



# Uncoupled spatiotemporal patterns of seed dispersal and regeneration in Pyrenean silver fir populations



Ester González de Andrés <sup>a,b</sup>, J. Julio Camarero <sup>c,d,\*</sup>, Isabel Martínez <sup>e</sup>, Lluís Coll <sup>f,g</sup>

<sup>a</sup> Departamento de Ciencias del Medio Natural, Universidad Pública de Navarra, Campus Arrosadía S/N, E-31006 Pamplona, Spain

<sup>b</sup> Departamento de Ecología, Facultad de Ciencias, Universidad Autónoma de Madrid, C/Darwin 2, E-28049 Madrid, Spain

<sup>c</sup> ARAID-Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, Apdo. 202, E-50192 Zaragoza, Spain

<sup>d</sup> Department of Ecology, Fac. Biology, University of Barcelona, Avda. Diagonal 645, E-08028 Barcelona, Spain

<sup>e</sup> Department of Conservation Biology, Estación Biológica de Doñana (EBD-CSIC), C/Américo Vespucio s/n, E-41092 Sevilla, Spain

<sup>f</sup> Forest Sciences Center of Catalonia (CTFC), Ctra. Sant Llorenç de Morunys km. 2, E-25280 Solsona, Spain

<sup>g</sup> CREAF, Centre for Ecological Research and Forestry Applications, Autonomous University of Barcelona, Bellaterra E-08193, Catalonia, Spain

## ARTICLE INFO

### Article history:

Received 25 November 2013

Received in revised form 28 January 2014

Accepted 30 January 2014

Available online 21 February 2014

### Keywords:

Canopy openness

Dispersal kernel

Masting

Recruitment

Regeneration niche

Spanish Pyrenees

## ABSTRACT

Silver fir (*Abies alba*) reaches its southwestern distribution limit (rear edge) in the Pyrenees, where it forms highly fragmented populations threatened by drought-induced die-off. Therefore, we need a better knowledge of regeneration patterns and processes (seed production and dispersal, regeneration niche) of such rear-edge stands to assist their long-term conservation. Seed rain patterns were studied in two structurally contrasting sites: an even-aged pure stand (Las Eras) and an uneven-aged mixed silver fir-beech (*Fagus sylvatica*) stand (Gamüeta) over 8 and 12 years, respectively. Seed production experienced a greater synchrony in years of high seed production than when crops were low, suggesting masting behavior in both sites. Seed inverse modeling methods resulted in dispersal curves differing between sites, with estimates of mean dispersal distances of 9.9 and 21.5 m for the pure and mixed stands, respectively. Long-term sampling of seed dispersal and production was complemented with an analysis of silver fir regeneration niche. Seed and seedling patterns were spatially uncoupled, emphasizing the relevance of microsite filtering of regeneration. Understorey light environment was the main factor explaining seedling emergence and mortality. Our study provides a mechanistic basis and a methodological approach for understanding the colonization ability of Pyrenean rear-edge silver fir stands and similar tree populations.

© 2014 Elsevier B.V. All rights reserved.

## 1. Introduction

Forest dynamics depend largely on tree regeneration which is influenced by biotic and abiotic factors acting at different spatial and temporal scales (Clark et al., 1998a). Seed production and dispersal, germination and seedling establishment are among the main processes determining successful tree recruitment (Dovčičak et al., 2003). Constraints acting on tree regeneration include low amount of viable seeds, restricted spatial extent of seed dispersal and reduced availability of suitable microsites for seedling establishment (regeneration niche *sensu* Grubb, 1977). At an individual level, seed production is directly related to tree size (Greene and Johnson, 1994). However, there are other factors affecting seed production at wide spatiotemporal scales (stand, decades) such as

\* Corresponding author at: ARAID-Instituto Pirenaico de Ecología, CSIC, Avenida Montañana 1005, Zaragoza E-50192, Spain. Tel.: +34 976 716031; fax: +34 976 716019.

