l'information publiée peuvent constituer une bonne base pour les modèles sans effet qui peuvent être calibrés par la suite lorsque l'information quantitative détaillée sur le changement du couvert forestier sera disponible.

Mots-clés: modèle probabilistique, matrice de transition, biome boréal, écologie du paysage

Introduction

The North American boreal forest biome covers over 420 million ha (UN-ECE/FAO 2000). This forest cover is subject to constant change, resulting in what is commonly referred to as a "shifting mosaic" (Clark 1991, Baker 1993), reflecting large-scale disturbances, such as forest fire (e.g., Heinselman 1981), insect epidemics (e.g., Holling 1992), and timber harvest (e.g., Harvey *et al*. 1995). Given the significance of the North American boreal forest in conserving biodiversity (e.g., Roberts and Gilliam 1995) and maintaining global carbon budgets (Price and Apps 1995), consequences of forest cover change are wide-ranging and need to be better understood. Knowledge of forest cover change, especially in a quantitative and spatially explicit form, is critical for a variety of modelling tasks, including assessing productivity (Van Cleve and Viereck 1981, Paré and Bergeron 1995), determining effects of disturbances (Flannigan *et al*. 1998, Bergeron 2000), monitoring timber supply (Bergeron and Harvey 1997), and understanding the implications of climate change (Landhausser and Wein 1993, Kasischke *et al*. 1995).



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Natural resource managers are faced with new challenges in achieving sustainable forest landscape management in the

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boreal biome. To help them maintain natural disturbance regimes in support of sustainable timber harvesting, large-scale models that can predict forest cover change under different management scenarios and disturbance regimes are needed. However, developing a unified landscape model for the whole boreal biome is a difficult task. The published knowledge on boreal forest succession provides a starting point, by helping us to outline model structure and further calibration requirements for particular forest management areas and sub-regions. Indeed, the literature provides a variety of case studies (e.g., Viereck 1970, Dix and Swan 1971, Bergeron and Dubuc 1989, Cumming *et al.* 2000) and a variety of techniques to analyze and quantify forest succession (Shafi and Yarranton 1973, Heinselman 1981, De Grandprè *et al.* 1993, Burton and Cumming 1995, Flannigan *et al.* 1998).

To further the goal of developing a landscape-level boreal forest cover change model, we explored how the published data on boreal forest succession could be synthesized for landscape dynamics modelling needs.

Review Of Published Data on Boreal Forest Cover Succession in North America

More than 400 publications were selected from popular bibliographic databases, using forest cover succession as the primary criteria, with less emphasis on stand-level variables such as non-tree species, nutrient cycling, habitat supply, biomass productivity, and physiological processes. A complete list of these publications is provided in Yemshanov and Perera (2001).

Upon further review, we selected the 175 publications that provided quantitative data on forest succession based on original information from field-based studies (e.g., Dix and Swan 1971, Carleton 1982, Bergeron and Dubuc 1989, Bergeron and Danserau 1993, Viereck *et al.* 1993, Lavoie and Sirois 1998, Bergeron 2000), literature reviews (e.g., Heinselman 1981, Weinstein and Shugart 1983, Schmidt *et al.* 1996), compilations of expert opinion (e.g., Lutz 1956, Chambers 1995), and forest species inventories (e.g., Reid 1974, Wall 1982, Carleton and Gordon 1992).

Representing succession for large-scale landscape modelling purposes

In this paper, we consider the modelling of forest cover change as a probabilistic discrete state transition process, a concept that often appears in the modelling literature (Rejmanek *et al.* 1987, Baker 1989, Flamm and Turner 1994, Muller and Middleton 1994, Trabaud and Galtie 1996, Jin and Wu 1997, Childress *et al.* 1998, Logofet and Lesnaya 2000, Yemshanov and Perera 2002). Probabilistic transition models treat forest cover as a system of discrete states, where forest cover change is modelled as a replacement of these states over time. Numerically, this process can be formalized using a transition probability matrix (e.g., Horn 1975, Acevedo *et al.* 1995, Li 1995, Logofet and Lesnaya 2000). Future forest cover composition $W_{(t+1)}$ at time interval $t+1$ can be predicted from current land cover composition at time t and a matrix of transition probabilities:

$$W_{t+1} = W_t \mathbf{P}_t, \tag{1}$$

where W_t is a $1 \times n$ state vector at time t, $\mathbf{P}_t$ is a $n \times n$ matrix of transition probabilities consisting of p_{ij} values, n is the maximum number of discrete states, and p_{ij} gives the probability of transition from discrete state i to state j between time t and $t+1$ $(i,j \le n)$:

$$\mathbf{P}_t = \begin{bmatrix} p_{11} & p_{12} & \cdots & p_{1n} \\ p_{21} & p_{22} & \cdots & p_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ p_{n1} & p_{n2} & \cdots & p_{nn} \end{bmatrix}. \tag{2}$$

For any given time t $(t = 1,2, \ldots k)$, the transition probabilities follow these conditions:

$$\begin{cases} p_{ij}(t) \ge 0, \forall i, \in 1, \ldots N \\ \sum_{j=1}^{N} p_{ij}(t) = 1 \end{cases} \tag{3}$$

When the number of discrete steps increases, a model may converge from its initial state $\mathbf{W}_{(0)}$ into a steady state $\mathbf{W}_{(\infty)}$, limiting distribution (Karlin 1968):

$$\mathbf{W}_{(\infty)} = \lim_{t \to \infty} \mathbf{W}_{(0)} \mathbf{P}^t \tag{4}$$

Temporal behaviour of the transition probabilities can be addressed by considering the time v_i when state i is being replaced by state j (Howard 1971). Logofet and Lesnaya (2000) used a time-dependent model, where each probability of discrete state persistence p_{ii} depended on the length of time spent in state i: v_i. p_{ii} was calculated from v_i as:

$$v_i = \sum_{n=0}^{\infty} p_{ii}^n = \frac{1}{1 - p_{ii}} \tag{5}$$

As a result, each discrete state has finite v_i, and for any given time interval t, $t < v_i$:

$$p_{\mathrm{ii}} = 1 - 1/v_{\mathrm{i}} \tag{6}$$

Another approach is to consider p_{ij}, the probability of discrete state i being replaced by state j, as dependent on the time spent in state i : p_{ij} (Acevedo *et al.* 1995). The time-dependency of p_{ij} can be modelled via v_{ij}, the lag time the model was in state i until being replaced by state j:

$$v_{ij} = \sum_{i=1}^{n} p_{ij} h_{ij}(t) \tag{7}$$

Here, v_{ij} represents the sum of lag time densities h_{ij} for each time interval t, $t < v_{ij}$, and corresponding transition probabilities p_{ij}. The lag time densities $h_{ij}(t)$ of transition from state i to j can be found for each time interval t, $t < v_{ij}$, by fitting them to a probability distribution function (Acevedo *et al.* 1996).

