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Can seed production and restricted dispersal limit recruitment in *Pinus pinaster* Aiton from the Spanish Northern Plateau?

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ABSTRACT

Natural regeneration faces increasing difficulties in dry forests from the Mediterranean basin, including for normally well-regenerating species such as maritime pine (*Pinus pinaster* Aiton). In this paper, we studied female fertility, seed dispersal and spread rates in *P. pinaster* from the Spanish Northern Plateau, where natural regeneration failure is a main concern for forest managers. For this purpose we periodically collected data from seed traps and trees located at two core locations across several years. We found significant variation in interannual cone production, with the best seed trees being the same across years. In addition, we found highly skewed distributions of female reproductive effort and large fertility differences across stands located few kilometres away. Annual seed dispersal kernels fitted lognormal or 2Dt models depending on the stand analysed, with median dispersal distances between 14 and 25 m. Kernels fitted for maximum dispersal periods showed an outstanding intraseasonal variation of median dispersal distances, from 10 to 54 m, in association to variable patterns of rainfall and maximum wind speed. The amount of seed produced appeared to be enough to guarantee the natural regeneration of the stands during the typical 20-year regeneration period. Colonisation simulations concluded that Mediterranean maritime pine has a notable dispersion capacity, which is strongly influenced by levels of fecundity and, especially, by the number and frequency of long-distance dispersal events. The latter play a key role in tree dispersion processes through enlarging the occupied area and fostering the invasion of abandoned crop land.

1. Introduction

The regeneration phase is a key part of sustainable forest management, as it determines the feasibility of most silvicultural treatments and the quality of the goods and services provided by the forest (Gordo et al., 2012). It also conditions the future development of the stand. Therefore, understanding natural regeneration processes of plant species is an important prerequisite for their conservation and management (Guarigata and Pinard, 1998). Stand regeneration is a complex process driven by the interplay of multiple abiotic and biotic factors (Tíscar Oliver, 2007), involving different stages in the life cycle of plants. The success of each one, with the seed and seedling stages recognised as the most important (Houle, 1996), depends in turn on the interactions of many site factors (Kitajima and Fenner, 2000).

Seed dispersal is one of the central processes in the dynamics and evolution of plant populations (Ouborg et al., 1999), operating at multiple temporal and spatial scales (Nathan, 2001). In plant populations, seed dispersal is the predominant stage at which plants move in space (Schupp and Fuentes, 1995; Nathan and Muller-Landau, 2000), generating the initial spatial pattern of new individuals. Besides, the process has tremendously important implications at multiple scales of organisation: for the survival, growth and reproduction of individuals; for the composition, structure and dynamics of populations and communities; and for the persistence, evolution and geographical distribution of species (Nathan, 2001). Thus, spatiotemporal patterns generated during the seed stage are critically important to plant dynamics (Nathan et al., 2001; Nathan and Muller-Landau, 2000; Schupp and Fuentes, 1995), in particular long-distance dispersal (Nathan et al., 2002; Nathan and Muller-Landau, 2000). As a result, a more realistic incorporation of seed dispersal in forest dynamic models is needed

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(Nathan et al., 2001). However, models of tree spread have rarely been implemented for pines (Prévosto et al., 2003; Lavi et al., 2005), and very few deal with *Pinus pinaster* (Higgins et al., 2001; Thuiller et al., 2005).

Maritime or cluster pine (*P. pinaster* Aiton) is one of the most iconic species of the western Mediterranean forest landscape. In Spain, it is the most widely distributed native pine (~600,000 ha of natural populations) and also the most widely used in reforestation. Maritime pine has been planted in temperate regions within and outside its natural range mainly because of its commercial importance and easy acclimation. In fact, outside its natural range, this species is considered one of the most relevant invasive plants in the world (Lowe et al., 2004). In the light of this, ecological information from natural populations of the species, in particular that related to seed dispersal and recruitment can be very useful for developing population dynamic and spread models (Rodríguez-García et al., 2010).

Success or failure of maritime pine regeneration is influenced by debris accumulation, and herbaceous and moss cover (Rodríguez-García et al., 2010). Nevertheless, water availability from precipitation is the most limiting factor for recruitment (Rodríguez-García et al., 2010, 2011; Ruano et al., 2009). Generally, post-harvest natural regeneration of this species is considered easy. However, nowadays, natural regeneration in large parts of *P. pinaster* distribution, such as on the dry (sandy) soils of the Spanish Northern Plateau, is not achieved satisfactorily, with several examples of poor regeneration (González-Alday et al., 2009; Serrada et al., 2008; Rodríguez-García et al., 2010). This limitation may compromise the sustainability of these stands, forcing alternatives such as seeding or planting (Gordo et al., 2012). Regeneration problems in dry sites will likely get worse by effect of global climate change, since seasonal droughts are expected to become longer and more intense. In these sites, an adequate amount of seed dispersed to suitable places results central to ensure natural regeneration.

