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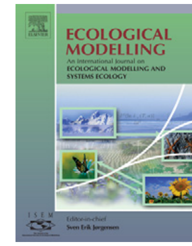

Review

The representation of allelopathy in ecosystem-level forest models

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ABSTRACT

Allelopathy is one of the factors that determine interactions among plants. Allelochemicals have been found in many forest ecosystems, but the importance of allelopathy depends on forest type and environmental conditions. Despite the wide presence of this phenomenon, few forest models have incorporated a representation of allelopathy, but its inclusion should be considered in forest models dealing with environmental stress, exotic plant invasions and ecological succession. Multiple factors influence allelochemical production and toxicity, including nutrient availability, soil moisture and texture, solar radiation, and temperature. Ecosystem-level effects of allelopathy include changes in germination rates, inhibition of seedling growth, mycorrhizal function, insect and bacterial growth, inhibition of nitrification or litterfall decomposition and dieback of mature trees. To illustrate some potential consequences of incorporation some aspects of allelopathy, in an ecosystem-level model, a virtual experiment was carried out with the forest ecosystem-level model FORECAST. This revealed different effects of allelopathy on several ecological variables depending on the type of allelopathic influence simulated. In addition, this experiment showed the utility of ecosystem-level models to simulate, if not directly the allelopathic interactions, at least the ecological effects of allelopathy at the ecosystem level. Overall, my work points out that researchers and forest managers should think carefully about the need to include allelopathy as a way of improving the accuracy of forest models and ecosystem-based decision support tools.

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1. Introduction

Models that represent forest development, from an ecosystem perspective, are proving to be the most suitable tools to assess the sustainability of forest practices. Although different types of forest models have been used for this purpose, hybrid models are possibly the most useful in forest management, because they combine the advantages of processes models and historical bioassay models to compensate for the shortcomings of both approaches (Kimmins, 2004). In order to study the biophysical consequences of forest management at an ecosystem level, a model should represent the most important components that integrate the forest ecosystem in question, independently of the level of complexity of such a model. Among these components, forest soil is the primary component influenced by silviculture practices, because it is an important nutrient and water reserve. Forest soil is a complex environment where multiple biogeochemical processes are superposed at the same time, and as a consequence many models only simulate soil processes through empirical growth modifiers, and therefore they cannot assess biophysical sustainability in ecosystems where moisture and nutrients play a key role in ecosystem sustainability. One of these processes is allelopathy, defined as the effects produced on growth and development of target plants caused by chemicals produced by donor plants (Rice, 1984). For some ecosystems the omission of allelopathy may act as a significant limitation on a model.

Historically, the study of allelopathic interactions has been focused mainly on relationships between crops and weeds (Pellissier and Souto, 1999), and recently, the chemistry and mode of action of allelochemicals has been studied (Einhellig, 2004). However, studies about allelopathic relationships in forest soils are still scarce and dispersed, possibly due to the difficulty of the separation of allelochemical effects from other factors, especially nutrient competition (Weidenhamer et al., 1989; Wardle et al., 1998). Nevertheless, several studies have identified the importance of allelopathy in forest ecosystems. For example, Rietveld et al. (1983) have reported premature birch (*Betula papyrifera* Marsh) death in mixed plantations with walnut (*Juglans nigra* L.). Problems of conifer regeneration caused by ericaceous understory species have also been described (Mallik, 2003). These examples show the importance of chemical interactions among plants in forest development and, therefore, show the necessity of including these relationships in forest models dealing with similar situations.

The first theoretical representation of allelopathic relationships was proposed by Maynard-Smith (1974), using a modified Lotka–Volterra competition model. Improvements and refinements of this model have been used to analyze allelopathy in plant communities and algae (Dubey and Hussain, 2000; Liu et al., 2003; Solé et al., 2005), and Einhellig and co-workers have developed conceptual models of about the mode of action of allelochemicals (see Einhellig (2004) for more references). Other contributions include theoretical models of allelopathy as a continuous time Markov process (Lanchier, 2004), separation of allelopathy from competition (Weidenhamer et al., 1989; Nakamaru and Iwasa, 2000), clarification of the ecophysiological foundations of allelopathy (An et al., 1993; Mukhopadhyay et al., 1998); allelochemical transport characterization and climate effects (Cheng, 1995; An et al., 2002); and simulation of external factors such as target plant density or fire (Weidenhamer et al., 1989; Newton and Weetman, 1994; Mallik, 2003). The development of allelochemical concentration in decomposing plant residues may be the most developed aspect in simulations of allelochemical interactions (An et al., 2002; Sinkkonen, 2003). Despite these theoretical developments, and the verified importance of allelopathy in some forest ecosystems, modelling studies that try to quantify the role of allelochemical interactions in ecosystems are scarce. Analytical models of allelochemicals in soil have generally not yet been integrated with other ecological factors in stand-level models. In this review, references to the simulation of allelopathy in forest models have only been found for FORCYTE-11 (Kimmins et al., 1990) and FORECAST (Kimmins et al., 1999). In grasslands, Goslee et al. (2001) developed improvements in the ECOTONE model to include allelochemical interactions among native and invasive species. This lack of representation of allelopathy in ecosystem models may be due to the complex mode of action of allelochemicals, which can influence processes at all levels of biological organization levels and, as a consequence, because of the lack of a comprehensive conceptual model of allelochemical interaction at the stand-level. Furthermore, there are other factors that should be taken into account in addition to the ones related to allelochemical production and toxicity. To include allelopathic relationships in ecosystem models it is neces-