Discrete-state transition models have been used to predict vegetation succession and land cover change at various spatial extents: i.e., from individual species to landscape-scale patterns

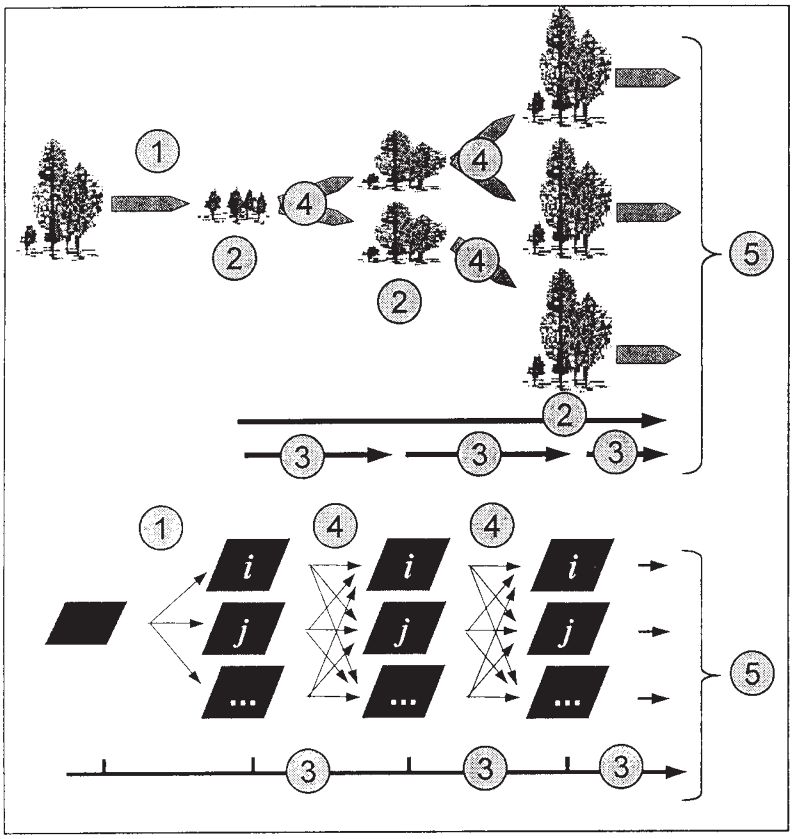

Fig. 1. Knowledge required to conduct forest succession modelling at large scales: 1 – Initial conditions; 2 – Post-disturbance pathways; 3 – Temporal details; 4 – Probabilities of forest cover change; 5 – Effects of geographic location and ecological site conditions; *i,j* – discrete states.

(Horn 1975, Bellefleur 1981, Rejmanek *et al.* 1987, Baker 1989, Muller and Middleton 1994, Trabaud and Galtie 1996, Childress *et al.* 1998). Although these transition models require fewer parameters than the stand-level gap models (Urban *et al.* 1999), they still require data to derive transition probabilities and model structure (i.e., time-dependent, or first-order, definition of discrete states). One convenient source of such data is the published literature. However, the use of published literature requires that several issues be considered:

The first issue relates to information about the scale of the process. At large scales, the process of forest succession does not closely match that of stand succession in its strictest sense (e.g., Spurr and Barnes 1980) nor the tree-by-tree replacement process (e.g., Horn 1981), but addresses the change in forest cover at coarse spatial resolution. Overall, forest succession information can be categorized into five basic groups that are relevant to developing models of forest cover change (Fig.1):

- **Initial conditions** include the effects of previous disturbances and the pre-disturbance forest cover composition on post-disturbance forest cover change (Fig. 1-1);
- **Pathways of post-disturbance forest cover change** describe the possible successional trajectories at the level of species composition in the canopy or forest classification unit (Fig. 1-2);
- **Temporal details** include aspects of succession such as periods of species persistence in the canopy and timing of successional steps. (Fig. 1-3);
- **Probabilities of post-disturbance forest cover change** refer to characterizing successional phases that can be depicted with discrete states, using a probabilistic process. For example, a simple sequence of successional phases, such as A->B, assumes that the probability of B replacing A equals 1. Any other ramifications, e.g., C<-A->B, lead to the probabilistic process (Fig. 1. 4); and
- **Effects of geographic location and ecological site conditions on forest cover change** can be spatially linked using detailed descriptions of geographical location and ecological site conditions in field case studies (Fig. 1-5).

The second issue relates to the discrete states in a transition model required to adequately portray forest cover change in a landscape. The choice of discrete states must correspond to the available spatial data. For example, when forest cover data are derived from classified satellite imagery, only broad classes of canopy composition can be distinguished. In this case, direct use of stand-level field knowledge of succession to develop discrete state models is not an option.

The use of tree species dominance in the canopy to define the discrete states may be appropriate when forest communities have simple canopy structures and low tree species diversity. For example, in the boreal biome succession is often reported as dominant tree species replacement in the canopy (e.g., Viereck 1973, Neiland and Viereck 1977, Woods and Day 1977, Bergeron and Dubuc 1989, Morneau and Payette 1989, Bergeron 2000, De Grandprè *et al.* 2000). In addition, the specific autecological responses of boreal tree species to disturbances have been widely studied (e.g., Heinselman 1981, Sims *et al.* 1990, Payette 1992) and can be used to separate early from late-successional stages.

Tree species dominance can be easily recognized and measured directly through field studies (Carleton 1982, Johnson and Fryer 1987, Viereck *et al.* 1983) or indirectly through aerial photograph interpretation over large areas (Jeglum and Boisson-

Table 1. Succession papers available in the literature categorized by spatial scale and disturbance type studied

Disturbance type	Fire		Natural ageing		Harvest		
Spatial scale	Species	Forest type	Species	Forest type	Species	Forest type	Total
Individual tree	–	–	3	–	8	–	11
Stand	39	7	28	2	18	–	94
Forest classification unit	–	2	–	–	–	–	2
Landscape	–	–	–	2	–	–	2
Total	39	9	31	4	26	–	109

neau 1977, Sayn-Wittgenstein 1978). Using dominant tree species as descriptors of boreal forest cover change is also advantageous because of its compatibility with operational spatial data sources, such as forest resource inventories (e.g., Gillis and Leckie 1996).

