Forest Systems
26 (2), e07S, 13 pages (2017)
eISSN: 2171-9845
https://doi.org/10.5424/fs/2017262-11200
Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria O. A., M. P. (INIA)

RESEARCH ARTICLE

OPEN ACCESS

Factors affecting cone production in *Pinus pinaster* Ait.: lack of growth-reproduction trade-offs but significant effects of climate and tree and stand characteristics

Felipe Bravo[1,2], Douglas A. Maguire[3] and Santiago C. González-Martínez[4]

[1]Sustainable Forest Management Research Institute, Universidad de Valladolid - INIA, Spain. [2]Universidad de Valladolid, Escuela Técnica Superior de Ingenierías Agrarias, Dept. Producción Vegetal y Recursos Forestales. Avda de Madrid 44, 34004 Palencia, Spain. [3] Oregon State University; College of Forestry; Dept. of Forest Engineering, Resources and Management. Corvallis, OR, USA. [4]UMR1202 BioGeCo: Biodiversity, Genes & Communities, Cestas, France.

Abstract

Aim of study: Our main goal is to determine the relationship between cone production and radial growth in *Pinus pinaster* Ait. under different climatic conditions across the Iberian Peninsula.

Area of study: Coca Intensive Sampling Plateau, Northern Plateau (Spain).

Material and methods: Cone counts were conducted on an intensive monitoring plot in Coca (North-Central Spain) during the years 2000, 2006 and 2007. A ZIP (zero-inflated Poisson) model was adjusted for simultaneously estimating the probability of obtaining crop cones and its amount. The Northern Atlantic Oscillation (NAO) index was used as explanatory variable, together with a wide variety of tree and local stand variables. Climate (as evaluated by NAO), local stand density (here estimated from the six nearest trees), tree size and vigor, competition and growth efficiency significantly influenced both occurrence and intensity of cone production.

Main results: ZIP models for predicting reproductive effort seems an adequate tool to predict reproductive responses to climatic fluctuations and the resulting future species distribution in the face of climate change, as well as to identify silviculture actions that would promote reproductive success in naturally-regenerated stands, list and discuss relevant results (including numeric values of experimental results).

Research highlights: Climate, stand density and tree conditions (size and vigor, competition and growth efficiency) influence significantly both cone occurrence and intensity of fruiting as shown by a ZIP model. As the climate variables included in the model (based on Northern Atlantic Oscillation, NAO) are general and easily obtained, the proposed model has practical applicability to predicting *Pinus pinaster* cone production in the Iberian Peninsula.

Additional keywords: ZIP model; NAO; Mediterranean; silviculture; dendrochronology.

Abbreviations used: AIC (Akaike's Information Criterion); BA_6 (basal area based on the 6 nearest trees); BAL (basal area in larger trees); CL (crown length); CP (crown projection area); CSA (crown surface area); DBH (diameter at breast height); dpi (dots per inche); LAI (leaf area index); NAO (Northern Atlantic Oscillation); NCAR (National Center for Atmospheric Research); NCEP (National Centers for Environmental Prediction); QIC (quasi-likelihood information criterion); SLP (normalized sea level pressures); Wi (Akaike weight); ZIP (Zero Inflated Poisson).

Authors´ contributions: Conceived and designed the study; ran and interpreted the analysis and wote the document: FB. Provided most of the data: SCGM. Discussed the methods and the results and reviewed the document: DM and SCGM.

Citation: Bravo, F.; Maguire, D. A.; González-Martínez, S. C. (2017). Factors affecting cone production in *Pinus pinaster* Ait.: lack of growth-reproduction trade-offs but significant effects of climate and tree and stand characteristics. Forest Systems, Volume 26, Issue 2, e07S. https://doi.org/10.5424/fs/2017262-11200

Supplementary material (Figs. S1 & S2, Table S1) accompanies the paper on FS's website.

Received: 09 Feb 2017. **Accepted**: 02 Oct 2017.

Funding: Spanish Government through its scientific mobility program to FB.

