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**Extreme climate conditions limit seed availability to
successfully attain natural regeneration of *Pinus pinaster* in
sandy areas of Central Spain**

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1 TITLE PAGE

2 1. TITLE OF THE PAPER

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35 ABSTRACT

36 Natural regeneration comprises different sub-processes, each of them driven by specific
37 climatic and stand-related factors, which determine the success of natural regeneration. The
38 objective of this study was to investigate the seed availability of maritime pine. To meet this
39 objective seed rain was monitored for four different levels of stand density at the experimental
40 site of Cuéllar, Spain, during a ten-year period. A generalized linear mixed model was fitted
41 to test the effects of climatic variables and stand density on the annual seed production and
42 seed rain. The climatic covariates were chosen among those thought to affect the key
43 physiological phases governing these sub-processes: minimum temperature in October two
44 years before dispersal (cone growing), April precipitation one year before dispersal (cone
45 growing) and October-November precipitation one year before dispersal (cone maturation).
46 No climate variable related to flowering or seed rain process was significant. Moreover, stand
47 density was considered through a spatially explicit index called seed-source index. Primary
48 cone growth was limited by extreme cold events. Absence of precipitation limits secondary
49 growth while it appears to hinder final cone ripening. It turns out that seed production and
50 seed rain may be a bottleneck for natural regeneration of *Pinus pinaster* under low stand
51 densities, especially under extreme climatic scenarios.

52 KEYWORDS

53 Climate change; generalized linear mixed model; Mediterranean ecosystem; natural
54 regeneration; seed limitation

55 INTRODUCTION

56 It is well established that natural regeneration methods contribute to effectively and
57 economically perpetuate natural ecosystems in the long term (Barnes et al. 1998). As a
58 result, silviculture treatments that favour natural regeneration are one of the main issues in
59 sustainable forest management, especially in Mediterranean forests, where disturbances like
60 fire or grazing may cause erosion and extreme climatic conditions can compromise natural
61 regeneration success (Scarascia-Mugnozza et al. 2000).

62 Natural regeneration consists of different sub-processes such as seed production, seed
63 dispersal, seed storage and predation, seed germination and establishment. Multiple factors
64 can affect each one of these sub-processes, and may determine natural regeneration success.
65 Consequently, it is crucial to identify these factors and determine their influence on the entire
66 process (Price et al. 2001).

67 Seed production and dispersal are particularly relevant in natural regeneration since they
68 initiate the whole process. Seed dispersal directly depends on the amount of seeds produced,
69 the availability of appropriate dispersal agents and the maximum distance over which seeds
70 can be dispersed (Price et al. 2001). In addition, these sub-processes have been reported to
71 play a major role in seedling spatial distribution so they are widely considered as key
72 processes to understand forest dynamics (Dovčiak et al. 2005; Nathan and Muller-Landau
73 2000).

74 Maritime pine (*Pinus pinaster* Ait.) is a western Mediterranean species of great economic,
75 ecological and aesthetic value. This is especially true for the Castilian Plateau in central
76 Spain, where this species covers more than 114 000 ha, which represents about 7.5% of the
77 species' European distribution. In Spain, *Pinus pinaster* natural regeneration has been studied
78 in post-fire conditions (Calvo et al. 2007; Fernández et al. 2008; Vega et al. 2009, 2008) and

in natural stands not affected by serious disturbances (González-Alday et al. 2008; Miguel Pérez et al. 2008; Rodríguez-García et al. 2011, 2008; Ruano et al. 2009; Del Peso et al. 2012). Studies in natural stands have focused on the Castilian Plateau's stands. Although some authors suggested that natural regeneration of *Pinus pinaster* was overall sufficient in this region (Miguel Pérez et al. 2008), a large array of conditions has been reported: from scarce or even null (González-Alday et al. 2009; Ruano et al. 2009) to excessive regeneration (Rodríguez-García et al. 2008). The ecological and silvicultural factors behind this variability remain unclear, their study being hindered by the lack of long-term monitoring data (Bravo et al. 2012). The knowledge of interannual *Pinus pinaster* seed rain pattern and the contribution of this sub-process to regeneration success or failure are particularly poor.

