ECOLOGICAL MODELLING 203 (2007) 464–474

available at www.sciencedirect.com

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journal homepage: www.elsevier.com/locate/ecolmodel

Modelling seed dispersal to predict seedling recruitment: Recolonization dynamics in a plantation forest

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ARTICLE INFO

Article history:
Received 3 August 2006
Received in revised form
7 December 2006
Accepted 11 December 2006
Published on line 24 January 2007

Keywords:
Inverse modelling
Seed dispersal
Seedling recruitment
Seed trap
Abies alba
Fagus sylvatica

ABSTRACT

The extend to which seed dispersal influences seedling recruitment is of major importance for forest dynamics. In non-equilibrium situations, seed dispersal might be of even further importance as it is a major determinant of the rate and composition of secondary succession. We modelled primary seed dispersal in a planted pine–spruce stand intensively recolonized by *Abies alba* and *Fagus sylvatica*, an ecological situation commonly found throughout southern Europe. We then evaluated the role of primary seed dispersal in seedling emergence and recruited seedling density. Using a seed trap experiment and inverse modelling methods, we calibrated short- and medium-distance seed dispersal functions. The relationship between the density of dispersed seed, the density of emerging seedlings and microsite characteristics were assessed using generalized linear models. The cumulative distribution function of seedling-to-nearest-adult distances made it possible to test the concordance between seed rain patterns and seedling spatial distributions. Seed production was highly variable between years for *A. alba* and *F. sylvatica*. Seed dispersal was shown to be locally restricted (median dispersal distance of 13.2–19.2 m for *A. alba* depending on the year and 6.49 m for *F. sylvatica*). Model prediction was considerably increased when seed production was directly assessed (and not indirectly estimated using diameter, for example). The number of *A. alba* seedlings that emerged in 1999 was positively correlated with the number of seeds dispersed in 1998 and with the local density of *Picea abies* adults, and negatively correlated with grass cover. The spatial distribution of seedlings was less aggregated around adult trees than expected from seed dispersal models, but significantly different from random beyond 6 m to the nearest adult for *F. sylvatica* and 26 m for *A. alba*. Thus, seed rain patterns are only partially responsible for recruitment dynamics in our model forest. Our study demonstrates that inverse modelling methods are well suited for the study of seed dispersal at the local scale, especially when a direct count of seed production can be made, and are therefore of particularly high interest in forests where several successional stages are present.

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0304-3800/$ – see front matter
doi:10.1016/j.ecolmodel.2006.12.008

1. Introduction

Predicting the local distribution of new recruits in a plant community has long been a major challenge in ecology. The distribution of seedlings results from several processes: adult fecundity, seed dispersal, spatial distribution of suitable microsites, pre- and post-dispersal seed predation, and intra- and inter-specific competition (e.g. Harper, 1977; Janzen, 1970; Clark et al., 1998; Nathan and Müller-Landau, 2000; Van der Wall et al., 2005). The relative importance of each process might be variable according to ecological requirements and biological traits of species, overall plant community density and composition, successional status within the community, density of seed predator populations and temporal fluctuations in climatic factors (Clark et al., 1999a). The regeneration dynamics of plant communities can thus be considered as a temporal and spatial sequence of different stages, from seed production to recruited seedlings, interacting with biotic and abiotic factors (Clark et al., 1999a; Nathan and Müller-Landau, 2000).

Over the last decades, most experimental studies of seedling recruitment have focused on just one stage (but see Herrera et al., 1994; Jordano and Herrera, 1995; Clark et al., 1998; Uriarte et al., 2005). For example, sowing experiments made it possible to describe microsites suitable for seed germination (De Steven, 1991a) and early seedling survival (De Steven, 1991b). However most of them only provided partial understanding of natural regeneration dynamics, because they assumed that seed rain was unlimited and homogeneous (but see Clark et al., 1998). Likewise, calibrating dispersal functions was not sufficient to measure the existence of recruitment limitations in plant communities, without knowledge of the spatial distribution of safe sites (Jordano and Godoy, 2002) and their saturation threshold (Nathan and Müller-Landau, 2000). Integrated approaches combining information on seed dispersal and seedling establishment are needed to better understand recruitment processes (Schupp, 1995; LePage et al., 2000).