E-mail address: [jjcamarero@ipe.csic.es](mailto:jjcamarero@ipe.csic.es) (J.J. Camarero).

stand density, tree-to-tree competition or climatic conditions triggering reproductive events or prolonging seed dormancy (Greene et al., 2002; Debain et al., 2003, 2007; van Mantgem et al., 2006).

Seed production often fluctuates from year to year, especially in the case of masting tree species, in which there is a synchronous production of many seeds at irregular intervals in the same population (Silvertown, 1980; Herrera et al., 1998). Some of the causes of masting are related to climatic variability, resource matching, success in pollination and predator satiation (Janzen, 1971; Kelly, 1994; Kelly and Sork, 2002). Besides seed fecundity, seed dispersal patterns are a critical component in the spatial variation of tree recruitment (Ribbens et al., 1994; Nathan and Muller-Landau, 2000). Seed density almost invariably declines leptokurtically with distance to the parent tree, so the offspring are clustered near the source and extended distribution tails usually represent rare long-distance dispersal events (Clark et al., 1998b; Stoyan and Wagner, 2001).

Some microsites are more suitable for seed germination and seedling survival than others, and that suitability depends on microtopography, canopy cover, understory type or presence of decayed wood (Beckage et al., 2000; Dovčiak et al., 2003). Therefore, the regeneration niche concept is central because it defines the requirements for a high chance of success in the replacement of mature trees (Grubb, 1977). The regeneration niche includes multiple interacting filters of tree recruitment such as canopy cover in temperate forests (Runkle, 1981) or soil water availability in drought-prone Mediterranean forests (Marañón et al., 2004). Habitat requirements of recruits also change throughout the different regeneration stages since young seedlings may heavily depend on water availability while older saplings require more light (Dovčiak et al., 2003). Further, interactions between adults and seedlings of other tree species constitute a complex balance between competition and facilitation, depending on factors such as abiotic stress or tree density (Callaway and Walker, 1997). Successful recruitment might be also expected to be higher at some distance of parental trees where predator pressure decreases as seed and seedling density do (Janzen, 1970). Therefore, the importance of seed dispersal or selective recruitment in specific microsites may be differently magnified by factors acting sequentially on seed germination and seedling establishment.

Here we assess the importance of seed production and dispersal as related to seedling establishment for the regeneration of Pyrenean silver fir (*Abies alba*) forests. To get a deeper insight on regeneration processes of these forests is very relevant because they constitute the south westernmost limit (rear-edge) of the species distribution area in Europe. Rear-edge populations, which frequently gather rare ecotypes and genotypes, are typically restricted to specific drought-prone habitats as compared with more central localities (Hampe and Petit, 2005). Therefore, studying the regeneration of rear-edge populations is of great interest because they portray ecological scenarios which may develop in more northern core areas under warmer or drier conditions (Castro et al., 2004). Besides, western Pyrenean silver fir forests are experiencing drought-induced die-off processes and they are also highly fragmented due to their past historical use for logging, both threatening their persistence and regeneration (Camarero et al., 2011). In addition, bioclimatic envelope models predict significant reductions of the Pyrenean silver-fir area due to intensified warming at the end of the 21st century (Serra-Diaz et al., 2012). Hence, the study of regeneration of rear-edge Pyrenean silver fir forests is crucial to assess their ability to recruit, migrate and colonize new territories in a warmer and drier climatic scenario.

Our aim is to characterize the spatio-temporal patterns of seed production, seed dispersal and seedling establishment of silver fir in two Pyrenean forests with contrasting structure and composition. Our specific objectives are: (i) to analyze the temporal variation of seed production in Pyrenean silver fir and its relation to regional climatic conditions, (ii) to determine the spatial patterns of seed dispersal and characterize seed dispersal curves, and (iii) to relate the spatial patterns of seedling establishment with environmental (canopy openness, substrate) and biotic variables (seed deposition, basal area) with the aim of describing the species' regeneration niche.

