Guidelines for modeling natural regeneration in boreal forests

by Juan A. Blanco^{1,2}, Clive Welham¹, J.P. (Hamish) Kimmins¹, Brad Seely¹ and Daniel Mailly³

ABSTRACT

Natural regeneration is recognized as an important component of forest management. Field studies are usually combined with conceptual and mathematical models as the most effective way to understand and predict natural regeneration. In the case of the boreal forest, several important issues arise in the design of regeneration models and are reviewed here. The most important concerns the trade-off between complexity and portability. Complex models may mimic natural systems more closely than do simpler models, but this realism comes at a cost in terms of the volume of data necessary for their calibration. A second issue is that most regeneration models have been scaled to problems at the tree and stand level, but recent interest in landscape-level issues requires models applicable to this higher spatial scale. Finally, the conceptual framework underlying most regeneration models may need to be revisited in light of recent efforts to depict vegetation dynamics under changing climatic regimes. It is unlikely that any single modeling approach will prove adequate for modeling natural regeneration under all conditions, and we provided guidelines as to how to create effective regeneration models.

Key words: climate change, disturbance, ecological models, forest regeneration, seedlings

RÉSUMÉ

La régénération naturelle est reconnue comme étant un élément important de l'aménagement forestier. Les études sur le terrain sont habituellement combinées à des modèles conceptuels et mathématiques pour constituer la manière la plus efficace de comprendre et de prédire la régénération naturelle. Dans le cas de la forêt boréale, plusieurs points cruciaux surgissent lors de la conception des modèles de régénération et font l'objet d'une révision ci-après. Le plus important porte sur l'équilibre entre la complexité et la transférabilité. Les modèles complexes peuvent reproduire les systèmes naturels plus fidèlement que ne le pourraient des systèmes plus simples, mais ce réalisme est dispendieux compte tenu du volume de données nécessaire à la calibration. Un deuxième point tient au fait que la plupart des modèles de régénération ont été élaborés pour identifier les problèmes au niveau de l'arbre et du peuplement, mais l'intérêt récent porté aux enjeux à l'échelle de l'écosystème requiert des modèles utilisables à cette plus grande échelle. Finalement, le cadre conceptuel sous-jacent à la plupart des modèles pourrait requérir une révision à la lumière des récents efforts de représentation de la dynamique des végétaux en fonction de la modification des régimes climatiques. Il est peu vraisemblable qu'une seule approche de modélisation s'avèrera adéquate pour modéliser la régénération forestière sous toutes les conditions possibles et nous élaborons des lignes directrices indiquant comment créer des modèles effectifs de régénération.

Mots clés : changements climatiques, perturbation, modèles écologiques, régénération forestière, semis

Introduction

A major goal of forest management is to sustain productivity and desired levels of biological diversity. Regeneration has been defined as the renewal of a forest crop by natural, artificial, or vegetative means, including all the ecological processes that affect seedling establishment, growth and mortality until the crop is 1.3 m high (CFS 1995). Regeneration is a critical component of sustainability and there is a substantial history of research on both natural and management-assisted forest renewal (Smith *et al.* 1997). Much of classical silviculture evolved as a means of solving regeneration problems, and the importance of forest regeneration in determining the biological diversity of future forests has been emphasized (Bergeron *et al.* 1998). Unfortunately, examples abound of regeneration efforts that failed or were inadequate (Lavender *et al.* 1990, Curtis *et al.* 1998), and the lack of

appropriate silvicultural prescriptions to ensure success continues to impede progress towards sustainable forest practice in some forest types. In the boreal forest, achieving regeneration objectives and satisfying regeneration regulations has often relied on the use of one or more of genetically improved plantation stock (Rainville *et al.* 2003), herbicides, and brushing (Biring *et al.* 1999, Thompson and Pitt 2003, Boateng *et al.* 2006). For economic and environmental reasons, reliance on intensive techniques is giving way to an emphasis on natural regeneration. Methods are now being employed, for example, to encourage vegetative regeneration particularly in deciduous species, exploit the aerial seed banks of jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP), and to utilize the seedling banks of black spruce and balsam fir (*Abies balsamea* [L.] Mill.) (Greene *et al.* 1999).

¹Department of Forest Sciences, University of British Columbia, 3041 – 2424 Main Mall, Vancouver, British Columbia, V6T 1Z4.

²Corresponding author. E-mail: juan.blanco@ubc.ca

³Direction de la recherche forestière, Ministère des Ressources naturelles et de la faune, 2700 rue Einstein, Québec, (Québec) G1P 3W8.

Disturbances are important factors in regenerating boreal forests. Fire, insects, diseases and wind are the principal natural disturbance agents in most natural forests (Groot *et al.* 2001). Anthropogenic disturbances such as harvesting, site preparation or understory management affect recruitment of natural regeneration and have different implications in management such that natural regeneration can be both positive and negative. For example, on a conifer cut-block the presence of only a few mature *Populus* could result in high aspen suckering, which could interfere with conifer establishment, growth and mortality. To ensure the greatest chance of success, natural regeneration efforts must be grounded in established ecological principles. Ecological processes that govern regeneration dynamics and their interaction are inherently complex, however, and determining the contribution of a particular process to the overall regeneration event is difficult. One way to represent this complexity is through the use of models.