Correspondence: should be addressed to F. Bravo: fbravo@pvs.uva.es

Introduction

Plant reproductive effort in any given year comes at a cost in terms of carbon allocation, resulting in tradeoffs with other traits that affect reproductive fitness more indirectly, such as growth and survival (Thomas, 2011). Against a backdrop of rapid environmental change, these tradeoffs can constrain and influence adaptive evolution. For instance, Etterson & Shaw (2001) found that among-trait genetic correlations that are antagonistic to the direction of selection can slow down genetic responses to climate change. Reproductive allocation, defined as the proportion of total resources used in reproductive structures (Bazzaz *et al.*, 2000), have shown size dependency (Sugiyama & Bazzaz, 1998). Moreover, tradeoffs between reproductive allocation and vegetative growth have been reported in plants with contrasting life-histories (*e.g.* Sánchez-Humanes *et al.*, 2011). Climent *et al.* (2008) showed that intense cone yield is not compatible with rapid vegetative growth in Aleppo pine (*Pinus halepensis* Mill) while Barringer *et al.* (2013) found similar results for *Quercus* species in California. Shifts in resource allocation that affect traits other than vegetative growth are also evident. For example, Sampedro *et al.* (2011) reported a significant negative genetic correlation between *Pinus pinaster* Ait. growth and defensive investment. These results support the existence of selective pressure to sacrifice growth rate when resources are demanded for ecophysiological functions more 'urgently' required to optimize reproductive fitness, such as direct allocation to reproductive structures or to defense chemicals that enhance the probability of survival. Defenses structures (*i.e*, resin) require a sufficiently large and permanent resource allocation that tree growth is reduced more on poor sites than on high productivity sites (Ferrenberg *et al.*, 2015). *P. pinaster* genetic variability is therefore related to differential aboveground resource allocation and resistance to pest attacks (Di Matteo & Voltas, 2016). In this regard, (Moreira *et al.*, 2015) observed wide intra-specific genetic variation in *P. pinaster* with regard to resource allocation to inducible defenses. According to partitioning theory trade-offs are expected between allocation sinks when resources are limited.

In forest trees, inverse correlations between size and cone production have been found for both conifers and angiosperms at the tree level (see, for instance, Eis *et al.*, 1965; Selas *et al.*, 2002; Monks & Kelly, 2006), but also at the branch level within trees (Tappeiner, 1969; Fox & Stevens, 1991; Hasegawa & Takeda, 2001). Moreover, a carry-over effect has been documented for the reduction of tree growth after intense fruit production (Thomas, 2011). The observed negative tradeoff between reproductive versus vegetative structures in forest trees may have important implications. For example, phenotypic selection of trees based on growth and wood quality (*e.g.* straight stems) in breeding programs may result in reduced reproductive allocation, but current evolutionary models suggest that increased fertility would be essential for in situ population survival in the face of climate change (Gomulkiewicz & Holt, 1995; Gomulkiewicz & Houle, 2009; Alberto *et al.*, 2013).

Environmental fluctuations can mediate growth-reproduction tradeoffs and complicate interpretation of causal mechanisms. Bell (1980) states that environmental factors with opposite effects on growth and reproduction can produce spurious negative tradeoffs between these two responses. From a slightly different perspective, Knops *et al.* (2007) concluded that observed growth oscillations associated with seed production were due to direct effects of rainfall on each, and that once this effect was removed, no tradeoffs were evident between radial growth and reproduction. Thus, attempts to evaluate tradeoffs for resource allocation must necessarily account for climatic and other mediating factors, while recognizing that differential response to the same environmental cues may have evolved as an adaptive mechanism for optimizing reproductive fitness under enviromental variability.

Extensively-managed natural stands and intensively-managed forest plantations of *P. pinaster* are distributed throughout the Mediterranean basin where they are adapted to regional edaphic and climatic factors. But in some cases seed sources have not been selected to match environmental conditions at the plantation site. Outside its natural range, *P. pinaster* is considered a potentially invasive species (Lowe *et al.*, 2000). *P. pinaster* initiates cone primordia toward the end of the third growing season before seed production and release from the cone; therefore, the sequence of weather conditions during the four years prior to cone maturation may be important for the occurrence of a cone crop and the relative number of cones produced (Mutke *et al.*, 2005; Philippe *et al.*, 2006; Calama *et al.*, 2011).