The study of seed dispersal in the Mediterranean basin has traditionally focused on the spatial patterns of different species: *Pinus pinaster* (Juez et al. 2014); *Pinus pinea* (Manso et al. 2012), *Pinus halepensis* (Nathan and Ne'eman 2004), *Abies alba* and *Fagus sylvatica* (Sagnard et al. 2007). Surprisingly, the effect of climate on seed production, which may determine seed rain temporal dynamics, has been overlooked. Currently, there is increasing agreement on the critical influence of climate on the key physiological stages of cone ripening in coniferous species, either limiting or boosting seed production (Calama et al. 2011; Keyes and Manso 2015; Mutke et al. 2005).

Although there is no evidence yet, this may also be the case for *Pinus pinaster*, given the two-year cone maturation period and the harsh climatic conditions of the Castilian Plateau. More specifically, flowering occurs in spring of the first year, leaf buds emerge in April and female strobili develop in May; cone growth typically takes place after the first summer; and final cone ripening occurs by the second autumn. Seed are dispersed over spring and summer immediately after completion of ripening (Auñón and Tadesse 2000; Rodríguez Soalleiro et al. 2008).

The main objective of this study was to quantify the effect of climate on the interannual pattern of *Pinus pinaster* seed production and seed rain. To meet this objective, seed rain was monitored for four different levels of stand density at the experimental site of Cuéllar, central Spain, during a ten-year period. The climatic variables thought to affect the physiological phases of cone ripening were tested in a generalized linear mixed-effects model. Our hypotheses were that (1) the interannual seed production and seed rain pattern is climate-mediated; (2) stand density has a positive effect on the overall amount of dispersed seeds; (3) seed limitations can be found after clearcuttings and extreme climate conditions. We expect that the findings derived from this study will contribute to our understanding of the impact of climate on seed production and seed rain for different levels of density. In turn, this will help define the most appropriate forest management strategy for ensuring natural regeneration in this type of forest.

MATERIALS AND METHODS

1. STUDY AREA AND MONITORING PROCEDURES

The experiment was carried out in a natural *Pinus pinaster* stand at the long-term experimental site of Mata de Cuéllar, Segovia, central Spain (41° 22'N, 4° 29' W, see Figure 1). The site is located in a flat, sandy region characterized by a semi-arid Mediterranean climate, with a strong summer drought and a period of potential frost of at least three months. Mean annual precipitation is 610 mm and mean annual temperature is 11.2 °C. The floristic community within the stand is composed of continental Mediterranean annual species typical of central Spain, *Micropyrum tenellum* (L.) Link, *Sedum amplexicaule* DC., *Vulpia myuros* (L.) C.C. Gmelin, *Lupinus angustifolius* L., with patches of shrubs, *Lavandula pedunculata* Miller and *Helichrysum italicum* (Roth) G. Don, and isolated stone pine trees (*Pinus pinea*).

Silviculture in the area is traditionally based on natural regeneration following a seed-tree system adapted to resin production, leading to low stand densities.

The experimental site consisted of ten 70 x 70 m plots that were established in 2004 for an integrated analysis of maritime pine regeneration. Four treatments were tested in a split-plot design: control and 3 harvest intensities (25%, 50% and 100% reduction of initial basal area) (Table 1), where one plot corresponded to the control and the harvest intensities were replicated three times. The average basal area of the plots before harvest was 17.4 m² ha⁻¹. In each plot, nine seed traps (1m x 1m) were located following a systematic design (Figure 1) in order to collect dispersed seeds every month from 2004 to 2013. Seed traps are raised from the ground approximately 30 cm, the base is made by a grid to recollect the seeds and it is covered by a wire mesh to avoid seed predation.