Natural regeneration of boreal forests includes processes such as seed production, seed dispersal, germination rates, seedling establishment and early seedling growth and mortality (bold boxes, Fig. 1). Models of natural regeneration have been developed that vary from the conceptual (Lieffers *et al.* 1998, Messier *et al.* 1998, Greene *et al.* 1999) to the mathematical (Botkin 1993; Greene and Johnson 1999, 2000; Calogeropoulos *et al.* 2003). These models have been used to explore a broad range of issues from how natural regeneration patterns define the subsequent response of forests to disturbance to the potential effect of global climate change on plant recruitment and community structure (Dixon *et al.* 1990, Botkin 1993, Attiwill 1994). To reliably predict how climate change might impact plant communities is contingent upon how well the relationship between regeneration dynamics and climate is understood (Shugart *et al.* 1992, Peng and Apps 1997, Price *et al.* 1998). The boreal forest ecoregion possesses a special set of physical and biotic features (biophysical determinants) that may pose significant challenges to regeneration efforts of some valuable species, such as spruce. The objective of this paper is to provide suggestions concerning the most important issues that should be taken into account when modeling regeneration in boreal forests, and provide guidelines for implementing regeneration into forest models in the boreal region.

Fig. 1. Conceptual model of factors influencing seedling recruitment in boreal forests (oval boxes) and items suitable to be simulated as pools (square boxes). Main chain of events in regeneration is highlighted in bold case. The group of factors directly related to climate change is drawn in dotted lines.

Biophysical Determinants of Regeneration

As can be seen in Fig. 1, to successfully replace a stand with a new population of trees by natural means, a chain of main events must happen. First, trees must produce pollen in a sufficient quantity to ensure production of a viable seed population. Seeds must then be dispersed and only those that land in suitable habitat can germinate and sustain growth (bold lines, Fig. 1). This series of events is subject to the physical and biological factors (the biophysical determinants, in ovals in Fig. 1) unique to each site. Several reviews of the biophysical determinants of regeneration have been conducted (Zasada *et al.* 1992, Greene *et al.* 1999, Gromtsev 2002) and thus only a brief description is provided here.

Climate

The boreal forest region is characterized by a wide range of climatic conditions, ranging from extremely cold, dry continental regimes in interior Alaska and Siberia to warm, moist conditions in eastern Canada and Fennoscandia (Bonan 1992). Hogg (1994) showed that the distribution of vegetation in the Canadian boreal forest was closely related to climatic regimes, particularly moisture. Climatic, microclimatic and climate-related effects that need to be considered when modelling regeneration include reduced light availability due to shading, soil moisture deficits associated with frozen soils, reduced nutrient availability from low rates of nutrient cycling in cool soils, frost, and low growing-season air temperatures (Shugart 1984, Botkin 1993; see below).

Light

The high latitude of the boreal forest ecoregion (ranging from 50°N to 65°N) and the resultant low sun angle mean that trees cast a longer shadow at high latitudes and so shading of an area is related as much to tree height as crown radius (Bonan and Shugart 1989). In a study of gap dynamics in a high latitude *Larix gmelinii* (Rupr.) Rupr. forest, for example, Ban *et al.* (1998) found that obliquely projected gaps were more important than vertically projected gaps in explaining regeneration patterns. This means that in comparison with forests at lower latitudes, only relatively large disturbances can produce a significant increase in radiation load on the forest floor (Shugart and Smith 1996).

The tall, narrow crowns characteristic of northern conifers tend to create relatively small gaps when individual trees die, with only a small impact on light at the ground level (Oliver and Larson 1990). Position within a gap can be important; the north side of a gap receives more light than the south side (Wright *et al.* 1998). Small gaps in the canopy often persist, however, because the crowns of surrounding trees expand only very slowly into the gap. Consequently, the gap is usually filled by recruitment from below rather than extension of side branches (Oliver and Larson 1990). Competition for light between seedlings and understory vegetation can be intense and is an important source of seedling mortality (Duchesneau and Morin 1999, Duchesneau *et al.* 2001, Bi *et al.* 2007). In boreal forests that include a deciduous component, gaps tend to close faster as a result of lateral branch expansion. A detailed review of light dynamics in boreal forest gaps can be found in McCarthy (2001).

Root distribution

In boreal forest soils, below-ground gaps are often smaller than canopy gaps, because: (1) in conifers lateral root spread is usually greater than branch spread (Kimmins 2004); (2) deciduous species such as trembling aspen (*Populus tremuloides* Michx.) respond to the formation of canopy gaps by suckering, and then rapidly expanding their root system to occupy below-ground gaps (Anderson *et al.* 2001), and (3) understory shrubs and grasses often develop a considerable root biomass even if above-ground growth is suppressed (Kimmins *et al.* 2004). Soil processes are often little affected by the creation of small gaps, as compared to microclimatic effects (Denslow *et al.* 1998). Consequently, when a canopy gap is formed, competition for soil resources may be reduced much less than competition for light (Harrington 2006, Bi *et*

al. 2007). Regeneration models that focus solely on light competition will over-predict vegetation response to the canopy gap on sites where competition for below-ground resources is an important determinant of productivity.

Soil temperature and moisture

Soil temperatures and associated conditions vary widely across the boreal forest region. In more southerly regions and on south-facing slopes, soils tend to be warmer and free of permafrost. Scattered permafrost soils are typical of interior Alaska and the western Canadian boreal forest. Central and eastern Siberia and northern Canada tend to have extensive cold, permafrost soils (Bonan 1992). Cold soils result in reduced water uptake by trees because of lower hydraulic conductivity, higher root resistance, and increased water viscosity. Soil temperature (and particularly permafrost) limits root penetration and ultimately, seedling growth (Fig. 1). Sucker production in trembling aspen is also significantly reduced at low soil temperature (Anderson *et al.* 2001). Lack of available soil moisture is often the major cause of seedling mortality and, hence, regeneration failure (Greene *et al.* 1999).