Beyond data from meteorological stations, indices of atmospheric mass distribution can help to provide integrated predictors for broad scale climate in terrestrial ecosystems. The Northern Atlantic Oscillation (NAO) refers to the atmospheric mass distribution between the Arctic and the subtropical Atlantic and has a strong impact on the European climate, including that of the Iberian Peninsula (where low NAO leads to a humid growing season; Martín-Vide & Fernández-Belmonte, 2001), as well as that of the eastern coast of North America. NAO can be assessed through an index based on the pressure differences between a northern location (usually Iceland) and more southern locations (usually the Azores Islands or the Portuguese coast). This type of general climate index provides an integrated measure of seasonal weather and offers potentially better description of coarse-scale regional climatic variability than finer-scale averages of specific local variables (Hurrell & Deser, 2009). Stenseth *et al.* (2003) advocated the use of indices of atmospheric mass distribution because they (1) show a coarse-scale spatial correlation with weather patterns, (2) simplify model selection by integrating climate effects from a small number of variables, (3) improve model predictability, (4) integrate net climate impacts on organisms better that simple temperature or precipitation values and (5) are easily available (most of them from the internet) for long-time frames.

Changes in atmospheric mass distribution, as reflected by NAO, can impact a variety of ecological processes and functions, including phenology, growth and reproduction (Menzel, 2003; Stenseth *et al.*, 2003; Wang & Schimel, 2003). Only a few studies have documented the general effects of NAO atmospheric distribution on forest trees. Tree ring growth in the Mediterranean forests is negatively related with NAO in winter, as reported in *Fagus sylvatica* L. (Piovesan & Schirone, 2000), *P. pinaster* (Bogino & Bravo, 2008), *Quercus ilex* L. (Campelo *et al.*, 2009) and *Pinus halepensis* Mill. (Pasho *et al.*, 2011). In Northern Europe, Lindholm *et al.* (2001) found that NAO in winter was positively correlated with *Pinus sylvestris* L. tree-ring growth. Interestingly, Piovesan & Adams (2001) found a significant correlation between seed production and the NAO index from the previous year among a number of beech species worldwide (*F. sylvatica* from Europe, *Fagus grandifolia* Ehrh. from eastern North America and *Fagus crenata* Blume from Japan). In addition, birch (*Betula ssp*) pollen production was correlated with the NAO index, with stronger correlation among sites in the United Kingdom than in Poland (Stach *et al.*, 2008).

Despite the ecological significance of fitness tradeoffs, the general consensus that global climate impacts these tradeoffs, and the wider availability of atmospheric mass distribution indices, to our knowledge no study has linked these three concepts. Establishing this link is especially important in the case of tradeoffs between reproduction and growth due to the high ecological and economic importance of these biological processes. The high intraspecific variability of cone production previously reported for *P. pinaster* (Tapias *et al.*, 2004; Juez *et al.*, 2014), along with the wide fluctuation in annual weather conditions that it typically endures, highlight the potential of this species as a case study for elucidating tradeoffs in resource allocation that may have ecological and economic importance. Moreover, a strong correlation has been recently reported in this species between environmental variables and minimum tree size required for production of female reproductive structure, probably reflecting environment-dependent costs of cone production (Santos-del-Blanco *et al.*, 2012).