(Insert Table 1 and Figure 1)

2. DATA ANALYSIS

2.1 Response variable

In order to analyse interannual seed production and seed rain dynamics of maritime pine, we selected the number of seeds collected each year in each seed trap as response variable. Considering that each trap covers an area of 1 m², the response variable is actually a seed density (seeds/m²). This variable is a count and consequently we assumed it followed a Poisson distribution. Therefore, a Poisson regression model based on a log link function was used. Let us denote plots, traps and years with indices i, j and k , respectively, such that $i = 1, 2, \dots, 10, j = 1, 2, \dots, 9$ and $k = 1, 2, 3 \dots 10$. Then,

$$y_{ijk} \sim \text{Poisson}(\lambda_{ijk})$$

$$\lambda_{ijk} = \exp^{\mathbf{x}_{ijk}\boldsymbol{\beta}}$$

where y_{ijk} is the number of seeds collected in trap j of plot i over year k , λ_{ijk} is the expectation of the Poisson distribution, $\mathbf{x}_{ijk}$ is a row vector of covariates possibly affecting dispersal and $\boldsymbol{\beta}$ is a column vector of parameters.

2.2 Explanatory variables

In order to test our first hypothesis, different explanatory climate variables were evaluated to represent the potential climatic drivers of seed production. Preliminary Pearson correlations between a number of potential predictors and the response variable were computed. As a result, 17 candidate climatic variables were selected according to the key physiological processes involved in cone ripening:

- Flowering (two years before dispersal): total precipitation and days of precipitation in April and May; maximum wind velocity in May; mean and maximum temperature in April; frost days in May. Frost days are defined as those days with minimum temperature lower than 0 °C.
- Primary growth (two years before dispersal): minimum temperature in October; frost days in October; Walter's summer drought index (Walter 1973). This index is assessed as: (mean daily temperatures from June to August) – (0.333 x (mean daily rainfall from June to August)). Higher values indicate more intense drought. Walter's index has been used to analyse the effects of summer drought on the reproduction of other Mediterranean species (Espelta et al. 2011, 2008) and maritime pine seed predation (Ruano et al. 2015).

• Secondary growth (one year before dispersal): total precipitation in April; frost days in March and severe frost days in March. Severe frost days are defined as those days with minimum temperature lower than -5°C.

• Final cone ripening (one year before dispersal): total precipitation in October and November.

• Seed release: precipitation days in May; maximum wind velocity in summer; mean temperature in August; frost days in April.

Climatic data were obtained from a nearby meteorological station managed by the Instituto Tecnológico Agrario de Castilla y León, placed to approximately 20 km from the experimental site (www.inforiego.org).

In addition to climate drivers, seed production and seed rain are likely affected by stand density in the close vicinity of the traps. It can reasonably be expected that higher stand density around a particular trap would lead to a greater number of seeds. A spatial explicit index similar to competition index in growth modeling (Weiskittel et al. 2011) was defined to account for this tree density-distance effect. For the sake of clarity, we will refer to this index as the seed-source index.

The seed-source index was calculated for each seed trap as the sum of the inverse distances between the seed trap and all potential seed sources. Trees within a 20-m distance from each seed trap were considered as seed sources. We chose this distance in the light of the estimated dispersal distance of *Pinus pinaster* for the Castilian Plateau in the existing literature (Juez et al. 2014).

2.3 Model fitting and evaluation

The traditional Poisson regression model relies on the assumption of independence. However, given the experimental design and the permanent plots, it could be reasonably expected that the observations from the same trap, plot and year were not independent. The mixed-model approach is one method among others that makes it possible to address this issue of dependent observations through the specification of random effects. Random effects are actually error terms that account for some unobserved explanatory variables at the trap, plot and year level (Gregoire 1987). The mixed-model approach has been widely used in forestry (e. g. Calama and Montero 2007; Collet et al. 2001; Manso et al. 2013).