The objectives of this study are (1) to describe seed dispersal patterns in Mediterranean maritime pine (*P. pinaster* Aiton) from the Spanish Northern Plateau at different spatial and temporal scales, (2) to estimate its potential spread rates and (3) to analyse ecological implications of the described spread capability, in special those related to natural regeneration success and forest management. To achieve these objectives, we first developed a multiyear study of fecundity and seed dispersal in natural populations of this species using modelling techniques based on the spatial distribution of seeds (seed shadows) to simultaneously estimate fecundity and seed dispersal kernels. Second, we used the forest simulation model SORTIE-ND (Murphy, 2008) to assess *P. pinaster* spread rates under diverse cases of stand fertility, long-distance dispersal (LDD), and forest structure. Our study contributes to the understanding of the role of seed dispersal in the complex process of natural regeneration of *P. pinaster* in central Spain.

2. Materials and methods

2.1. Study site and sampled stands

The study was conducted in two natural *P. pinaster* stands (Coca, 41°16N, 4°29W; and Cuéllar, 41°22N, 4°29W) with a density ca. 110 trees/ha. Both are located in a flat sandy region in Mediterranean Central Spain (Fig. 1) and have trees 25–150 years old. Management is based on natural regeneration following a shelterwood system adapted to resin production.

2.2. Meteorological data

Meteorological data for Cuéllar were extracted from daily measurements recorded in the Spanish forest damage monitoring network (level II, 2004–2007) corresponding to this locality (Directorate for Nature Affairs and Forest Policy, www.marm.es). For Coca, rain data were taken from AEMET (Spanish National Meteorological Agency, http://www.aemet.es/). Specifically, we used the following variables: precipitation, maximum and mean temperature, and maximum and mean wind speed. Temperature and wind data for 2007 were not available for Coca.

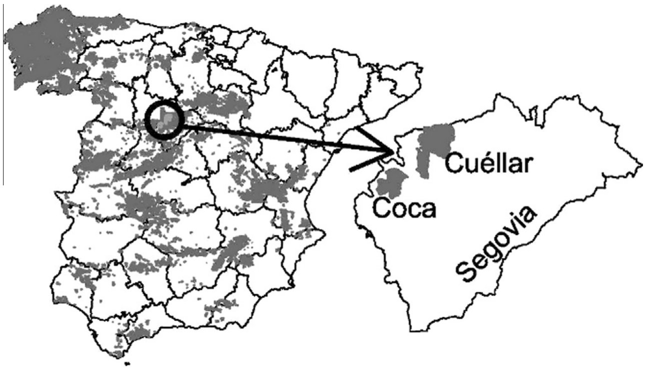

Fig. 1. Location map of experimental plots. The distribution range of *Pinus pinaster* (native and introduced) in Spain in also given (in grey on the map of Spain).

2.3. Experimental design and measurements

Seed dispersal was studied in Coca during the years 2000, 2006 and 2007 (Co00, Co06 and Co07, respectively) and in Cuéllar from 2004 to 2007 (Cu04, Cu05, Cu06 and Cu07). In the year 2000, we placed 28 square ($1 \times 1\ \text{m}^2$) traps in a 30 m radius plot in Coca. As numbers of collected seeds were low that year, in 2006 and 2007 seed deposition was measured by placing 45 traps of bigger size ($1.5 \times 1.5\ \text{m}^2$), which were situated in a 75 m radius plot. Traps in Coca were visited weekly from May to October, covering the main seed dispersal period, and all seeds were collected and counted. In Cuéllar, we placed 90 square ($1 \times 1\ \text{m}^2$) traps across an area of 11.4 ha. Seeds were collected in Cuéllar every 15 days from January 2004 to December 2007.

In both stands, polar coordinates of all trees and traps were taken, and age, total height and diameter (at 1.30 m) were measured. To get an estimate of the relative contribution of each tree to the seed crop, cones on all trees were counted in Coca ($n = 362$) in the springs of 2000 (Miguel-Pérez et al., 2002), 2006 and 2007, and on a large tree sample in Cuéllar ($n = 212$) in the spring of 2004. In Co00 and Cu04 only the cones in half of the crown were counted, using a conversion coefficient to estimate the cones on the whole crown (Miguel-Pérez et al., 2002). All traps were protected from seed predators with a net of 1cm^2 mesh.

2.4. Seed dispersal kernels

In absence of molecular marker data, modelling techniques (conventionally named ‘inverse modelling’, IM) were used to adjust dispersal kernels. We built a classical seed dispersal model by assuming all trees dispersed their seeds according to a probability density function for the random dispersal distance r. Three dispersal kernels with two unknown parameters (namely the scale parameter u and the shape parameter p) were examined and compared. (1) The exponential kernel that was developed by Ribbens et al. (1994) and later modified by Clark et al. (1998), whose equation we use here:

$$f(r) = \frac{p}{2\pi u^2 \Gamma(2/p)} \exp\left[-\left(\frac{r}{u}\right)^p\right],$$

(2) the lognormal kernel (Greene and Johnson, 1989):