Our main objective was to determine the relationship between cone production and vegetative growth in Mediterranean *P. pinaster* in the context of concurrent fluctuations in climatic conditions. Radial growth at breast height served as the surrogate for vegetative growth in our analysis, and two facets of cone production were considered, including simple occurrence of cones as a binary response and intensity of cone production as an actual count of cone numbers. To accomplish the stated objective, several different general hypotheses were tested:

1) Cone production (occurrence and intensity) is driven by tree size, local stand density (here estimated from the six nearest trees), inter-tree competition and climate. Five alternative climatic mechanisms were proposed: (a) cone production (occurrence and intensity) is affected by climate during the current and each of the three previous years; (b) cone production (occurrence and intensity) is affected by climate during only the third year before cones reach maturity; (c) cone production (occurrence and intensity) is affected by climate in the third year before cones reach maturity; in addition cone occurrence is also influenced by climate in the second year before cones reach maturity; (d) cones intensity, also known as cone set, is influenced by climate in the third year before observed cone count, along with the size, local stand density, and competition covariates, but cone occurrence is influenced only by climate (no size or stand structural variables) during the third year before cone maturity; (e) cones intensity is influenced by climate in the second year before observed cone count, along with the size, local stand density, and competition covariates, but cone occurrence is influenced only by climate (no size or stand structural variables) in the third year before cone maturity.

2) After accounting for tree size, local stand density (six nearest trees), inter-tree competition, and climate effects on cone occurrence and cone intensity, the marginal effects of crown attributes, tree radial growth and growth efficiency can explain a significant part of the residual variability in cone production.

Testing of the hypothesis above was done by constructing zero-inflated Poisson (ZIP) regression models and selecting the model with the strongest statistical evidence using standard Akaike's Information Criterion (AIC) criteria. Then, the marginal effects of individual-tree crown attributes, tree radial growth, and growth efficiency on reproductive effort were assessed, to test the null hypothesis that reproductive-growth tradeoffs are lacking in this widespread Mediterranean conifer.

Material and methods

Study area

The data were collected from an experimental plot situated in a natural maritime pine (*P. pinaster*) forest located at 755–810 masl in a flat sandy region in the Castilian Plateau, central Spain (latitude 41º16'N and longitude 4º29'W). Rotation age has been approximately 100 years under a shelterwood system adapted to resin production. In this system, the regeneration period varies from 20 to 25 years in length. Climate is dry Mediterranean, with an annual rainfall of 401 mm and mean annual temperature of 11.2 ºC. Vegetation is dominated by *Corynephorus canescens* (L.) P. Beauv., *Stipa* spp., *Retama sphaerocarpa* (L.) Boiss., *Lavandula stoechas* L., *Thymus mastichina* L., and isolated trees of *Pinus pinea* L. A detailed description of the site was given by Nanos *et al.* (2004).

Tree data

In 2000, a circular plot (radius=100 m) was installed in a mature stand within the study area where only dead trees had previously been removed during thinning operations. On all mature trees (380) the following data were collected: spatial position (polar coordinates, to nearest 0.1 m), ring count age, total height (to nearest 0.1 m), number of cones and diameter at breast height (DBH) to nearest 0.1 cm. Coordinates were measured with a total station. In 2006 and 2007, additional cone counts were conducted on the same trees. Number of cones was estimated on each tree by visual count (see details in Miguel *et al.*, 2002). For each tree, BAL, *i.e.*, the basal area in trees larger than the subject tree (Wykoff, 1990), was computed as an index of competition from above and basal area of neighboring trees (BA_6) was calculated as an index of two-sided competition. Both BAL and BA_6 for each subject tree were computed by considering only the six nearest trees. Crown dimensions of each tree were estimated with Lizarralde's (2008) crown equations (see Fig. S1 [suppl] for details). Tree dimensions (stem and crown) were assumed to have experienced no change over the course of the study (from 2000 to 2007) because the stand studied is mature and well over its maximum growth period.