The heterogeneity of seed rains is now considered a major determinant of natural regeneration dynamics (e.g. Nakashizuka, 2001). However, integrated studies were previously limited by difficulties in measuring seed dispersal. In natural uneven-aged forest communities where individual seed shadows overlap and fecundity varies among adult trees, measuring seed dispersal has been considered an impossible task until fairly recently (Ribbens et al., 1994; Clark et al., 1998). Increasingly refined statistical methods (Ribbens et al., 1994; Clark and Ji, 1995; Clark et al., 1998, 1999a), and the development of spatially explicit forest dynamics models (Pacala et al., 1996) now make it possible to quantify seed shadow patterns within forest communities and to measure the role played by seed dispersal in natural regeneration dynamics. Indeed, although several processes might interact simultaneously to shape a spatial pattern and limit the ecological information that can be drawn from spatial statistics, spatial analysis of fully mapped data can help us to better understand the demographic dynamics of plant populations when using clearly identified ecological hypotheses (Barot et al., 1999; Pélissier and Goreaud, 2001).

Most studies of natural regeneration dynamics have focused on closed-canopy, late-successional forests, where competition and microsite distributions were more important than seed dispersal limitation (but see Dalling et al., 2002). In this study, our goal is to investigate the early stages of regeneration dynamics in a forest characterized by several successional stages, where seed dispersal can determine the speed of recolonization as well as the initial composition of the recolonizing forest community (Grubb, 1977; Howe and Smallwood, 1982; Willson, 1993). Natural recolonization of plantation forests and old fields by late-successional forest tree species is currently occurring on a wide scale in many southern European mountainous regions since the middle of the 20th century (Rameau, 1992). We studied seed dispersal and recruitment of new seedlings of silver fir, *Abies alba* (Mill.) and European beech, *Fagus sylvatica* (L.), two shade-tolerant, late-successional species, recolonizing a planted pine (*Pinus uncinata*) and spruce (*Picea abies*) stand on Mont Ventoux, south-eastern France. Calibrating seed dispersal using seedling distribution is not straightforward as seedling distribution is a function of multiple processes, and not just seed dispersal. In this study, we calibrated primary seed dispersal functions for both *A. alba* and *F. sylvatica* using a seed trap experiment and we evaluated the effect of the primary seed rain and microsite characteristics on seedling emergence in *A. alba*. We show that inverse modelling approaches are powerful for calibrating seed dispersal and greatly improved when seed source production potential is thoroughly described.

2. Material and methods

2.1. Study species and study site

A. alba and *F. sylvatica* are two keystone tree species in low to mid-altitude European mountainous forest ecosystems. Both are shade-tolerant late-successional species that form mixed forests over a broad range of ecological conditions from sub-Mediterranean to upper Montane bioclimatic regions. *A. alba* only regenerates from seeds (it is an obligate seeder) and produces winged seeds dispersed by wind. *F. sylvatica* reproduces both by seeds (beech nuts) and by root sprouting. Beech nuts are relatively heavy, highly nutritious and consumed by many vertebrate species. Twenty-six species of birds and 17 species of mammals feeding on beech seeds were recorded by Turcek (1961 and 1967, in Nilsson, 1985). Although beech nuts' primary dispersal is by gravity, their most important dispersal vector is by scatter-hoarding animals.

The study was conducted on Mont Ventoux (44°11′N; 5°17′E), a calcareous mountain located at the south-westernmost tip of the Alps. By 1850, it was almost entirely deforested due to over-grazing by sheep and goat. Mixed *A. alba*–*F. sylvatica* forests were reduced to small forest islands in the most inaccessible parts of the mountain. The decrease of grazing combined with the reforestation efforts undertaken in the early 20th century (using mostly pine and spruce) made it possible for *A. alba* and *F. sylvatica* to gradually recolonize the planted stands.