However, the use of dominant species to define discrete states is appropriate only when dominance can be easily recognized in the canopy and associated with specific successional stages. For the special case of mixedwood forest types, where the dominance cannot be clearly recognized, a different approach can be used. For example, synthetic forest classification units (FCU) may be applied as discrete states of the model. FCUs are useful for forest management, where they are used to distinguish forest stands based on canopy species composition and ecological site conditions (OMNR 1996).

The third issue is the spatial resolution used for modelling. Tree species dominance is resolution-sensitive. When the spatial resolution of a model corresponds to individual trees (e.g., 0.01– 0.1 ha), single-tree dominance criteria can be used. For coarser spatial resolution (e.g., 1 ha), when the probability of species mixtures in the canopy may increase, it may be necessary to develop special FCUs based on canopy species combinations. In addition, constraints such as resolution of forest inventory databases must be considered when defining discrete states.

Information on forest cover change in the literature

We reviewed 175 publications for relevant modelling information that they could provide as discussed above. Of these, 109 contained data representing succession in terms of tree species dominance or other coarser-scale categories such as forest ecosystem classification units (see Appendix 1). Over 50% of these reported successional process in textual form, using dominant species at discrete stages of succession as qualitative descriptors (e.g., Viereck 1973, Neiland and Viereck 1977). Another 20% presented succession in graphical form, illustrated by either line graphs of the process or forest profiles (e.g., Johnson and Rowe 1977, Viereck 1983). Only about one third of the reports included quantitative data on succession, such as relative species abundance over time (Bergeron and Dubuc 1989, Lavoie and Sirois 1998, Bergeron 2000).

Most studies (86%) focused on forest stands (Table 1), with only a few (2%) reporting succession processes at larger spatial extents.

Below, we describe the published knowledge on forest cover change using five categories (Fig. 1).

Initial conditions: The type and characteristics of disturbances that initiated succession were well documented by most field case studies (Black and Bliss 1978, Heinselman 1981, Bergeron and Dubuc 1989, Johnson and Fryer 1987, Payette *et al*. 1989, De Grandprè *et al*. 2000). Natural disturbance history of the boreal forest has been reconstructed using various methods, primarily from dendroecological data (Bergeron and Charron 1994) and historical inventories (e.g., Payette *et al*. 1989, Bergeron and Danserau 1993, De Grandprè *et al*. 2000). Historical aerial photographs and inventories also provide references to past clearcuts, fires, windthrow events, and insect outbreaks (Arseneault 2001). However, the question of how disturbance severity affects forest cover change at large scales remains unclear (Zasada *et al*. 1987, Landhausser and Wein 1993).

Pathways of post-disturbance forest cover change: This parameter is also well documented, although it is represented in different ways in the literature. The three most common representations are:

- Textual data describing forest succession as a phased sequence based on disturbance type, severity, and the time since the disturbance (e.g., Ritchie 1956, Zoltai 1975, Bertrand *et al*. 1992);
- Visual representation of succession as a scheme or pathway graph. Usually, the sequence of discrete states is reported in a deterministic way without any reference to probabilities of occurrence (e.g., Johnson and Rowe 1977, Viereck 1983); and
- Quantitative data showing changes in forest composition over time, e.g., forest composition, species abundance, basal area, biomass, stem density (Bergeron and Dubuc 1989, Viereck *et al*. 1993, Lavoie and Sirois 1998, Bergeron 2000).

Most of the knowledge is reported at the stand scale; very few studies assess succession at larger scales (e.g., Weinstein and Shugart 1983, White and Mladenoff 1994, Schmidt *et al*. 1996, Zhang *et al*. 1999).

Information on pre-disturbance vs. post-disturbance forest cover change is of practical interest for modelling post-disturbance forest cover dynamics. Quantitative data comparing pre- and post-disturbance forest cover composition are rare in the literature (e.g., Delaney and Cahill 1978, Bergeron and Gagnon 1987, Thomas and Wein 1985, Sirois and Payette 1989). Indirect references to this type of data were found in some successional schemes and pathway diagrams (e.g., Lutz 1956, Viereck 1973, Neiland and Viereck 1977). Sometimes the description of pre-disturbance forest composition has been generalized (e.g., Jarvis 1960) or simplified to the few most typical forest classification units (e.g., Heinselman 1981). Some papers also reported pre-disturbance vs. post-disturbance forest composition for only short-term studies of early post-disturbance establishment (e.g., Methven 1973, Chrosciewicz 1988). Many studies that reported post-disturbance successional pathways did not provide details on pre-disturbance vs. post-disturbance forest composition (e.g., Day and Harvey 1981, Heinselman 1981, Carleton 1982, Foote 1983, Bergeron and Dubuc 1989, Payette 1992). However, authors of the more recent studies (e.g., Cumming 2001, Arseneault 2001) emphasized that pre-disturbance conditions could initiate different successional pathways of post-

Table 2. Succession papers in the literature classified by number of successional phases and duration of study for each disturbance type

Successional phases (number)	Duration succession studied (years)																							
	Fire								Natural aging								Harvest							
	1–5	5–20	20–50	50–100	100–200	200–300	Non-specific	Total	1–5	5–20	20–50	50–100	100–200	200–300	Non-specific	Total	1–5	5–20	20–50	50–100	100–200	200–300	Non-specific	Total
1–2		1	2	1	2	1	1	8		5		1	1	1	2	10	2	5	1		1		1	10
3-4	2	1	1	2	1	3	4	14				1	1		2	4	3	3						6
5–7				1	5	2	1	9				1		1	1	3				1	1			2
8–11						3		3					1	3		4		1						1
Non-specific	2	1	1		2	1	7	14			1			3	10	14		3					4	7

*Shading indicates data with 20-year or better temporal accuracy

fire succession in the boreal forest. While published studies on post-fire forest succession and long-term succession due to natural ageing were frequent, long-term quantitative information about natural ageing following harvest was lacking.