Preliminary models were fitted for each explanatory variable to identify which one of them had an influence on the response. During this step, power (x^2 , $x + x^2$), logarithmic ($\log x$, $x + \log x$) or square root ($\sqrt{x}$, $x + \sqrt{x}$) transformations of the variables were tested too. In a second step, the variables and transformation identified during the first step were sequentially included in the model. Several covariates were rescaled to avoid numerical problems. Both steps were assisted by a visual assessment of standardized residuals to make sure there were no unaccounted trends left in the model. Because climatic variables are usually correlated, we did not test all of them at the same time. Once the standardized residuals showed no persistent trend, plot, trap and year random effects were specified on the model intercept and the resulting mixed model was refitted. After several trials, only the plot and trap random effects were kept. The fixed effects structure was revised when needed. Competing models were compared in terms of Akaike's Information Criterion (AIC) (Akaike 1973) and statistical significance was set at $\alpha=0.05$. The resulting generic model could be expressed as

$$\lambda_{ijk} = \exp^{x_{ijk}\beta + u_i + u_{ij}}$$

$$u_i \sim N(0, \sigma_{plot}^2)$$

$$u_{ij} \sim N(0, \sigma_{trap}^2)$$

where u_i and u_{ij} are two random effects common for the observations from the same plot and seed trap respectively. Random effects are assumed to be independent among levels and normally distributed with mean 0 and variances σ^2_{plot} and σ^2_{trap} , respectively.

Model accuracy and unbiasedness were evaluated through the root mean squared error (RMSE), mean error (E) and model efficiency (EF). Adding random effects in the model had a major consequence on the predictions. The expectation of the model conditional on the random effect is $E[y_{ijk} | u_i, u_{ij}] = \exp^{x_{ijk}\beta + u_i + u_{ij}}$. However, when the expectation of the model is marginalized over the distribution of the random effects it results that $E[y_{ijk}] \neq \exp^{x_{ijk}\beta}$. This is due to the nonlinear form of the function and it is commonly referred to as Jensen's (1906) inequality. Because we assumed that u_i and u_{ij} follow a Gaussian distribution and are independent from each other, this marginalization reduces to the back-transformation of a log-

transformed variable (see Duan 1983): $E[y_{ijk}] = \exp^{x_{ijk}\beta + \frac{\sigma^2_{plot} + \sigma^2_{trap}}{2}}$.

In order to check whether the Poisson assumption held, theoretical frequencies from marginalised model predictions were evaluated and compared with the observed frequencies in the data as suggested in Lambert (1992) and Fortin and DeBlois (2007). All statistical analyses were performed in R (R Development Core Team 2014).

RESULTS

The fitted model proved accurate, the bias and the root mean square error being relatively small. No major departures from the assumption of Poisson distribution were found. The random effects notably improved the model goodness-of-fit (AIC=9278.9 without random effects; AIC=7128.3 with random effects). The estimated variances of the plot and seed trap

random effects were $\hat{\sigma}^2_{plot} = 0.0139$ and $\hat{\sigma}^2_{trap} = 0.1248$, respectively. The best model in terms of AIC was:

$$E[\widehat{y_{ijk}}] = \exp^{\widehat{\beta}_0 + \widehat{\beta}_1 \cdot SSI + \widehat{\beta}_2 \cdot \log(SSI+1) + \widehat{\beta}_3 \cdot \frac{Tmin_{Oct}}{10} + \widehat{\beta}_4 \cdot \frac{P_{Apr}}{100} + \widehat{\beta}_5 \cdot \frac{P_{OctNov}}{100} + \widehat{\beta}_6 \cdot \log\left(\frac{P_{OctNov}}{100}\right) + u_i + u_{ij}}$$

where *SSI*: is the seed-source index; *Tmin_{Oct}*: minimum temperature in October two years before dispersal; *P_{Apr}*: April precipitation one year before dispersal; *P_{OctNov}*: October and November precipitation one year before dispersal (Table 2). Maximum likelihood estimates and their standard errors are shown in Table 3.