Soil fertility, nutrient cycling, and plant competition

Some boreal forest soils are fine-textured and quite productive (the lacustrine soils of western Canada, for example). Other soils are composed of infertile, coarse-textured material (i.e., the Canadian Shield and much of the Finnish boreal region). In addition to texture, fertility is greatly affected by soil temperatures. Cold soil results in slow rates of organic matter decomposition and nutrient cycling, which is compounded by the fact that litterfall tends to be low in nutrients (from high rates of nutrient translocation). Competition for nutrients can be severe (McCarthy 2001), and tree growth can be severely limited on sites dominated by Ericaceous shrubs (*Vaccinium* spp., *Kalmia angustifolia* L., *Gaultheria shallon* Pursh, *Rhododendron* spp., and/or *Ledum groenlandicum* Oeder; Messier and Kimmins 1990, Prescott and Weetman 1994, Mallik 2003). These shrubs are strong competitors for nutrients because of their high root/shoot ratios and allelopathic effects (Prescott and Weetman 1994, Mallik 2003) (Fig. 1). Allelopathy is seldom taken into account when simulating forest ecosystems despite its importance in limiting tree productivity in some ecosystems (see Blanco 2007). In the prolonged absence of disturbance, Ericaceous shrubs can replace a closed forest and constitute the climax community (Kimmins 1996).

Nurse logs

Large, well-decomposed logs can provide an important substrate for seedling survival. How nurse logs actually improve natural regeneration is not fully understood but they may provide an improved thermal environment for seedling roots, elevate seedlings above competing herbs and shrubs, or represent a safe site against pathogens that kill over-wintering seeds (Harmon and Franklin 1989, Zhong and Van der Kamp 1997). Although nurse logs may be important for early seedling establishment, decaying logs are a nutritionally poor substrate for seedlings and consequently their initial growth is generally slow, at least until roots can penetrate the underlying mineral soil.

Seed production and timing of seed release

Climatic conditions during bud development, pollination and embryonic development have a strong influence on seed production and dormancy (Sarvas 1968, Henttonen *et al.* 1986). Extremes in humidity can result in low pollination rates and thus poor cone crops (Owens 1987). Regeneration success for many species is also strongly dependent on the timing of seed release. Availability of appropriate seedbeds and competition-free sites may last only a few years following a disturbance and species arriving after this time may be at a strong disadvantage (Greene *et al.* 1999). Timing of seed maturation occurs in 1 of 3 categories: (1) seeds that mature in summer and disperse during the current growing season, (2) seeds that mature in late summer but disperse during the dormant season, and (3) seeds that mature in late summer with the potential for significantly delayed dispersal (Leadem 1997). Among boreal trees, deciduous species are typical of the first category, while category 2 is exemplified by white spruce (*Picea glauca* [Moench] Voss) and balsam fir. In the last category are species with serotinous or semi-serotinous cones, such as black spruce, jack pine, and lodgepole pine (*Pinus contorta* Doug ex. Loud.). These species can retain seeds within cones for many years; cones open either gradually or when exposed to the high temperatures produced by wild fire.

Germination, seedling establishment, and growth

Germination success and even sapling establishment have been linked directly to the abundance and quality of seedbeds (Lepage *et al.* 2000). In general, the critical feature affecting seedbed quality is its capacity to supply moisture to the seedling root zone, though substrate temperature may also be important (Groot *et al.* 2001). Variation in seedbed quality may be simply a consequence of different moisture regimes because substrates comprised of low-porosity material (e.g., mineral soil) generally support greater tree seed germination than high-porosity seedbeds (e.g., thick duff) (Greene and Johnson 1999). Another important factor is the legacy of vegetative composition on the site (its ecological fingerprint; Kimmins 1990), which can determine the spatial pattern of local soil microenvironments and, ultimately, the abundance and distribution of seedlings (Binkley and Valentine 1991, McIntire *et al.* 2005).

Seedling growth rate is a function of how effectively it acquires resources. As the size of a seedling increases and its organs of resource capture (roots and leaves) are spread over a larger area, carbon allocation may change accordingly (Ingstad and Kähr 1985, Gower *et al.* 1995, Luxmore *et al.* 1995) as morphology is adjusted to forage more efficiently for resources. The relative importance of light, moisture and nutrients in determining carbon allocation in seedlings varies between early and late successional species (Canham *et al.* 1996), presumably reflecting the different relative abundance of, and competition for, these resources at different seral stages (Burton 1993, Lauenroth *et al.* 1993). In natural regeneration, rapid initial growth of roots and shoots is an advantage. Seedlings that grow slowly are in danger from desiccation of the upper soil layers, and overtopping by more rapidly growing competitors. Tolerance of competition and moisture stress are strategies that can partially compensate for slow early growth (Groot *et al.* 2001). Competition from herbaceous or woody species with commercial tree species is an important problem (Harvey *et al.* 1993). Although competi-

tion can reduce and delay seedling growth, site preparation significantly reduces the time needed to establish a new stand (Burgess *et al.* 2001). Reducing competition can also stimulate release of advance regeneration. For some boreal species (i.e., *Quercus rubra* L.) the shade provided by an overstory provides better conditions for germinating and early growth (Crow 1988).

Seed pathogens, predators, and herbivores

Studies of regeneration have frequently overlooked the effects of seed pathology and predation, and the role of herbivores in the recruitment and survival of tree seedlings. As noted above, the benefit of nurse logs in some forest types may be due to a preponderance of seed fungal pathogens on the forest floor (Zhong and Van der Kamp 1997). In the boreal forest, red squirrels (*Tamiasciurus hudsonicus* Erxleben) are an important seed mortality agent, while in clearcuts deer mice (*Peromyscus maniculatus* Wagner) and southern red-back voles (*Clethrionomys gapperi* Vigors) can occur in sufficient numbers to significantly reduce seedling recruitment by consuming large numbers of viable seed (Moses and Boutin 2001).