Temporal details: It was important to determine the number of discrete successional phases that can be extracted from published data. Most papers provided stages of succession (Viereck *et al*. 1993) or changes in composition of dominant tree species over post-disturbance time (e.g., Bergeron and Dubuc 1989, Chambers 1995, Bergeron 2000, De Grandprè *et al*. 2000). Regardless of disturbance type, most studies reported five or less distinct successional stages (Table 2).

Other temporal details on forest cover change at larger scales found in the literature included forest cover composition and the dates of consecutive studies (Van Cleve and Viereck 1981, Weir and Johnson 1998), generalized schemes of large-scale forest cover replacement (e.g., Pastor and Mladenoff 1992), and time steps of forest cover transitions (Weir and Johnson 1998, Zhang *et al*. 1999).

Also important was the temporal accuracy for different lengths of successional periods. Because most landscape models predict forest cover change with 10- to 20-year time steps (Baker 1999, He and Mladenoff 1999), this time interval can be used as a guideline for a data search of the literature. We determined how well temporal details on succession can be used in landscape modelling as follows: Papers with quantitative successional data were categorized by the duration of succession reported and the number of successional stages that were referenced or could be extracted from reported data. Then the data range with 20-year or shorter intervals was identified (Table 2, shaded). The literature was most detailed for post-fire succession, whereas the temporal details for post-harvest and natural ageing succession were less detailed. Also, post-fire succession has been studied for periods longer than other types of disturbance in the boreal biome. However, most reports that provided successional data beyond 200 years were less detailed than short-term studies.

Successional time variables (i.e., persistence times of specific successional phases, timing of replacements) also varied greatly (Table 2). This variation may be partially explained by the influence of early post-disturbance conditions on successional pathways (Cumming 2001). The lack of data on historical low-severity disturbances adds uncertainty to estimates of successional pathways. Our literature review also revealed the difficulties of estimating the severity of historic burns and finding evidence of the post-fire residual stand, where data on low-severity fires were reconstructed mostly from fire scars and tree rings (Danserau and Bergeron 1993, Johnson *et al*. 1998).

Probabilities of post-disturbance forest cover change: Stand-level studies on boreal forest succession did not mention probabilities of forest cover change (Johnson and Rowe 1977, Neiland and Viereck 1977, Viereck 1983) but rather assumed that they were deterministic replacements. Only a few recent papers on large-scale forest cover change presented the probabilities of forest cover replacement (White and Mladenoff 1994, Weir and Johnson 1998, Zhang *et al*. 1999).

Effects of geographic location and ecological site conditions on forest cover change: Abiotic factors, such as climate, significantly control the structure of boreal forest ecosystems (Viereck *et al*. 1983, Bergeron and Dubuc 1989, Bonan and Shugart 1989, Hogg 1994). Our review indicated that the literature provides adequate description of the geographic and site ecological conditions and their relation to forest cover change. Fig. 2 illustrates the geographical distribution of field case studies across North America reported in the literature we reviewed. Almost half of these were post-fire studies (Table 2).

Traditionally, successional pathways were represented by common ecosite types (Carleton *et al*. 1985, Hogg 1994), grouped by moisture, soil richness (Ritchie 1961, Bergeron and Dubuc 1989, Heinselman 1981, Kneeshaw and Bergeron 1996), and basic terrain features (e.g., uplands, lowland, river valleys; Heinselman 1981, Jeglum 1983, Host *et al*. 1987). The effect of ecological site conditions can be determined by comparing successional pathways among different site types and geographical locations. Another important spatial characteristic is the breadth of geo-climatic conditions and site types reported in the studies (Table 3). In general, the case studies reported fewer than five different ecological site types.

Some papers address succession for areas adjacent to the southern boundary of the boreal biome, e.g., the Great Lakes-St. Lawrence forest (e.g., Heinselman 1973, 1981; Woods and Day 1976, 1977). These studies were included for consideration only if they provided data about the succession of tree species common in the boreal zone.

In addition, we also found papers that reported the effects of landscape fragmentation on forest cover change in other temperate forest zones (Zipperer *et al*. 1990, Li *et al*. 1993, Mladenoff *et al*. 1993, Malanson and Cairns 1997). Many biotic agents of forest succession, e.g., seed dispersal (Zasada *et al*. 1992, Greene *et al*. 1999) and re-colonization of disturbed areas (Kneeshaw and Bergeron 1996, Galipeau *et al*. 1997), have a

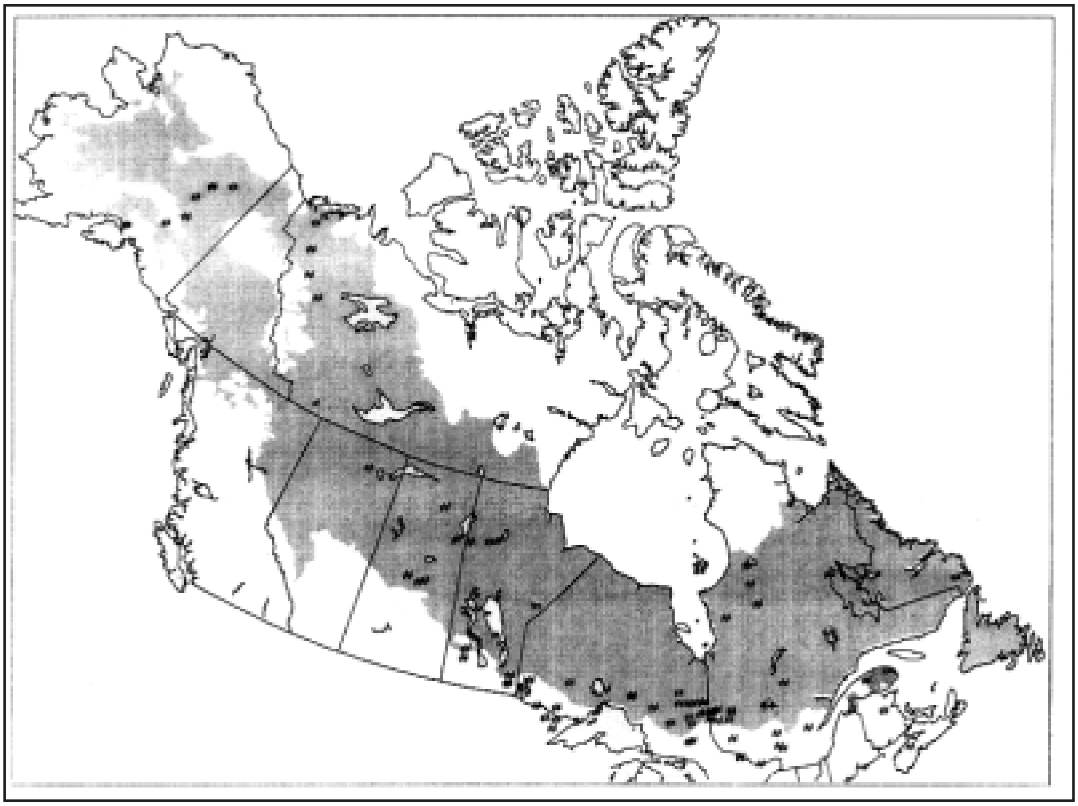

Fig. 2. Geographical distribution of case studies selected from the literature to provide input data for the forest cover transition model. Shading represents boreal zone.