(Insert Table 2 and 3)

The effects of the explanatory variables on the response variable are presented in Figures 2 and 3. For each harvest intensity, predicted seed densities and their confidence intervals were generated over the observed range of each climatic variable in the study area while setting all the other covariates to their mean values. As regards climate, October minimum temperatures had a negative effect on predicted seed densities two years later (Figure 2a). This corresponded to the beginning of cone primary growth. In regard to secondary growth, predicted seed densities increased along with April precipitation one year before dispersal (Figure 2b). Concerning final cone ripening, an optimal value of October and November precipitation (50 mm approximately) was found to maximize the predicted seed densities (Figure 2c). This optimum occurs close to the lower limit of the recorded precipitation range of October and November. Beyond this value, increasing precipitation seems to reduce seed density.

In the case of the seed-source index, predicted seeds and its confidence intervals were produced considering the mean value of the index for each harvest intensity and the mean value of the climatic variables (Figure 3). It turned out that an increase of the index induced an increase of seed densities which ranged from 11 to 29 seeds/m². The trend appeared to be slightly quadratic or asymptotic.

The predicted seed density for the 50%-harvest intensity (22 seeds/m²) was twice that of the clearcutting treatment (11 seeds/m²). Predicted seed densities in 25%-harvest intensity and in the control were around 30 seeds/m², which was three times larger than those predicted in the clearcutting treatment (Figure 3). There were no significant differences between the 25%-harvest intensity and the control (Figure 2).

(Insert Figures 2 and 3)

DISCUSSION

Very few studies have addressed the seed availability, being mainly focused on the identification of spatial patterns, either as a result of a physical process (Barbeito et al. 2008; Clark et al. 1999; Manso et al. 2012), a wind-mediated process (Bullock and Clarke 2000; Dovčiak et al. 2005; Greene and Johnson 1989) or an animal-mediated process (Westcott et al. 2005). The main constraint in the assessment of the climate effect on seed dispersal is the scarcity of long-term time series that fully depict plant response to climatic conditions. With few exceptions (e.g. Mutke et al. 2005, Calama et al. 2011, Keyes and Manso 2015), most studies on seed dispersal are based on short-term monitoring (e.g. Hamann 2004). Here, a 10-year seed rain time series has been used, a period that represents half the usual regeneration period for *Pinus pinaster* in operational management units. The length of this time series

contributes to the strength of this work. Despite this, our experimental design shows some weaknesses. For instance there is only one experimental site and only one control plot. Moreover plots are very close in some cases or some seed traps are too close to trees outside the plots, affecting the correct identification of the seed source.

We can confirm our first hypothesis of a climate-mediated interannual seed production pattern. Specifically all considered explanatory variables were exclusively related to cone growth and maturation. Rodríguez Soalleiro et al. (2008) asserted that flowering in *Pinus pinaster* is affected by light, temperature, precipitation and drought. We tested the effect of precipitation, wind velocity or frosts as potential surrogates but none of them were found to be significant in our analysis. Similarly, we did not find any association between climatic variables and seed rain. Apparently, high temperatures may favour cone opening (Nathan et al., 1999; Tapias et al., 2001) although this may refer serotinous species and the local provenance of this study is weakly serotinous. Serotinity in Mediterranean ecosystems can be a key question for seed dispersal pattern. Some Mediterranean species are adapted to fire ensuring regeneration after it. This is the case of serotinous cones, which are able to hold mature seeds for dispersal after fire forming a long-term canopy seed bank (Daskalakou and Thanos 1996; Tapias et al. 2001). Moreover during this period, when mature seeds are in the cones before seed release, predation could affect seed availability. In this case *Pinus pinaster* can be serotinous or non-serotinous because there is a high intraspecific variability (Tapias et al. 2004). Castilian Plateau provenance is considered as weakly serotinous (Tapias et al. 2004, 2001). In addition, no fire occurred in our experimental site, at least during the last 10 years. In this respect, its serotiny is not expected to have played a significant role during the study period.