In 2011, 113 trees were selected by expert judgement to cover the range in cone yield and were cored to obtain radial increments. DBH for these 113 trees ranged from 25.3 cm to 62.7 cm while cone counts ranged from 0 to 78 (see more details in Table 1). Cores were polished and scanned at high resolution (2000 dpi) with an Epson Expression 1640 XL scanner with 0.01 mm accuracy. Tree rings were measured using WinDendro© V 6.5C version (Regent Instruments). COFECHA program 6.06P version (Grissino-Mayer 2001, www.ltrr.arizona.edu) was used to assess data accuracy by calculating correlation indices between ring-width series and identifying errors such as missing or false rings. At the end of this process, a 15-year growth series (from 1996 to 2010) was obtained for each tree. Tree-ring width from the cone count years and the three years previous to each cone count were extracted from each growth series. Only 105 trees per year (104 in year 2000) were used in the final analysis. Trees were classified into four social classes according to their relative BAL: dominant (if BAL was in the bottom quartile, *i.e.* lowest values), codominant (if BAL was in the second to smallest quartile), intermediate (if BAL was in the third to smallest quartile) and suppressed (if BAL was in the largest quartile, *i.e.*, highest BALs). The cone count frequencies are presented in supplementary documentation (whole data set in Fig. S2 [suppl]). As a surrogate for growth efficiency different alternatives were computed from annual ring increment, including basal area growth per unit crown projection area (CP), growth per unit crown surface area (CSA), and growth per unit LAI_s.

Climatic data

NAO data were obtained from the Climate Analysis Section, National Center for Atmospheric Research, NCAR (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based). Monthly and Seasonal NAO indexes are based on the difference of normalized sea level pressures (SLP) between Ponta Delgada, Azores and Stykkisholmur/Reykjavik. As of April 2003, the Ponta Delgada station stopped reporting, so to continue this time series NCAR staff substituted it by the nearest National Centers for Environmental Prediction/National Center for Atmospheric Research, NCEP/NCAR reanalysis grid point (see details at http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.html). The correlation between a monthly time-series constructed with the Ponta Delgada observational data and one constructed with NCEP/NCAR reanalysis data was, according to NCAR information, 0.99 for the period from 1948 to 2003. NAO data from the cone count years (t=0) and the three previous years (t=1, t=2 and t=3) were extracted from the full dataset. NAO_{winter} was computed as the average of the consecutive December, January and February NAOs).

Statistical analysis

Determining correct variance-covariance structure

Because the data included three non-consecutive measurements from each tree, potential autocorrelation within trees could lead to biased estimates of variances and incorrect p-values for statistical tests. Four different variance-covariance structures, typically used in ecological studies (Barnett *et al.*, 2010), were tested in a model for cone occurrence (binomial regression) and in a model for cone intensity (Poisson regression): independent, exchangeable, unstructured and autoregressive of order one. The models with alternative variance-covariance structures were fitted by SAS Proc GENMOD and compared by the quasi-likelihood information criterion (QIC) proposed by Pan (2001). No evidence could be found for significant autocorrelation in the pooled data, so further data analysis was pursued assuming independence of observations.

Zero-inflated Poisson model (ZIP model)

A zero-inflated Poisson (ZIP) model (eq. 1) proposed by Lambert (1992) was fitted to test the five hypotheses proposed in the Introduction. The ZIP model consisted of two parts: one to estimate the occurrence of cone production by using a logistic model and other to estimate the cone set or intensity of the reproduction event (number of cones) by using a Poisson model. The ZIP model fitted by SAS Proc COUNTREG had the following form:

$$P(Y = y_i|x_i, z_i) = \begin{cases} \theta \;\; if\; y = 0 \\ (1-\theta)f(y) = (1-\theta)\left(\frac{\mu_i}{1+\alpha\mu_i}\right)^{y_i}\left(\frac{(1+\alpha y_i)^{(y_i-1)}}{y_i}\right)e^{\left(\frac{-\mu_i(1+\alpha y_i)}{1+\alpha\mu_i}\right)}x, if\; y > 0 \end{cases} \quad (1)$$

where y_i is the observed cone count, θ represents the probability of observing no cones (y_i=0) modeled via a logit link function (eq. 2 below) and $f(y)$ indicates the probability mass function for a Poisson function with expected mean μ (eq. 3) and variance equal to $\mu\,(1 + \alpha\mu)^2$.

$$logit\ \theta = log\left(\frac{\theta}{1-\theta}\right) = \sum x_i\beta_i \quad (2)$$

$$\mu_i = e^{\sum x_i\gamma_i} \quad (3)$$

where x_i are the covariates representing climate, tree size, stand density, and inter-tree competition and β_i and γ^i are parameters estimated from the data. Expected cone occurrence (θ) and expected cone intensity (μ_i) are not assumed to be affected by the same covariates.