## 2. Materials and methods

### 2.1. Study species and site

Silver fir (*A. alba* Mill.) is one of the tree species with larger biomass and height (up to 40 m) in the Spanish Pyrenees, where its distribution area reaches the southwestern limit (Fig. 1). There, this species dominates subalpine and montane forests, mainly on

northern and northwestern slopes of mesic and humid sites with fresh and deep soils (Blanco et al., 1997). Most Pyrenean silver fir forests were subjected to selective logging up to the late 1950s when their exploitation for timber greatly decreased (Camarero et al., 2011).

Silver fir is a monoecious and shade-tolerant conifer (Ruiz de la Torre, 2006). It regenerates from seeds that are winged and dispersed by wind from upright cones (Ruiz de la Torre, 2006). Cones ripen from September to October, and they are located in the upper third of the crown from where seeds are released until May. Silver fir bears fruit every year although it is known that seed production varies greatly between years and in mast years the seeds may present higher germination potential than in years of low crop amount (Ruiz de la Torre, 2006). Seeds produce a resin with high monoterpene content, which constitutes up to about 20% of the fresh mass of seeds (Čermák, 1987). This resin is related to seed predators deterrence, defenses against pathogens, protection of the embryo from drying, and the deep physiological dormancy experienced by silver fir seeds, which usually germinate in spring under wet conditions (Kolotelo, 1998).

The study was conducted on the upper part of Ansó Valley (Parque Natural de los Valles Occidentales, western Aragón, Spain; Fig. 1), where beech (*Fagus sylvatica* L.) or Scots pine (*Pinus sylvestris* L.) can coexist with silver fir. Other less abundant species in these forests are *Sorbus aucuparia* L., *Sorbus aria* (L.) Crantz, and *Betula alba* L. We studied two structurally different sites located in Gamueta (42°53' 55"N, 0°47'59"W, elevation 1395–1415 m a.s.l.) and Las Eras (42°52'40"N, 0°48'18"W, elevation 1320–1350 m a.s.l.) (Fig. 1). Gamueta is a mature and mixed silver fir-beech forest, while Las Eras is a young and pure silver-fir forest with higher tree density than Gamueta (see Table 1 for a list of characteristics of each stand). The soils of both study sites are basic and derived from marls and limestones.

The climate in the study area is temperate and subjected to oceanic influence (wet winter and spring seasons) with a high rainfall amount distributed throughout the year, and fog and snow are frequent in winter. Mean temperature is 8.5 °C, with December (1.9 °C) and August (15.8 °C) being the coldest and warmest months, respectively. Total annual rainfall is 1843 mm, and July and August are the driest months. Ground may be covered by snow from November until March, and average wind speed during the dispersal season (September–May) is 2.07 m s<sup>-1</sup>.

### 2.2. Adult location and seed shadows

Two 900-m<sup>2</sup> square plots (30 m × 30 m) were established in each stand. The first plot (Gamueta) was set in fall 2001, whereas the second one (Las Eras) was set in fall 2005. We measured the location (coordinates *x*, *y*) and size (diameter at breast height – dbh–, total height) of all adult trees (dbh > 20 cm, individuals over 1.3 m in height) and seedlings (individuals with height < 0.5 m) located within the plots, as well as within a buffer zone 10-m wide surrounding the plots.

At the beginning of the study we placed 36 seed traps in each plot following a regular 5-m grid (Fig. 2). Traps were cylindrical containers of 0.014 m<sup>2</sup> circular collecting surface coated with fine mesh bags and placed 0.5 m above the ground. Seeds were monthly or bimonthly collected from traps during the dispersal season (September–May) until fall 2012, resulting in 12 and 8 years of seed rain estimates in Gamueta and Las Eras, respectively. We grouped seeds depending on whether they were collected in autumn (September–November) or in winter–spring (December–May) to determine when the most seed fall occurs. Then, seed density (seeds m<sup>-2</sup>) was calculated on annual or seasonal basis considering the amount of seeds collected in each trap. We determined the number of predated seeds collected within

Download English Version:

<https://daneshyari.com/en/article/86648>

Download Persian Version:

<https://daneshyari.com/article/86648>

[Daneshyari.com](https://daneshyari.com)