The positive effect of precipitation during the period of secondary cone growth points out that water stress is a limiting factor for seed production in *Pinus pinaster* in the Castilian Plateau.

These findings coincide with those of Mutke et al. (2005) and Calama et al. (2011) for *Pinus pinea* in the same area. Also, Calama et al. (2011) observed a negative effect of the number of days with severe frost during the first winter after cone initiation. Interestingly, we found that the higher the minimum temperature in October of the first year, the lower the predicted number of seeds was.

Brunet et al. (2009) carried out different regionalized climate scenarios for 21st century in Spain. The different regional models used in that study agree on an increase of the minimum, maximum and mean temperatures throughout the country. In contrast, predictions on precipitation trends are not as consistent. Nevertheless, a slight reduction of precipitation in the western half of the Iberian Peninsula and a slight increase in the eastern half is expected (Brunet et al. 2009). As it applies to our case, mean temperature in autumn is expected to increase between 2°C and 6°C while precipitation in spring may decrease between 20 and 50 mm. As a result of both effects, seed rain could be strongly reduced. However, this reduction effect might be partly compensated for by the effect of precipitation in autumn, which is expected to decrease by 40 mm. In the light of these predictions, it is clearly necessary to further analyse the effect of climate change on seed dispersal process.

Our findings are based on the response of seed rain to current climatic normals. For example, autumn conditions are informative of *Pinus pinaster* seed rain because there are key physiological processes that usually take place in that season. However, climatic forecasts for the Mediterranean region in the next years could change the behavior of the species, bringing forward or delaying processes as mega- and micro-sporangia production or cone maturation. In fact, evidences of changes in species ranges has already been observed (Thuiller et al. 2008). In the case of coming with climate change predictions significant climatic variables obtained in the present work could change because species phenology could change too, so it would be necessary to review species biology.

Our results also confirm our second hypothesis, since stand density is one of the main drivers for seed production and seed rain. On the other hand, low stand density in a given area may result in local seed limitation. For example, Lucas-Borja et al. (2012) observed an increasing number of collected seeds along with stand density in a *Pinus nigra* forest in Central Spain. On the other hand, higher stand density may lead to an overall decrease in the number of dispersed seed due to competition. This is the case of *Pinus pinea* stands located in the Castilian Plateau (Calama et al. 2011; Manso et al. 2014). Our results confirm these trends: as stand density increases as measured through the seed-source index, the marginal gain in seed density decreases. If a denser stand had been available in our study, a seed density decrease with respect to the control plot might have been found. In any case our index, assessed similarly to classic competition indexes, has worked well for predicting seed availability.

In the light of the aforementioned findings, a critical question remains unanswered: when considering the temporal dimension, can seed production and seed rain be a bottleneck for natural regeneration of *Pinus pinaster* in the Castilian Plateau? According to Matney and Hodges (1991) a recruit density of 2000 seedlings/ha is the minimum requirement for successful natural regeneration. However, a density of between 1000 and 1500 viable trees/ha may be considered satisfactory in stands with abiotic stress (Rodríguez-García et al. 2010). Several factors can negatively affect the subsequent stages of the regeneration process after dispersal, namely predation of the dispersed seeds and the limiting climatic conditions occurring in the Mediterranean ecosystems during the initial months of seedling establishment (Miguel Pérez et al. 2008). The impact of predation, germination failure and seedling survival in the specific case of *Pinus pinaster* can be analysed taking other experiments carried out in the same experimental site into account: Ruano et al. (2015) studied the effect of predation on belowground seed bank. They observed mean percentages of seed predation around 75% for control and clear cutting plots, around 86% for 25% harvest intensity plots and around 92%

for 50% harvest intensity plots. Moreover, Ruano et al. (2009) analysed the effect of harvest intensity and summer water regimes on germination and seedling survival during 18 months. They observed percentages of germination around 40% for clearcut, control and 50% harvest intensity plot and around 60% for 25% harvest intensity plot. Furthermore, they found percentages of seedling survival around 13% for clear cut plot, around 25% for control and 50% harvest intensity plots and around 45% for 25% harvest intensity plot.