Ungulates and beavers (*Castor canadensis* Kuhl) can function as important biogenic disturbance agents, either retarding or accelerating succession depending upon their impact on regeneration (Reimoser and Gossow 1996). In Finland, a high moose (*Alces alces* L.) population is considered the most likely reason for Scots pine (*Pinus sylvestris* L.) plantation failures in the 1970s and 1980s (Läpäri and Löytyniemi 1988). Snowshoe hare (*Lepus americanus* Erxleben) populations in Canada have profound effects upon vegetation composition through excessive browsing of young seedlings (Krebs *et al.* 1995). Browsing pressure by several deer species has also been shown to significantly influence regeneration (Moore *et al.* 2004).

Disturbance

Different types of disturbance and their timing can have very different regeneration consequences. Greene *et al.* (1999) suggested 4 parameters that are necessary to model the recruitment process: 1) colonization distance (how far seeds must travel to the recruitment site), 2) return time (the length of time between disturbance events), 3) disturbance severity, and 4) specificity (the type of disturbance). Where there is a well-developed seedling bank, severe defoliation of overstory trees by insects or low-disturbance logging can increase available light and trigger seedling release leading to a complex stand structure. Complete overstory mortality by wind or fire usually creates an abundance of suitable seedbeds and increases light, moisture and nutrient availability, thereby facilitating the establishment of an abundant new seedling cohort. Fire is an important disturbance agent regulating the abundance and diversity of tree species in boreal landscapes (Payette 1992). Vegetation composition after a fire is a function of several factors, including pre-burn vegetation type and age, time of burn, fire severity, topography, and the post-fire climatic conditions (Viereck 1983, Bonan and Shugart 1989, Greene and Johnson 2000).

Anthropogenic disturbances can also affect regeneration processes. In clearcuts, radiation balance and energy budget in the seedbeds are altered significantly (hotter during the day and colder at night). Water balance at the soil surface can fluctuate.

tuate rapidly and widely, with the risk that regeneration microsites dry out beyond germinant tolerance (Farmer 1997). In many cases, the forest floor remains largely intact following harvesting. Understory vegetation can develop therefore rapidly from existing seedbanks and out-compete conifers and light-seeded hardwoods. One option is to break up the LFH layer and mix it with the mineral soil to disrupt understory regeneration and create suitable seedbeds for tree regeneration. This method has been used successfully for regenerating *Betula alleghaniensis* Britton (Farmer 1997) or *Pinus banksiana* Lamb. (Chrosiewicz 1990).

Scale of disturbance

Disturbances vary greatly in size. Small gaps are created by the death of individual trees, intermediate-sized patches by wind, fire or insects, and very large areas (100 000 ha or more) by wildfires and epidemic diseases or insect attacks (as the mountain pine beetle outbreak in British Columbia). The vast majority of fires are of intermediate and small size (Johnson *et al.* 1998). Although of low frequency, large fire events are an important feature for succession of boreal forests (Stocks *et al.* 2002). Small-scale and low-severity disturbances are strongly influenced by the species composition, structure and condition of the forest, whereas large-scale disturbances are relatively unaffected by these factors (Kuuluvainen 1994). Post-disturbance regeneration, however, depends more on the severity, scale and landscape pattern of the disturbance than on the pre-disturbance forest condition (Albani *et al.* 2006). Small-scale disturbance has an important role in maintaining a diverse forest structure and may result in higher species diversity within a given forested area (Kuuluvainen 1994). Large disturbances are also important agents of diversity because of spatial heterogeneity in severity, which in turn modifies the landscape pattern of successional pathways and age classes (e.g., Sirén 1955). In other cases, small-scale disturbances may perpetuate the regeneration and dominance of late-seral, shade-tolerant species (Mailly *et al.* 2000).

Constructing a model of regeneration in boreal forests

Traditionally, regeneration in boreal forests has been modelled in as an aggregated process that incorporates several events (bold boxes, Fig. 1). This simplification has been acceptable for current environmental conditions, but dividing regeneration into its component parts (seed production, dispersal, establishment, growth) will be important in efforts to simulate the effect of climate change (Price *et al.* 2001). Greene *et al.* (1999) listed 5 tree-related biotic parameters deemed fundamental to seedling recruitment: (1) tree basal area, (2) seed mass, (3) asexual reproduction capacity, (4) dormant seedbank, and (5) shade tolerance. Abiotic parameters such as light, temperature and moisture regime have an important influence on seedling development (Price *et al.* 2001). The importance of each factor should be carefully evaluated, however, to avoid an unnecessary increase in model complexity and data requirements, and to permit the inclusion of pre-existing data (Lauenroth *et al.* 1993). These key factors can be combined within a model in several different ways.

Static versus dynamic models

In a static model, time is the only factor determining when regeneration events occur. Growth and yield models are an example of this approach. These models do not simulate

regeneration explicitly. Instead, a cohort of new trees is simply added to the model based on long-term averages calculated from mensurational data (Vanclay 1995). This statistical approach to regeneration is usually based on relatively simple equations as, for example, in FVS (Dixon 2002) or TASS (Di Lucca 1999).

In dynamic regeneration models, values for the input variables are derived from simulation processes that can vary temporally (Ek and Brodie 1974, Vanclay 1995). In process-based models, for example, plant growth is driven by simulated material exchange processes (Hari *et al.* 1982, McMurtrie and Wolf 1983, Bossel and Schäfer 1989). The rate of change in plant size (and thus its potential for seed production) therefore depends upon plant size at a given time and the processes influencing the size-specific net uptake rate of resources. In addition, in early seedling establishment, rapid initial growth of roots and shoots is an advantage, because it reduces the dangers from drying of the upper soil layers or from the development of more rapidly growing competitors. Dynamic models can also simulate the influence of changing environmental conditions on seed germination and seedling growth (Price *et al.* 2001). By varying the intensity, type, and frequency of disturbance combined with species-specific factors such as the amount and frequency of seed production, dispersal and germination rates, a number of different regeneration pathways can be produced. (Noble and Slatyer 1980, see Fig. 1). Several models of succession have been developed that explicitly incorporate these factors (Cattellino *et al.* 1979, Noble and Slatyer 1980, Seely *et al.* 2008).