Table 3. Succession papers in the literature categorized by disturbance type and number of specific site conditions studied.

Type of disturbance	1–2 groups	3–4 groups	5–7 groups	8–11 groups	> 11 groups	Non-specific	Total
Natural ageing	24	5	1	–	2	16	48
Fire	3	–	–	1	2	6	12
Fire and natural ageing	5	7	1	3	2	5	23
Harvest	10	1	3	1	3	3	21
Harvest and natural ageing	1	1	–	1	–	1	4
Harvest and fire	–	1	–	–	–	–	1
Total	43	15	5	6	9	31	109

spatial component. Some, such as distance from seed source, size of disturbance, and post-disturbance forest cover pattern, have already been used in studies of forest cover dynamics (Clark 1991, Pastor *et al.* 1999).

Use Of Published Knowledge on Succession in Large-scale Landscape Modelling

As indicated above, existing knowledge about boreal forest succession provides only generalized information on forest cover change. However, in order to build a transition model of forest cover change, we need adequate information for the development of transition probability matrices $\mathbf{P}_t$ (Eq. 2) for given geographical locations and site conditions. As forest cover change is considered a time-dependent process (sensu Acevedo *et al.* 1995, Urban *et al.* 1999, Logofet and Lesnaya 2000), the assumptions of time dependence of p_{ii} or p_{ij} (Eqs. 5–7) would require additional parameters from the literature. To maximize the utility of the information in the literature, we examined the following approaches of synthesizing successional knowledge into a transition probability matrix:

- Using raw multi-temporal data (i.e., measurements of species composition for study sites) or proportions of successional phases versus successional time;
- Using outputs from fine-scale individual-based (gap) models of forest dynamics as a data generation engine; and
- Using data representing a mixture of semi-quantitative estimates, textual citations and expert opinion on succession.

These approaches are discussed in detail below.

Using raw multi-temporal and proportional data

This technique generates transition matrices with p_{ij} directly from multi-temporal field-collected data (e.g., chronosequences of permanent plots, forest cover maps, satellite images, and aerial photographs). For each discrete time interval, Δt, transition probabilities can be calculated from the transition frequencies z_{ij} of replacement from discrete state i by state j during Δt:

$$p_{ij} = \frac{z_{ij}}{\sum_j z_{ij}} \tag{8}$$

This approach is common in studies of change detection in landscapes (Childress *et al.* 1998, Zhang *et al.* 1999) and vegetative composition (Balzter 2000). Since non-summarized raw spatial data are used in the calculation of p_{ij}, this technique produces the least biased results.

Sometimes, the only successional data available relate to the change of proportions between discrete states over time. Common examples are historical inventory records of forest canopy composition (Reid 1974) and summaries of species composition change over post-disturbance time (Black and Bliss 1978, Bergeron 2000). These data permit determination of approximate values of transition probabilities via optimization procedures using linear programming. The p_{ij} values are constrained to the interval [0;1] and attempt to reproduce input data proportions (more details can be found in Lee *et al*. 1970, Usher 1992, and Balzter 2000). Only proportion data (relative composition of specific forest cover types and their changes at certain time intervals) are needed to derive the transition probabilities, and these data are readily available in the literature. For example, canopy species composition change diagrams (e.g., Bergeron 2000) can be used to define these proportions. However, this technique assumes that transition probabilities do not change over time (i.e., first-order Markovian), and, therefore, does not account for the time-dependent nature of post-disturbance forest cover change.

Using stand-level gap models as a data generation engine

Another approach is to use finer-scale (patch- and individual-based) mechanistic models of forest succession to generate the successional pathways or chronosequences of forest canopy composition. Successional data in the literature have been widely used to design and calibrate individual-based (gap) models of forest dynamics (Bugmann 1996, Kienast *et al*. 1999, Mailly *et al*. 2000). In fine-scale gap models, stand development is simulated within sample plots by calculating establishment, growth, and death of individuals as deterministic processes. The model outputs resemble inventory tally sheets with characteristics of individual trees. These outputs can be scaled up to the forest cover level and used to parameterize large-scale probabilistic models (Acevedo *et al*. 1995, Urban *et al*. 1999).

This approach uses gap model outputs as surrogate "experimental" data to calculate transition probabilities. Acevedo *et al*. (1996) described the parameterization of a time-dependent transition model from simulated outputs of a spatially explicit version of the ZELIG stand-scale model (Urban and Shugart 1992, Urban *et al*. 1999). The technique requires a thorough calibration of gap models for large areas. The ecological factors included in most gap models vary greatly (Bugmann *et al*. 1996). The latest gap models have tended to replace simple combinations of climate-dependent and climate-independent processes with increasingly detailed formulations (Lexer and Hönninger 2001). However, few studies were found that evaluated the significance of how these new formulations improve the prediction of long-term forest dynamics (i.e., Bugmann and Martin 1995).

Using semi-quantitative data to define the structure of the transition model

The previous two approaches require detailed data sets or well-calibrated stand-level successional models for large regions. Many of the data found in the literature provided only a semi-quantitative outline of succession, for example, pathways or timing. This information may be insufficient for direct calculations of transition probabilities. Instead, it can be used to define the structure of the transition model, i.e., the temporal boundaries of forest cover change (when cover replacement begins and ends, and when the maximum cover value is reached) and the discrete states, and to differentiate forest cover change by combinations of ecological site conditions. To derive transition probabilities from these limited data, assumptions of how transition probabilities would behave within the defined temporal boundaries must be used. These assumptions can be derived from published case studies and knowledge of tree species autecology. Species tolerances to disturbance or age dependency of tolerance are examples of such assumptions.