Taking into account these percentages, it is possible to obtain a rough estimate of the required seed rain to reach the threshold of 2000 seedlings/ha for successful establishment. Seed densities of around 5 seeds/m² for 25% harvest intensity plots, around 9 seeds/m² for control plots, around 18 seeds/m² for clearcut plots and around 25 seeds/m² for 50% harvest intensity plots would be necessary to ensure a successful regeneration. According to our results, current seed rain could be enough in the control and 25% harvest intensity, even if less favourable climatic conditions occurred. However, natural regeneration may fail in the other cases. Mean predicted seed rain in 50% harvest intensity plots was around 23 seeds/m², becoming progressively lower under more extreme climatic events. When clearcutting is carried out, seed rain does not seem abundant enough regardless of the climatic conditions. In this case, the estimated density of established recruits is lower than 1200 seedlings/ha for a seed rain density of 10 seeds/m².

In terms of forest management, the present study can support decision making related to *Pinus pinaster* natural regeneration. Whether seed production and seed rain is a bottleneck for natural regeneration is clearly related to harvest intensities, which validates our third hypothesis. Because interannual pattern of seed production is climate dependent, good conditions may eventually compensate for harvest intensities while harsh conditions will inevitably lead to regeneration failure. This is the case of the 50%-harvesting operation,

which is a widely-applied silvicultural practice in the study area. Therefore forest management should reduce harvest intensities in this area to assure natural regeneration.

Our knowledge on the impact of climate may help anticipate restoration treatments in order to alleviate these constraints. For example, a positive effect of scarification on seedling emergence has been reported for temperate and continental pine forests (Boucher et al. 2007; Karlsson and Nilsson 2005; Nilsson et al. 2006) and in the Mediterranean area (Prévosto and Ripert 2008). In fact, scarification is usually recommended in the event of insufficient natural regeneration in *Pinus pinaster* stands (Rodríguez Soalleiro et al. 2008). Given that seed dispersal takes place in summer and that our model can predict seed rain several months in advance, scarification can be prescribed during the winter prior to dispersal if need be. This way, it could be possible to improve the seedling emergence after a year of higher seed rain carrying out a soil scarification the previous winter.

The main interest of this work was to analyse the impact of climatic factors on the between-years pattern of seed production and seed rain. Although the spatial dimension has been taken into account, our approach presents some limitations in this respect. Commonly, tree-related variables such as diameter at breast height, crown size or height are used as a proxy of individual tree fecundity (de-Lucas et al. 2008; González-Martínez et al. 2006). Unfortunately, we could not consider any of these variables when assessing our seed-source index because we did not have enough measurements. Nevertheless, the proposed index provides, at least, consistent and unbiased inference on the effect of local stand density on seed rain.

Pinus pinaster plantations were established in the southern hemisphere (mainly in South Africa and Australia) where it can escape from plantations and spread into native ecosystems (Rouget et al., 2004). It is for this reason that *Pinus pinaster* has been considered one of the world's worst invasive tree species (Lowe et al. 2004). It would be necessary to repeat this

type of experiments to generalize our results outside or even inside its natural range due to *Pinus pinaster* high variability in terms of ecotypes, plasticity and habitat conditions.