Deterministic versus stochastic models

Another important decision when designing a model is whether the value for each variable is represented explicitly, or probabilistically. In deterministic models, the input values contain no associated error whereas in stochastic models the outcome varies randomly within limits specific to the input variables and associated processes (see Pukkala 1988). There are several ways to implement stochasticity: (1) a pseudo-random uniform number between 0 and 1 is drawn and applied to a regeneration function (as in JABOWA II, for example; Botkin 1993) or, (2) as a random draw from well-established probability distributions (Greene and Johnson 2004). Stochasticity may be especially important in modelling processes that exhibit considerable inter-annual variation. Examples include seed production in *Picea glauca* (Moench) Voss and *Fraxinus nigra* Marsh. Intervals between bumper crops in these species can vary from 4 to 8 years (Groot *et al.* 2001).

Process-based and mechanistic models

Process-based models simulate the structure and function of a forest ecosystem using mathematical representations of the underlying biological processes that control the behaviour of the ecosystem (Godfrey 1983). Mechanistic models, in contrast, focus on the interactions between process variables to define model structure (DeAngelis and Mooij 2003).

A key assumption of process-based models is that the properties of a given process and the interdependency between processes can be determined outside of their functional environment (see Blake *et al.* 1990). Tree growth, for example, is represented by simulating one or more of photosynthesis, carbon allocation, respiration, growth regulation, and intra-tree transport (see, for example, Godfrey 1983,

Dixon *et al.* 1990). Recruitment and regeneration modelling has often been overlooked in process-based models (Landsberg 2003). This may be a consequence of the many factors influencing regeneration. These include (see Greene *et al.* 1999): (1) the production of seeds and asexual stems, (2) the dispersal of seeds by wind (or the dispersion of asexual stems) as a function of distance from source, (3) dormant seed bank capacity, (4) organic layer depth as a determinant of germinant mortality and asexual bud response, and (5) shade tolerance as a partial arbiter of the density of advanced regeneration. As a consequence, in process models regeneration is usually modelled simply as a sequence of discrete steps (see Fig. 1) with survival rates assigned at each step (see Kurz and Apps 1999, for example). An alternative approach is to scale the relative influence of a given factor on the overall regeneration process (see Greene *et al.* 1999). Bonan (1989) developed a model to examine factors regulating the soil thermal regime of boreal forests, which was then integrated into a gap model of forest vegetation patterns. Regeneration was constrained by the same site conditions limiting tree growth (growing season temperature sums, available light, soil moisture, and nutrient availability) but with additional effects due to thickness of the forest floor organic layer and seed availability following fire. Another example of this approach is the PICUS model (Lexer and Honninger 2001). It simulates seed production as a function of species, tree size and absorbed light, and seed germination as a function of chemo-physical site properties and bioclimatic variables. Herb and shrub competition is rarely simulated in process-based models, and yet Bi *et al.* (2007) showed that when disturbance type and intensity were combined with alternative methods of regeneration (seeds or rhizome), this could result in very different outcomes for forest regeneration.

Mechanistic models integrate a large number of ecological processes. These models can be complex making it difficult to ascribe cause-and-effect relationships among input and output variables (Reynolds *et al.* 1993). Nevertheless, this approach can help conceptualize and formulate a better understanding of complex systems (Kimmins 2004). The impact of moisture on seedling recruitment of boreal tree species has been modeled mechanistically by assuming that initial root length is proportional to seed mass and that seedbeds can be classified according to their moisture retention capability (Greene and Johnson 1999). Other processes suited to a mechanistic approach are seed dispersal and seedling mortality (see Seely *et al.* 2008; Fig. 1).

Spatial versus non-spatial models

Until recently, most natural regeneration models were concerned primarily with predicting the demographics in a stand of structurally homogeneous plants (Price *et al.* 2001). These models usually provided no explicit consideration of spatial and temporal patterns in seedbed availability, spatial heterogeneity in light or soil resources, and how competition for those resources affected seed production and plant survival, although an exception is the SORTIE model (Canham *et al.* 1999). At higher spatial scales there are also processes that determine the pattern of seed distribution across the landscape. Landscape-level regeneration models have been developed (see Mladenoff and He 1999) but some scaling issues still need to be resolved (Fortin and Dale 2005).

A critical property of any regeneration/recruitment model

is the spatial scale over which it best applies (single tree, stand or landscape) and whether, as in the latter 2 cases, there is explicit representation of the spatial location of trees and other plants. Stand-level gap models, for example, are usually applied to small and medium-sized canopy gaps (JABOWA's neighbourhood plot size, for example, is usually set at 10 m × 10 m; Botkin 1993) but they contain no spatial representation of individual trees (but see Busing 1991, Mailly *et al.* 2000). This represents a significant limitation in northern forests where conifers have narrow crowns and their spatial relationship determines the actual gap size (Oliver and Larson 1990). In some models, the spatial interaction between trees has been simulated indirectly via its effect upon resource depletion (e.g., Wu *et al.* 1985, Mou *et al.* 1993, Pacala *et al.* 1993). The SORTIE model (Pacala *et al.* 1996), which was originally developed for hardwood forests in northeastern North America, has a recruitment submodel consisting of species-specific equations that predict the number and spatial locations of seedlings produced by a maternal tree (Ribbens *et al.* 1994).

Regeneration processes (seed dispersal, for example) that operate at landscape scales have an important influence on landscape structure and development, and therefore should be represented explicitly (Anderson and Kimmins 1999). Mladenoff and He (1999) developed a spatially explicit stochastic forest model (LANDIS) to simulate large landscapes over long time scales. In LANDIS, seed dispersal is modelled as the probability of seeds dispersing within an effective and maximum seedling distance in accordance with a negative exponential distribution. Seedling establishment is determined by a coefficient that scales seed abundance to how environmental factors favour one species over another. These factors are assigned from empirically derived probabilities or from the simulation results of models such as JABOWA (Mladenoff and He 1999). In the modelling approach used in the models HORIZON (Kimmins *et al.* 1998) and LLEMS (Seely *et al.* 2008), pixels in a raster-based map are classified into different regeneration classes that take account of species, seed weight, distance to seeds sources and wind direction.