Defining a time-dependent transition model from published data

We suggest that the following approach can be used to synthesize published data on boreal forest succession for use in large-scale forest cover change modelling. Two assumptions have to be made: First, large-scale change in boreal forest cover can be described in terms of canopy-replacing transitions, and, therefore, certain canopy composition types can be used as discrete-state descriptors (single species or species mixtures). Second, the probability of tree species dominance is dependent on the time spent by the current species at a given location (this probability follows the age-dependent nature of forest canopy replacement). Thus, the probability of discrete state persistence (p_{ii}) can be described by the probability distribution function $\xi(t)$:

$$p_{ii}(t) = \xi(t)\, p_{ii} \tag{9}$$

The next step is fitting of $\xi(t)$ into the temporal boundaries of succession, i.e., forest cover persistence times, and the shape of the $\xi(t)$ curve. Data from the literature are insufficient to define the shape of $\xi(t)$ exactly; however, they provide at least two temporal parameters of forest cover persistence (Fig.3):

- Maximum period of forest cover persistence under the given site conditions t_p
- The time interval, t_d, since forest cover establishment, when the probability of forest cover replacement by another cover type approaches 0.

By associating discrete states of the transition model with tree species dominance, t_p and t_d can be extracted from the literature. These time periods are measured using time since the current discrete state occupied a given location.

The temporal behaviour of p_{ii} within the intervals t_d and t_p (i.e., the shape of $\xi(t)$ curve) can be characterized by the time when the rate of current forest cover replacement reaches its maximum, t_{peak}. Assuming $p_{ii}(t) = \xi(t)\, p_{ii}$ at any time within $[t_d; t_p]$, (Eq. 9), the values $1 - p_{ii}$ for each discrete time step can be found by fitting the cumulative probability density function $\xi(t)\, p_{ii}$ to the time constraints t_d and t_p taken from the literature (Fig.3). A Gamma probability density function can be used following Howard (1971):

$$h_{ij}(t) = \frac{d_{ij}^{k_{ij}}\, t^{k_{ij}-1} \exp\left(-d_{ij} t\right)}{\left(k_{ij}-1\right)!}, \tag{10}$$

where d_{ij} is a first-order rate, k_{ij} is the order of the function, t is the lag time, and $h_{ij}(t)$ is the lag time density for replacement of i by j. The maximum of Gamma probability density function $h_{ij}(t)$ can be determined from t_{peak}. For each state, the param-

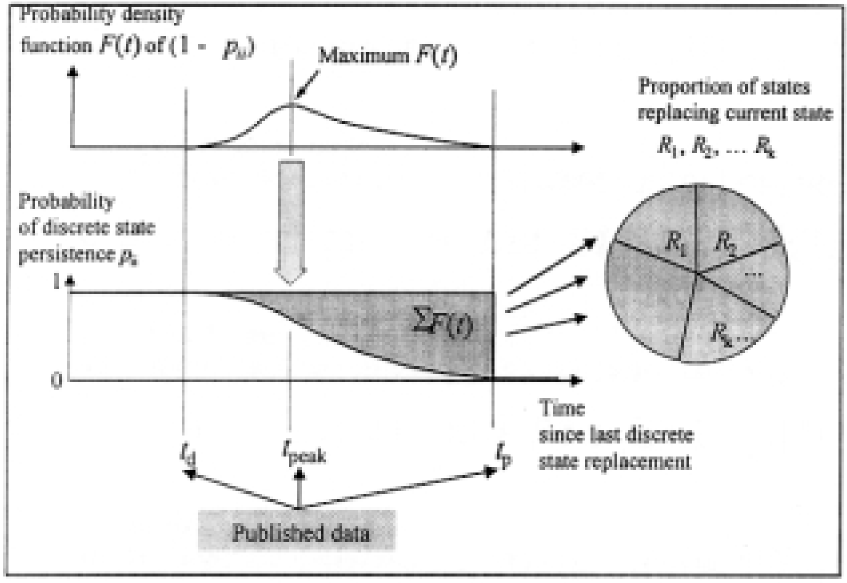

Fig. 3. Schematic representation of forest cover transitions: t_d – Time since establishment, when the replacement of one discrete state by another state begins; t_p - Maximum persistence time of the discrete state; t_{peak} – Time when rate of replacement of one discrete state by another reaches its maximum; $\Sigma F(t)$ – Cumulative values of probability density function $F(t)$; R_1, R_2, .. R_k – Proportion of states replacing current state.

eter estimation consists of the fitting d_{ii} and k_{ii} to minimize the deviation between the maximum of $h_{ij}(t)$ and t_{peak} taken from the literature.

The proportion of other forest cover types replacing a given forest cover type during post-disturbance succession (e.g., as found in Sirois and Payette 1989, Viereck *et al.* 1993, Bergeron 2000) can be used to define resulting proportions $R_{j1}, R_{j2},\dots R_{j(n-1)}$ of discrete states after a transition from the current state i into a set of states $j_1, j_2,\dots j_{(n-1)}$. Here n is the total number of discrete states in the model. Following Logofet and Lesnaya (2000), the transitions p_{ij} from state i to states $j_1, j_2,\dots j_{(n-1)}$ are constrained by proportions $R_{j1}, R_{j2},\dots R_{j(n-1)}$, and the condition of $R_{j1}+R_{j2}+\dots+R_{j(n-1)} = 1$ during the transition period (Fig.3). Thus, for each discrete time interval Δt, $t \in [t_d, t_p]$, p_{ij} were found as:

$$p_{ij} = R_i(1 - p_{ii}),\ j = 1,2,\dots n-1, \text{ and } R_{j1} + R_{j2} + \dots + R_{j(n-1)} = 1 \tag{11}$$

Because the literature did not provide the details characterizing temporal behaviour of specific p_{ij} transitions, it is difficult to consider time-dependence of each p_{ij} transition.

Variables such as climatic zone (Rowe 1972, Sirois and Payette 1991), soil moisture (Viereck 1970, Bergeron and Dubuc 1989), and nutrient status (Viereck *et al.* 1983) can be used to stratify the transition probabilities by ecological site conditions.

This technique is appropriate for deriving transition probabilities from the mixture of semi-quantitative and quantitative successional data, where some references may report only part of the required information. More details on the use of published knowledge on succession in probabilistic models of forest cover change are discussed in Yemshanov and Perera (2002).