CONSEQUENCES FOR MANAGEMENT

In the present study, we have analyzed the effect of climate on the interannual pattern of *Pinus pinaster* seed production and seed rain in the Castilian Plateau. The impact of climate over the entire seed production process has been studied, from flowering to seed release. Temperature seems to control primary cone growth, while absence of precipitation limits secondary growth. Contrastingly, precipitation appears to hinder final cone ripening. Interestingly, any climatic variable was apparently related to flowering or seed rain process.

Currently seed production and seed rain seem to be a bottleneck for natural regeneration of *Pinus pinaster* under intensive harvest intensities. Our results suggest that seed-limitation problems may arise with the 50% harvest intensity under extreme climatic scenarios, specifically with lower precipitation during spring and autumn. Moreover seed rain may not be enough to obtain a successful regeneration when clearcuttings are conducted. Therefore harvest intensity recommendations need to be revised, or at least, a homogeneous spatial distribution of the trees should be promoted.

In addition, it could be possible to improve natural regeneration success carrying out silvicultural treatments. According our results scarification could be applied to take advantage of summers with higher seed rain.

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TABLES

Table 1. BA: Basal area (m²/ha) and N: stand density (trees/ha) before and after harvest in the experimental site plots

Plot	harvest intensity	BA before harvest	BA after harvest	N before harvest	N after harvest
1	100%	16.64	0.00	136.73	0.00
2	25%	17.66	13.25	140.82	79.59
3	100%	17.89	0.00	126.53	0.00
4	25%	18.03	13.68	161.22	95.92
5	25%	21.35	16.06	173.47	124.49
6	50%	20.85	10.24	187.76	83.67
7	50%	14.06	7.01	114.29	44.90
8	50%	15.07	7.96	130.61	63.27

9	100%	18.91	0.00	153.06	0.00
10	0%	13.46	13.46	95.92	95.92

Table 2. Characteristics of the significant variables: sampling size (n), mean, maximum, minimum and standard deviation.

	n	Mean	Maximum	Minimum	Standard deviation
Seeds	900	16	114	0	15.269
Seed-source index (SSI)	90	0.823	2.789	0.000	0.583
TminOct (primary growth)	10	5.517	7.970	3.610	1.552
P _{Apr} (secondary growth)	10	46.10	82.63	20.40	17.323
P _{OctNov} (final ripening)	10	110.30	260.60	13.59	68.004

Table 3. Fitted fixed effects. Estimated parameters, standard error and P-value. AIC (Akaike's Information Criterion): 7128.3; BIC (Bayesian Information Criterion): 7171.5; log-likelihood: -3555.1.

Effect	Parameter	Estimate	Standard Error	P-value
Intercept	β_0	2.591	0.138	$<2*10^{-16}$
SSI	β_1	-1.612	0.384	$2.67*10^{-5}$
log (SSI + 1)	β_2	4.305	0.730	$3.64*10^{-9}$
TminOct (primary growth)	β_3	-0.421	0.070	$<2*10^{-16}$
P _{Apr} (secondary growth)	β_4	0.692	0.046	$<2*10^{-16}$

P_{OctNov} (final ripering)	β_5	-0.833	0.036	2.5×10^{-9}
$\log(P_{OctNov})$ (final ripering)	β_6	0.405	0.024	$< 2 \times 10^{-16}$

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FIGURE CAPTATIONS

Figure 1. Location of the experimental design with a climodiagram. Position of all the trees and stumps of the experimental site and position of the seed traps and nursery trays to control predation. Harvest intensity is indicated near each plot. Climodiagram from Rivas-Martínez and Rivas-Sáenz (1996-2009)

Figure 2. Predicted seed densities and their confidence intervals for each harvest intensity. Vertical long dash lines indicate the mean values of each climatic variable

Figure 3. Predicted seed densities and their confidence intervals for each mean value of the seed-source index for each harvest intensity

1674x1184mm (14 x 14 DPI)

350x812mm (96 x 96 DPI)

756x556mm (20 x 22 DPI)