Gap models

Modellers interested in regeneration at the stand level can use a gap model to simulate tree community development at a localized spatial scale, as well as community-level interactions resulting from depletion of common resources. Resource and environmental factors are used to constrain maximum seedling establishment rates (Shugart and Prentice 1992) though early seedling survival is generally not simulated explicitly (Urban and Shugart 1992).

A recent review (Price *et al.* 2001) indicated that only 2 gaps models, FORGRA (Jorritsma *et al.* 1999) and PICUS (Lexer and Honninger 2001), included all of seed production, dispersal, germination, and seedling establishment in the regeneration process. The gap model SIERRA (Mouillot *et al.* 2001) describes seed germination as a function of daily air temperature and simulates the sensitivity of the germination process to soil water availability. This model is capable then of representing interactions between climate and key below-ground plant and soil processes that have direct relevance to seedling establishment (Wulfschleger *et al.* 2001).

Early gap models of forest succession assumed that light was transmitted vertically through the forest canopy (Horn 1971, Botkin *et al.* 1972). In more recent models, the geome-

try of light transmission has been included and it exhibits a profound effect upon vegetation dynamics (Canham 1988, Canham *et al.* 1994), particularly at high latitudes. Three-dimensional approaches to modeling light transmission thus represent an important addition to regeneration models (Canham *et al.* 1994, Stadt and Lieffers 2000, Groot 2004). A good example is SORTIE (Pacala *et al.* 1993, 1996). This light-driven gap model tracks the fate and location of each individual tree and its recruitment submodel predicts the number and spatial distribution of seedlings using species-specific equations based on parent tree proximity, size and abundance (Ribbens *et al.* 1994).

In traditional gap models, seedling establishment has often been treated as a stochastic event with establishment rates assumed to be constrained by the same climatic factors that modify growth (Smith *et al.* 1992, Bonan and Shugart 1989). The validity of this assumption has been questioned (Pacala and Hurtt 1993, Dale and Rauscher 1994, Price *et al.* 2001), and model output is sensitive to even small errors in climate parameter estimates (Botkin and Nisbet 1992). Several modifications have been proposed. These include consideration of bud-break heat sum requirements, and temperatures necessary for induction of dormancy and cold hardiness (Burton and Cumming 1995). Kellomäki *et al.* (1992) have included a multiplier for frost damage in the SIMA model. Pukkala (1988) and Kellomäki and Väisänen (1997) have considered the effect of climate on seed crop, seed quality and seed germination. More recently, Lepage *et al.* (2000) used likelihood estimation techniques and the Poisson distribution to fit functions to empirical data in order to predict the overall density of seedlings in a quadrat, as a function of the area of each of the substrate types present and the distribution of parent trees. Predictions of seedling recruitment were weighted by cover and favorability of each substrate type under 4 levels of canopy openness. Parameter values were derived through statistical fitting procedures that represented the local site conditions encountered during field sampling.

Disturbances such as fire and its effect on forest seedling regeneration have been modeled in a variety of ways in gap models. Generally, the effect on tree mortality and consumption of the duff layer are modelled in relation to fire intensity (Keane *et al.* 1996). Bonan's (1989) boreal forest gap model simulated fire intensity as a function of fuel build-up, with tree size, species-specific fire tolerance, and fire intensity, as modifying factors. In models such as FIRE-BGC (Keane *et al.* 1996), fire intensity and rate of spread are modelled dynamically using simulated landscape features. The long-term consequences of the interaction between fire severity and seed production were explored by McIntire *et al.* (2005) in the stand-level model FORECAST. They showed that the loss of seed source legacies reinforced the dominance of disturbance-driven species.

Population, cohort or individual models

When the spatial features of regeneration are of interest (distance from seed sources, dispersion patterns, patch regeneration, or availability of suitable locations for establishment or seedling growth), the individual-tree approach is well suited to this type of modelling. In individual-tree models, seedling recruitment is usually a function of distance, position and size of the parent tree. It has been suggested that further work is required to elucidate the effects of propagule abundance and

dispersal (Busing and Mailly 2004). Another approach is to group individuals within size or age classes, and then simulate recruitment into each cohort, as was used in the REGSNAG model (Kupferschmid *et al.* 2006). This approach is useful because each cohort can be assigned different attributes (Kimmins *et al.* 1999). Although modeling regeneration with attributes and functions defined at the cohort level improves model realism, processes that differentially affect trees within a cohort (size-selective browsing, for example) are still not accounted for.

Spatial scale

The appropriateness of a given model and its complexity are dictated by the spatial scale at which it is applied. If forest composition and the main variables driving regeneration can be assumed to remain constant, regeneration and stand composition can be linked using a simple stand-level statistical relationship. This is unlikely to be the case, however, when the number and distribution of favourable microsites created after a disturbance changes over time (see Greene *et al.* 1999). Furthermore, assumptions of universal availability of propagules and environmental homogeneity are common (Busing and Mailly 2004), and yet Clark and Ji (1995) found that models assuming an unlimited supply of propagules were likely to overestimate species abundance.