Conclusions

The literature provides only generalized data for describing succession as a discrete state replacement process, with discrete states identified by tree species dominance in the canopy at large scales. Although most published studies were conducted at the stand level, the data they presented were sufficient to define temporal boundaries of forest cover replacements, i.e., persistence of forest cover types, and the sequence of their replacement in the canopy. However, details on long-term succession (200 years or more) are rare, as are data on the effects of pre-disturbance composition on post-disturbance successional pathways. As a result, the published succession knowledge can be used for large-scale landscape modelling as a null model to be calibrated using multi-temporal spatial data (e.g., permanent sample plots, historical aerial surveys).

We summarized basic methods of incorporating published succession knowledge into probabilistic landscape models that represent data on succession as a transition probability matrix. This method may be used objectively to incorporate succession knowledge into models that simulate disturbances (e.g., fire, insect diseases, and harvest) in boreal landscapes, and perhaps to standardize input and output of landscape-scale forest cover change models.

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Appendix 1. Summary of available literature on forest succession in the North American boreal biome and adjacent sub-boreal zones relevant to predicting forest land cover change

Author(s)	Year	Location	Disturbance type	Average length of succession (years)	Unique stages (number)	Groups based on site conditions (number)
Landscape-level spatial scale at forest type study resolution						
Schmidt *et al*.	1996	Generalized to Lake States (Michigan, Minnesota)	Natural ageing	13	1	8
Weinstein and Shugart	1983	Southern boreal forest zone, generalized to Lake States (Michigan, Minnesota)	Natural ageing	250	2	3
Forest type spatial scale at forest type study resolution						
Gauthier *et al*.	1996	Les Basses-Terres d'Amos, Quebec	Fire	220	9	4
Viereck *et al*.	1986	Alaska	Fire	Non-specific	Non-specific[1]	3
Tree stand spatial scale at forest type study resolution						
Abrams	1991	Northern lower Michigan	Fire	Non-specific	4	1
Bergeron and Danserau	1993	Lake Abitibi, Quebec	Fire	220	8	1
Dyrness *et al*.	1986	Generalized to Interior Alaska	Fire	200	6	2
Foster	1985	Southeastern Labrador	Fire	Non-specific	3	1
Johnson and Rowe	1977	Caribou Range, Northwest Territory	Fire and natural ageing	50 2	8	23
Pastor and Mladenoff	1992	Generalized to Great Lakes boreal hardwood zone	Natural ageing	Non-specific	5	Non-specific
Payette *et al*.	1989	Northern Quebec	Fire	60	6	1
Reid	1974	Mackenzie Valley, Alaska	Fire	120	6	2
Ritchie	1958	Northern Manitoba	Fire	Non-specific	5	Non-specific
Tree stand spatial scale at species study resolution						
Abrams *et al*.	1985	Northern lower Michigan	Fire and natural ageing	35	Non-specific	1
Alexander and Euler	1981	Wabigoon Lake, Ontario	Fire	Non-specific	3-4	5
Auclair	1985	Schefferville, Quebec	Fire	140	7	1
Auclair and Goff	1974	Generalized to southern boreal mixedwood, Wisconsin	Natural ageing	Non-specific	3	1
Baldwin	1977	Edmundston, New Brunswick	Harvest	10	3	5
Ball and Walker	1997	Manitoba Escarpment, Manitoba	Harvest	40	2	6
Baskerville	1965	Green River Watershed, New Brunswick	Harvest	10	1	2
Bergeron	2000	Lake Duparquet, Quebec	Fire and natural ageing	225	11	1
Bergeron and Charron	1994	Lake Duparquet, Quebec	Fire and natural ageing	75	5	38
Bergeron and Dubuc	1989	Lake Duparquet, Quebec	Fire	300	6	4
Bergeron and Gagnon	1987	Lake Duparquet, Quebec	Fire	200	2	22
Black and Bliss	1978	Inuvik, NWT	Harvest and natural ageing	Non-specific	Non-specific	4
Bonnor and Magnussen	1986	Algonquin Park, Ontario	Harvest	5	3	1
Brisson *et al*.	1988	Upper St. Lawrence area, Quebec	Natural ageing	20	1	1
Butson *et al*.	1987	Lake Nipigon, Ontario	Harvest	Non-specific	Non-specific	1
Carleton	1982	Swastika, Timiskaming district, Ontario	Fire	30	1	1
Carleton and Arnup	1993	Eastern Ontario	Fire	Non-specific	3	2

