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Modelling forest succession in two southeastern Canadian mixedwood ecosystem types using the ZELIG model

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ABSTRACT

The gap model ZELIG was validated for red spruce–balsam fir–yellow birch and yellow birch–sugar maple–balsam fir forest types in southern Quebec, Canada. Long-term historical data originating from the Lake Edward Experimental Forest, La Mauricie National Park, were used. The effect of the variation in plot size, representing the space within which trees uptake site resources, was also examined. Several species were included in both forest types: red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.), yellow birch (*Betula alleghaniensis* Britton), white birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.) and northern white cedar (*Thuja occidentalis* L.). The pattern of change in basal area growth varied among species, ranging from a steady increase to a more or less rapid decline. There was a good agreement between observations and predictions for yellow birch, red spruce, red maple, sugar maple, balsam fir and northern white cedar. Plot size had a significant impact on the dynamics of the different species. Depending on the species, the decline was accelerated, the amplitude of the fluctuations varied, or the maximum basal area reached changed. Predicted regeneration varied among species and the number of seedlings generally increased with increase in plot size. The pattern of development for most species was related to their life characteristics. The results highlighted the fact that there is a critical lack of knowledge and data on the dynamics of regeneration from the seedling to the sapling stages for the two forest types studied, which resulted in poor predictions for some species. As the life characteristics varied among species, the use of only one plot size for all species may not be realistic.

1. Introduction

Different types of models have been developed during the last few decades to predict the dynamics of forest ecosystems. The first models were developed in the 1960s and consisted of growth and yield models that predicted tree and stand productivity using variables that could be derived from inventory measurements. Growth and yield models focus on the prediction of the effect of management practices (Mohren and Burkhart, 1994). They are not based on a description of the mechanisms that govern tree and stand growth. The statistical methods used for their calibration aim at estimating the parameters that best fit the model components to observed data. Even though they can predict relatively accurately the short-term effects of silvicultural treatments, they cannot be used safely to predict the growth of forest ecosystems with

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characteristics that extend beyond the range of the data used for their calibration.

As technology development allowed more precise measurements of processes, such as photosynthesis, process-based models were developed to predict forest productivity by modelling the physiological processes that govern the allocation of carbon within trees and stands (e.g. Running and Coughlan, 1988; Running and Gower, 1991; Peng et al., 2002; Paul et al., 2003). Process-based models are considered as very flexible to predict the effect of disturbances, such as insect infestation or global change, because they focus on the description of the mechanisms that affect tree and stand growth. However, their calibration requires extensive ecophysiological and environmental data (Shugart, 1984; Landsberg, 2003). Thus, it may be difficult to use process-based models when environmental site conditions vary considerably or when several species are involved, as ecophysiological data are not usually measured extensively.

Gap models are a compromise between traditional growth and yield models and process-based models. They are considered as a suitable approach by forest ecologists to predict long-term forest dynamics, as they integrate the effects of climatic and site variables and of intra- and inter-specific competition (Bugmann, 2001). Although they integrate ecophysiological factors, they were developed to remain quite general in application. Also, gap models focus on modelling forest succession by integrating several demographic mechanisms, such as tree establishment, growth and mortality. The majority of gap models that have been developed over the last few decades were derived from the JABOWA and FORET models (Bugmann, 2001).

There is a rich body of literature that focuses on the development of gap models. Recent examples can be found in Gullison and Bourque (2001), He et al. (2002) and Song and Woodcock (2003). However, very few studies have dealt with the validation of forest succession models with historical data (e.g. Lindner et al., 1997; Yaussy, 2000; Mäkelä et al., 2000) because long-term records on the same forest ecosystems are extremely rare (Smith and Urban, 1988; Bugmann, 2001). The overall objective of the present study was to validate the gap model ZELIG for red spruce–balsam fir–yellow birch and yellow birch–sugar maple–balsam fir forest types in southern Quebec, Canada, using long-term historical data. The first specific objective was to examine for both forest types the sensitivity of ZELIG to variation in the size of the area within which individual trees compete for site resources. The second specific objective was to contrast the dynamics of the different species in the two forest types.

2. Materials and methods

2.1. *Study area*

The forest ecosystem types under study were located at the Lake Edward Experimental Forest (LEEF), which is located within La Mauricie National Park (46°45′N, 72°56′W), one of the national parks of the Government of Canada. This territory belongs to the Great Lakes-St. Lawrence forest region (Rowe, 1972). The landscape is quite variable, ranging from moderate hills to mountains with a maximum elevation of 431 m. Climatic conditions vary considerably throughout the year. During winter, temperature remains mostly below 0 °C and there is snow from November to April. Summers are characterized by warm temperatures, generally above 20 °C. Mean annual temperature is 2.5 °C, growing degree-days are between 2000 and 2600 for a growing season that lasts between 160 and 170 days. Annual precipitation varies between 900 and 1000 mm (Robitaille and Saucier, 1998).

The LEEF, established in 1918 by the Government of Canada, originally measured about 16 km^2 in area (Hatcher, 1959; Archambault et al., 2003). In 1918, the objective was to study the growth, mortality and regeneration following harvesting, as problems were identified when different silvicultural treatments were undertaken: insufficient softwood regeneration, increase in hardwood proportion, competition from mountain maple (*Acer spicatum* Lamb.) and other undesirable hardwoods. By 1936, 343 sample plots measuring 405 m^2 in area were established in a grid network, such that the sample plots were 201 m apart from each other. Measurements were conducted in 1936, 1946, 1956, 1967, 1995, 2001, 2003 and 2004. However, approximately half of the original sample plots were measured between 1994 and 2004. The network of sample plots was representative of most forest types that exist in the region. For the present study, two forest types were examined: the red spruce–balsam fir–yellow birch (RSYB) forest type and the yellow birch–sugar maple–balsam fir (SMYB) forest type (Table 1). Data from five uncut sample plots within each forest type were used for the present study. The forest surveys conducted in the different years differed slightly in their procedures. Before 1994, dbh and the number of live trees with dbh larger than 1.3 cm (0.5 in.) were tallied by 2.54 cm (1 in.) dbh classes. Dead trees larger than 9 cm in dbh were also measured. For the 2001 survey, vegetation and soil characteristics were measured by following the procedures outlined by Saucier (1994) for the description of forest ecosystems.

2.2. *Description of ZELIG*

ZELIG is a gap model based on the same basic principles as the JABOWA and FORET models (Urban, 1990, 2000; Urban et al., 1991). For the present study, ZELIG was selected because (1) it is an individual-tree model that includes realistic representations of tree and stand growth, (2) remains relatively general for application to different forest types, and (3) is adapted for uneven-aged mixed stands (see Urban, 1990). The main processes simulated by ZELIG include photosynthetic active radiation (PAR) interception, tree mortality, treefall gaps and regeneration establishment. The diameter increment for each tree species is computed by integrating the effect of potential growth reduced by environmental constraints. Potential growth consists of the maximum growth rate that a tree species can achieve under optimal conditions in the absence of competition. Environmental constraints include modifiers that account for the effects of changes in PAR conditions, temperature, soil moisture and nutrients. Individual-tree growth, mortality and regeneration are computed annually. Central to ZELIG is the concept of a grid square network that represents the space within which individual trees uptake site resources (Urban et al., 1991, 1999; Coffin and Urban, 1993). This space,