Ecosystem models designed to be more inclusive (by incorporating soil, tree and understory processes) and that include a regeneration component have been developed (Keane *et al.* 1996; Kellomäki and Väisänen 1997; Friend *et al.* 1997; Kimmins *et al.* 1998, 1999). These models have an explicit representation of many key ecophysiological processes and conditions dictating growth, carbon allocation, mortality and regeneration. Those models designed to address specific issues in forest ecosystem management have included linkages between tree and landscape level processes (the FORECAST and HORIZON models, for example; Kimmins *et al.* 1998), while others have emphasized the influence of climate change (Botkin and Nisbet 1992, Dale and Rauscher 1994, Price *et al.* 1998). Although some are primarily stand-level models, larger-scale processes are implicit in their regeneration component (Friend *et al.* 1997, Kellomäki and Väisänen 1997).

Another important consideration is the shift in management practice from stand-level considerations to the broader, landscape level (Andison and Kimmins 1999). This will necessitate the development of landscape models that incorporate the regeneration contributions of individual trees in the stand, the distribution of stands across the landscape, the dispersal of seed between stands, and the regeneration consequences of reserves and "connectivity corridors." One example of this approach is LLEMS, a GIS-based model in which growth and development of each stand (polygon) on the landscape is driven by the stand-level ecosystem model FORECAST (Kimmins *et al.* 1998, 1999; Seely *et al.* 1999). In LLEMS, natural regeneration in disturbed polygons is influenced by regeneration processes both within that polygon and in adjacent polygons. Finally, some models have been developed (CBM-CFS2; Kurz and Apps 1999) that simulate forest regeneration at the continental level. Although the simulation of regeneration in the CBM-CFS2 model is highly simplified, this may be a level of complexity appropriate to model objectives (see below).

The issue of model complexity

Regeneration models are much more complex when component processes are evaluated for individual seedlings, rather than cohorts or populations, and detailed temporal and spatial dimensions are included. Since complex models involve a larger number of parameters, more data are required for their calibration, thus rendering them less portable (Sievänen 1992, Keane *et al.* 1996, Friend *et al.* 1997). These disadvantages can be outweighed, however, by their generality and ability to predict regeneration under a range of environmental conditions.

The appropriate degree of complexity thus depends on the purpose of the model (Kimmins *et al.* 2008). If a regeneration model is to be used when environmental conditions are well-defined and the management period relatively short, a simple deterministic approach should suffice. Generating projections for new management scenarios or changes in climatic conditions, however, requires a model that also incorporates the key processes influencing regeneration. Ågren *et al.* (1991) have suggested the following steps in deciding how much complexity to include in a model: 1) determine the model's specific objectives, 2) identify the minimum number of variables needed to define the key components and processes of the system, and 3) evaluate whether this model satisfies the objectives. If model performance is below expectation, only then should more variables be added.

Final Considerations for Implementing Regeneration in Boreal Forest Models

Modeling regeneration under potential climate change

Marked changes in climate are expected to have a significant impact upon boreal forest ecosystems (Chapin *et al.* 1992, Keyser *et al.* 2000). The relationship between climatic factors and forest regeneration, however, is poorly understood (dotted lines, Fig. 1). To incorporate climate change effects within the context of forest regeneration, information is required on the effect of thermal regimes on flower development and seed production, the potential colonization rates of individual species, the ecophysiology of seed production and seedling establishment, processes of seed dispersal, storage and germination, and the sensitivity to climate and elevated CO₂ of species that reproduce vegetatively (Price *et al.* 2001). Several reviews of existing models have been conducted to determine their capability to simulate climate change effects. Price *et al.* (2001) have suggested that, among gap models, the major limitations are: (1) that ecological processes are not treated separately, (2) site conditions and seed availability are treated uniformly, and (3) insect and vertebrate herbivory are rarely accounted for. Wullschlegel *et al.* (2001) have argued that within the context of climate change, more attention is needed to below-ground processes. Specific areas for model improvement include better descriptions of the soil environment, including a multi-layered representations of soil water and nutrient availability, better information on biomass allocation to roots and root distribution within the soil profile, improved treatment of inter- and intra-specific competition for available soil resources, increased consideration of spatial processes as related to land-surface hydrology, and improved attention to above- and below-ground interactions.

Several methods have been developed that model vegetation response to changing climates but they do not deal explicitly with regeneration processes. This is likely because

most predictions of vegetation change to date have been done using global circulation models (versus regionalized or down-scaled interpolated output). To overcome this issue, Hogg and Schwarz (1997) combined a semi-quantitative regeneration index with a climatic moisture index specifically developed for several vegetation zones in western Canada to determine conifer distribution in 4 different vegetation zones. This approach may be promising because it uses readily available Global Circulation Model output directly in its calculation of regeneration success.

The "ideal" model of regeneration

The ideal regeneration model for boreal forests should be capable of simulating the effect on seedling recruitment of: (1) different types of disturbance—fire, windthrow, insect outbreak, forest harvesting, site preparation, and vegetation management—this should include variation in scale, pattern and severity since it is disturbance that creates the potential for recruitment; (2) stage of development, species composition, age and size class structure, slope, aspect, soil type and condition, the light profile, nutrient availability, temperature and moisture regime—these features define the biophysical environment for seedling recruitment; (3) the autoecology of tree and plant species, including seed production, dispersal and viability, light requirements and shade tolerances, temperature, moisture and nutrient requirements, and susceptibility to herbivory and pathogens—these features represent the recruitment potential of a given species; (4) Survival and growth of seedlings to maturity, including the effects of competition with herbs and shrubs in both above and below-ground; and (5) the effect of potential climate change. Fig. 1 illustrates these features and their relationships.