Appendix 1. Continued

Carleton and Maycock	1980	Northern and central Ontario	Natural ageing	Non-specific	2	Non-specific
Cayford and McRae	1983	Generalized to North American boreal zone	Fire	Non-specific	2	Non-specific
Chrosciewicz	1976	Southeastern Manitoba	Fire	Non-specific	Non-specific	1
Chrosciewicz	1983	Southeast of Winnipeg, Manitoba	Fire and harvest	10	1	3
Clayden and Bouchard	1983	Lake Abitibi, Quebec	Natural ageing	Non-specific	2	3
Cogbill	1985	Laurentian Highlands, Quebec	Harvest and natural ageing	200	2	8
Crowell and Freedman	1994	Kings County, Nova Scotia	Natural ageing	75	4	1
Danserau and Bergeron	1993	Lake Abitibi, Quebec	Fire	Non-specific	Non-specific	Non-specific
Day and Carter	1990	Temagami forest, Ontario	Fire and natural ageing	260	Non-specific	11
Day and Harvey	1981	Generalized to boreal mixedwood zone	Fire	125	4	Non-specific
Day and Woods	1977	Quetico Provincial Park	Fire	210	4	2
De Grandprè *et al*.	2000	North Shore region, Quebec	Fire	225	4	Non-specific
Delaney and Cahill	1978	Avalon Peninsula, Newfoundland	Fire	50	1	1
Dix and Swan	1971	Candle Lake, Saskatchewan	Natural ageing	100	2	4
Fiedler and Lloyd	1995	Generalized to Western Canada	Natural ageing	Non-specific	Non-specific	Non-specific
Foote	1983	South of Yukon River, Interior Alaska	Fire	200	6	2
Foster and King	1986	Southeastern Labrador	Fire	110	Non-specific	45
Galipeau *et al*.	1997	Abitibi's Hebecourt township, Quebec	Fire	68	3	4
Gauthier *et al*.	2000	Abitibi-Lake Matagami Lowlands, Quebec	Fire	225	10	2
Gauvin and Bouchard	1983	Mount Orford Park, Quebec	Natural ageing	Non-specific	Non-specific	8
Greene *et al*.	1999	Generalized to boreal North America	Harvest and natural ageing	Non-specific	Non-specific	Non-specific
Groot and Horton	1994	Northern Clay section, Iroquois Falls, Ontario	Natural ageing	Non-specific	Non-specific	40
Harris	1972	Afognak Island, Alaska	Harvest	20	Non-specific	Non-specific
Harvey and Bergeron	1989	Lake Abitibi, Quebec	Natural ageing	6	1	4
Harvey *et al*.	1995	Clay Belt, Quebec	Natural ageing	8	1	9
Heinselman	1973	Boundary Waters Canoe area, Minnesota	Fire	200	1	2
Heinselman	1981	Generalized to North American southern boreal biome	Fire	Non-specific	Non-specific	Non-specific
Hendrickson	1988	Petawawa Research Forest, Ontario	Harvest	4	1	2
Jarvis	1960	Goulais River Watershed, Ontario	Fire	46	4	2
Johnstone	1976	Hinton, Alberta	Harvest	10	Non-specific	1
Kayll	1968	Generalized to Canadian boreal zone	Fire	Non-specific	Non-specific	Non-specific
Kenkel	1986	Elk Lake, Ontario	Natural ageing	Non-specific	Non-specific	3
Kenkel *et al*.	1998	Northwestern Ontario	Natural ageing	250	5	12
Kittredge	1938	Generalized to southern boreal mixedwood	Fire and natural ageing	Non-specific	Non-specific	Non-specific
Kneeshaw and Bergeron	1996	Lake Duparquet, Quebec	Fire	200	7	1
Landhausser and Wein	1993	Inuvik, NWT	Fire	7	1	1
Lavoie and Sirois	1998	Chisasibi region, Quebec	Fire	6	3	4
Leduc *et al*.	1995	Lake Duparquet, Quebec	Natural ageing	220	8	4
MacArthur	1964	Gaspè Region, Quebec	Fire	20	Non-specific	1
Montague and Givnish	1996	Northern Wisconsin	Natural ageing	250	Non-specific	4
Morneau and Payette	1989	Hudson Bay area, Quebec	Fire	250	6	1
Moss	1953	Northwestern Alberta	Fire	Non-specific	4	Non-specific
Neiland and Viereck	1977	Alaska	Fire	220	4	Non-specific
OMNR	1997	Generalized to Ontario boreal biome	Harvest	100	5	19
Ritchie	1956	Northern Manitoba	Fire and natural ageing	Non-specific	Non-specific	Non-specific
Roberts and Powell	1988	Nashwaak watershed, New Brunswick	Harvest	6	1	16
Shafi and Yarranton	1973	Clay Belt, Ontario	Fire	50	Non-specific	Non-specific
Sims *et al*.	1990	Generalized to northwest Ontario	Fire and natural ageing	Non-specific	Non-specific	Non-specific
Sirois and Payette	1991	Northern Quebec	Fire	Non-specific	Non-specific	Non-specific
Steneker	1967	Riding Mountain, Manitoba	Harvest	10	Non-specific	Non-specific
St-Pierre *et al*.	1991	Reserve Ashuapmushuan, Quebec	Fire	5	Non-specific	Non-specific
St-Pierre *et al*.	1992	Lake Saint-Jean, Quebec	Fire	5	Non-specific	Non-specific

Appendix 1. Continued						
Strang	1973	Lower Mackenzie River, NWT	Fire	Non-specific	Non-specific	Non-specific
Timoney and Peterson	1996	Peace River Lowlands, Alberta	Harvest	Non-specific	Non-specific	Non-specific
Twolan-Strutt and Welsh	1997	Manitouwadge, Ontario	Harvest	200	6	1
Van Cleve and Viereck	1981	Tanana River, Alaska	Fire	300	5	3
Viereck	1973	Alaska	Fire and natural ageing	200	3	Non-specific
Viereck and Dyrness	1979	Yukon-Tanana Uplands, Alaska	Fire	5	3	1
Viereck *et al*.	1993	Tanana River, Alaska	Natural ageing	Non-specific	Non-specific	Non-specific
Wall	1982	Nova Scotia	Harvest	6	3	1
Weir and Johnson	1998	Prince Albert National Park, Saskatchewan	Fire	90	1	1
Whitney	1987	Northern lower Michigan	Natural ageing	140	1	2
Woods and Day	1976	Quetico Provincial Park, Ontario	Fire	Non-specific	2-4	Non-specific
Woods and Day	1977	Quetico Provincial Park, Ontario	Fire	250	Non-specific	Non-specific
Yarie	1981	Fort Yukon, Alaska	Fire	200	Non-specific	Non-specific
Yarie	1983	Porcupine River drainage area, Alaska	Natural ageing	Non-specific	Non-specific	Non-specific
Youngblood	1995	Fairbanks-Big Delta, Alaska	Fire	60	4	1
Zoladeski and Maycock	1990	Northwestern Ontario	Natural ageing	150	8-11	7
Zoltai	1975	Mackenzie River Valley, NWT	Fire	220	2	1
Individual-based spatial scale at species study resolution						
Bella and DeFranceschi	1972	Hudson Bay, Saskatchewan	Harvest	5	4	6
Bertrand *et al*.	1992	Matane, Quebec	Harvest and natural ageing	Non-specific	1	1
Cayford	1963	Sandilands Forest Reserve, Manitoba	Harvest	5	4	1
Chrosciewicz	1988	Candle Lake, Saskatchewan	Harvest	8	1	14
Cole *et al*.	1999	Fort Richardson, Alaska	Harvest	5	1	4
Deal and Farr	1994	Prince Wales Island, Alaska	Harvest	20	2	1
Ellis and Mattice	1974	Northwestern Ontario	Harvest	13	3	1
Fraser	1959	Petawawa Model Forest, Ontario	Harvest	9	9	8
Kneeshaw and Bergeron	1998	Lake Duparquet, Quebec	Fire and natural ageing	234	Non-specific	Non-specific
Payette and Filion	1985	Hudson Bay-Richmond Gulf, Quebec	Fire and natural ageing	Non-specific	Non-specific	1

[1]Study reports generalized data