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Simulating the impact of small-scale extrinsic disturbances over forest species volumetric light environment

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Abstract

Small-scale disturbances (SSD) creating canopy gaps are fundamental to successional dynamics in temperate forests. As gap-oriented management becomes very popular, spatial aspects of gap dynamics, especially the detailed impact of disturbances on the light environment for different species, remain understudied. The aim of this study is to evaluate this effect using the individual-based model SORTIE. Using different initial conditions, 10 simulated data sets, each representing temperate forests, were artificially disturbed using four disturbance sizes. For each 3D location of the simulation space, light availability was computed using the gap light index to create volumetric light data sets. The growth functions of the nine tree species incorporated in the simulation were mapped to each light data set, generating species-dependent 3D cubes illustrating the effect of small-scale disturbances over the different species according to their autecologic relationship to light. The general impact of the simulated SSD was assessed (1) by extracting the 3D boundaries associated to the absolute spatial influence of each replicated SSD and (2) by analyzing the variation of light inside and outside these boundaries, at different height levels. Results were compared for each disturbance size. The species response to different disturbance sizes was evaluated globally and also as a function of height levels under the canopy. This study revealed that the impact of different SSD schemes is highly variable among replicates. Nonetheless, results revealed that small size disturbances exhibit more heterogeneous impact. A threshold effect was detected around a disturbance size of 1000 m^2 suggesting a relative SSD impact that decreases for large SSD sizes. It was also found that species relationship is consistent between different disturbance schemes.

Keywords: Small-scale disturbance; Individual-based simulation; Forest management; Light environment; Spatial structure; Species expanded gap

1. Introduction

Most ecologists now recognize that local small-scale disturbances (SSD) are an important driving force of forest community change in many ecosystems of the globe (Bormann and Likens, 1979; Lorimer, 1980, 1984, 1989; Pickett and White, 1985; Withmore, 1989; Payette et al., 1990; Runkle and Yetter, 1987; Runkle, 1990, 1991; Belsky and Canham, 1994). Canopy openings are mainly created by natural death of trees (Barden, 1989) but may also originate from extrinsic factors such as windstorm and thunderstorm light burst. These different processes are responsible for a spectrum of SSD, varying in terms of size, shape and composition (Lorimer et al., 1988). In temperate ecosystems, depending on the source and the intensity

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of the underlying process that creates them, natural SSD sizes will range from <50 to 2000 m^2 (Runkle, 1982; Coates and Burton, 1997).

By increasing local light resources, appearance of small-scale disturbances is often associated to an important reconfiguration of tree light habitat with significant impacts on tree resource allocation, tree interactions, and ultimately successional processes. Natural SSD are necessary for almost all tree species to attain canopy status (Canham, 1988, 1989; Pouslon and Platt, 1989) through recurrent suppression and release episodes, and species-dependent resource integration strategies. Adaptive strategies range from the capacity to capture and convert sudden local light increase in terms of radial growth more efficiently (Wright et al., 2000) to the ability to survive long periods of light suppression and dramatically decrease the probability of mortality after only a slight increase of solar radiation (Kobe and Coates, 1997). Gaps play a major role in species coexistence by creating local ecological niches for particular species (Denslow, 1980; Brokaw and Schneider, 1989; Sipe and Bazzaz, 1994; Gray and Spies, 1996; Kupfer et al., 1997) or simply by adding some noise to the ecosystem dynamics (Brokaw and Busing, 2000). They constitute an important source of entry sites of new genotypes (Silvertown and Smith, 1988), and may enhance the resistance of some species to herbivory (Coley, 1993).

1.1. *The expanded impact of SSD*

Over the last two decades, knowledge about SSD patterns and processes has been significantly improved, due to several key pioneer field studies emphasizing discrete canopy gaps, at the disturbance level (Runkle, 1982, 1985; Brokaw, 1985; Canham, 1989, 1990; Payette et al., 1990). These studies played a major role in the characterization of many phenomena such as canopy gap replacement, gap closure processes and light resource distribution following the creation of canopy gaps (Runkle, 1991).

Traditionally, gaps were defined by the vertical projection of the canopy opening and were sometimes extended to the basis of the first-order neighbouring trees (Runkle, 1982). This discrete gap/non-gap paradigm has been highly criticized by some researchers (Canham, 1989, 1990; Lieberman et al., 1989) who proposed to reformulate the concept of SSD in terms of canopy closure continuum with an emphasis on the study of light "as it extends into progressively shadier conditions well beyond the absence of any recognizable opening in the forest" (Lieberman et al., 1989). The concept of expanded SSD explicitly rises the following question: what is the impact of a disturbance of a given size and shape inside and outside its discrete boundaries and how does it change through 3D space?

In the context of forest ecology, the impact of small-scale disturbances can be defined and measured either by focusing on the individual tree response to a canopy opening (Ménard et al., 2002a) or through a direct analysis of the light increase patterns generated by the disturbance. The first method represents the only way to assess the real immediate effect of a canopy opening on a specific individual, to investigate the effect of neighbouring trees and to relate individual response to other variables such as age classes, mortality probability, etc. On the other hand, a direct focus on light distribution allows one to assess the particular contribution of the impact generated by a single SSD to any specific spatial 3D location under the canopy, even when the impact is too small to be sensed by individual trees over geographic space.

The impact of a small-scale disturbance is highly dependent on the relative spatial position of the trees in a site, individual DBH, and species foliage opacity among other factors. For canopy disturbances smaller than around 300 m^2, Canham et al. (1990) demonstrated that the impact was also highly heterogeneous and strongly dependent on site latitude and site topography. They also showed that light distribution was changing inside and outside the gaps as a function of height under the canopy. SSD impacts also have different meanings for different species. To illustrate this situation, one may look at the spatial distribution of light over a simulated, deciduous forest stand. Light usually decreases irregularly from the center of an SSD. Two hypothetical species having a different sensitivity to light will be associated to two distinct SSD impact.

1.2. *The role of modelling*

In the field of SSD studies, spatially explicit cell-based and individual-based models (Judson, 1994) have been considered by many as an interesting complement to field surveys. Over the last decade,