Many attempts have been made to model natural regeneration (summarized in Table 1). Unfortunately, the processes involved are complex and modeling objectives vary so widely that no single approach may be sufficient. One proposed solution is to predict future species composition following disturbance from 3 vital attributes: method of arrival and persistence at a site; ability to grow to maturity in the new stand; and the time needed to reach critical life stages (Rogers and Johnson 1998). A second approach is to focus on seed production, asexual stem production, seed dispersal, germination, and advance regeneration (Greene *et al.* 1999). Both approaches require a strong link between regeneration processes and temperature, nutrient and moisture availability (Keane *et al.* 1996). A third approach is to develop a common conceptual framework from which a network of models can be developed (Acock and Reynolds 1990, Robinson 1998). Implementing a modular approach to modeling living systems could be facilitated by the sharing of information and models across the internet. An important step in this regard is the development of internet model registries (see, for example, <http://ecobas.org/www-server/index.html>), which include model descriptions, input requirements, and application histories. It may also be possible to integrate several types of models (including growth, mortality and regeneration sub-models) into a common modelling platform such as CAPSIS (Computer-Aided Projection for Strategies In Silviculture; de Coligny *et al.* 2004).

Regardless of which approach is utilized, model performance should be assessed by comparing predictions to an inde-

Table 1. Potential characteristics (not mutually exclusive) to be included in regeneration models

Model type	Characteristics	Method to simulate regeneration	Example	References
Static model	Only time determines when regeneration occurs	Regeneration simulated by long-term average calculated from mensurational data	Growth and Yield models TASS / TIPSy MULTIPLE PATHWAY	Di Lucca (1999) Cattellino <i>et al.</i> (1979)
Dynamic model	Regeneration is a function of more variables than time	Values for driving variables are derived from input data or through simulation processes	Process-based models Mechanistic models	Bossel and Schaffer (1989) Greene and Johnson (2000)
Deterministic model	Output determined precisely	Inputs values for the driving functions that simulate regeneration contain no error	FORECAST	Kimmins <i>et al.</i> (1999)
Stochastic model	Output represents a probabilistic value	Regeneration is a random function with an associated error	JABOWA II SIMA FORECE	Botkin (1993) Kellomäki <i>et al.</i> (1992) Kienast <i>et al.</i> (1999)
Process-based model	Use of mathematical representations of the underlying biological processes that control the behaviour of the ecosystem	Regeneration is simulated through a battery of equations connected to environmental factors	PICUS FORGRA FIRE-BGC FSV Series of equations	Lexer and Honninger (2001) Jorritsma <i>et al.</i> (1999) Keane <i>et al.</i> (1996) Dixon (2002) Greene and Johnson (1999)
Mechanistic model	Use of fundamental knowledge of the interactions between process variables to define the model structure	Regeneration and growth simulated as the result of one or more processes of photosynthesis, carbon allocation, respiration, intra-tree transport, growth regulation	FORCEE FORECAST HORIZON LLEMS	Kimmins <i>et al.</i> (1998) Kimmins <i>et al.</i> (1999) Seely <i>et al.</i> (2008)
Non-spatial model	No specific representation of individual trees locations	Simulation of effects of species interaction and resource availability	JABOWA II FORECAST	Botkin (1993) Kimmins <i>et al.</i> (1999)
Spatial model	Specific representation of location of trees and/or plants	Prediction of the number and spatial locations seedlings produced by a maternal tree	SORTIE PICUSPICUS	Pacala <i>et al.</i> (1996) Lexer and Honninger (2001)
Ecosystem model	Simulation of regeneration of several populations of trees and plants	Each population has different parameters to define the regeneration patterns (seed production, dispersal, establishment)	FORCEE FORECAST HORIZON LLEMS	Kimmins <i>et al.</i> (1998) Kimmins <i>et al.</i> (1999) Seely <i>et al.</i> (2008)
Population model	Simulation of regeneration of a population of a given species	Seed dispersal, germination and other processes are defined with population-level attributes. Usually used to study the influence of species composition on regeneration patterns.	FORSKA	Prentice and Leemans (1990)
Cohort model	Simulation of different cohorts which are regenerated at the same time	Each tree cohort is defined as a group of trees regenerating at the same time and/or space	REGSNAG FORECAST FSV Series of equations	Kupferschmid <i>et al.</i> (2006) Kimmins <i>et al.</i> (1999) Dixon (2002) Greene and Johnson (1999)
Individual model	Trees are individual items and are simulated independently from each other	Each tree is a potential source of seeds and each seedling establishes in an independent environment defined with tree-level attributes	FORCEE SORTIE	Kimmins <i>et al.</i> (1998) Pacala <i>et al.</i> (1996)
Gap model	Simulate tree community development at a localized spatial scale	Explicit representation of growth processes and community-level interactions resulting from depletion of common resources	FORGRA PICUS SIERRA SIMA FORECE	Jorritsma <i>et al.</i> (1999) Lexer and Honninger (2001) Mouillot <i>et al.</i> (2001) Kellomäki <i>et al.</i> (1992) Kienast <i>et al.</i> (1999)
Spatial gap model	Specific representation of location of trees and saplings	Regeneration simulated as a function of shade tolerance based on light levels calculated within the neighbourhood of a sapling	SORTIE SPACE DRYADES	Pacala <i>et al.</i> (1996) Busing (1991) Mailly <i>et al.</i> (2000)
Landscape model	Representation of regeneration at landscape level	Definition of pixels (entire stands or areas within stands) with different classes of regeneration in raster-based maps, by which one cell or stand influences another	LANDIS LLEMS	Mladenoff and He (1999) Seely <i>et al.</i> (2008)

pendent set of empirical data, a process referred to as validation or evaluation (Vanclay and Skovsgaard 1997; Yang *et al.* 2004; Blanco *et al.* 2005, 2007). Unfortunately, these data sets are rare or difficult to acquire. The problem could be simplified by developing models based on principles that emphasize and explore cause and effect relationships, and which can then be tested empirically (see Botkin 1993).

We have described many of the biophysical determinants that influence boreal forest regeneration and highlighted the central issues related to their implementation in forest models. It seems unlikely that any single model approach will be adequate for all purposes; the most appropriate model will depend primarily on its anticipated use. Table 1 summarizes the basic approaches that can be used to model regeneration.

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