Candidate ZIP models

To test the first set of alternative hypotheses (see end of Introduction) about response of cone occurrence and cone intensity to tree size, stand density, inter-tree competition and climate, five corresponding models were developed (Table 2). The best among the five candidate models was selected on the basis of AIC.

To test the second general hypothesis about marginal effects of crown attributes, radial growth and tree growth efficiency, another set of alternative models was developed (Table S1 [suppl]). New

Table 1. Summary of biometric data from 314 *Pinus pinaster* trees (104 trees for cone counts in year 2000 and 105 trees for cone counts in years 2006 and 2007). DBH is diameter at breast height (1.3 m), ΔRt is annual radial increment for year t (where t is number of years prior to cone counts), BA6 is basal area, and BAL is basal area in trees larger than subject tree. Dominants included 32 trees for each annual count (except for only 31 trees in the year 2000), codominants included 19 trees, intermediates included 23 trees, and the suppressed class included 31 trees).

Var	Mean	Max	Min	SD
DBH (cm)	41.7	62.7	25.3	7.5
Cones (number)				
Whole dataset	9.4	78.0	0.0	11.1
Dominants	10.4	8.0	0.0	13.2
Codominants	9.7	39.0	0.0	9.5
Intermediate	10.2	65.0	0.0	11.8
Suppressed	7.6	44.0	0.0	8.9
ΔR_0 (mm)	1.6	7.0	0.1	1.1
ΔR_1 (mm)	1.1	4.2	0.1	0.7
ΔR_2 (mm)	1.3	6.7	0.1	1.1
ΔR_3 (mm)	1.5	6.3	0.0	1.0
BA_6 (m^2/ha)	19.1	44.1	7.1	7.2
BAL (m^2/ha)	9.8	36.1	0.0	7.9

variables were included only in the intensity part of the model. Different variables were initially tested in the occurrence part of the model, but no improvements were achieved, suggesting that the occurrence model should include neither crown variables nor any radial growth or growth efficiency effects.

The final step in the analysis was to identify the best full model (*i.e.* the best model for explaining cone occurrence and cone intensity as a function of tree size, stand density, inter-tree competition, and climate), with the intensity portion of the model augmented by the best variables representing crown, growth and growth efficiency. The final model was selected on the basis of percentage reduction in AIC over the basic model (best model from Table 1). Percentage reduction in AIC (PRAIC) was computed as:

$$\text{PRAIC} = 100 \times [1\text{-}(\text{AIC}_{\text{Full}}/\text{AIC}_{\text{Basic}})] \tag{4}$$

Additionally, Akaike weight (W_i) was computed following the procedure presented by Johnson & Omland (2004). W_i provides a relative weight of evidence for each model and can be interpreted as the probability of model i is the best model for the observed data set. Equal values of W_i means that the performance of the models is equal.

Results

ZIP basic model

Winter NAO three years prior to cone maturation was the only variable tested that consistently had a significant influence on occurrence of cones. In contrast, tree size, inter-tree competition, and local stand density variables all contributed to explaining variation in cone intensity, along with winter NAO either during the year of cone primordia initiation (year t-3 in models 2, 3, and 4; Table 3) or during year of flowering (year t-2 in model 5; Table 3).

In model 5, all variables were significant and AIC achieved the lowest value (Table 3). Model 5 was therefore further considered as the base model for testing hypothesis 2 with regard to marginal effects of crown attributes, growth efficiency, and radial growth on cone count (ZIP full models, see below), starting with the following estimated forms for occurrence and intensity, respectively:

$$logit\,\theta = log\left(\frac{\theta}{1-\theta}\right) = -1.817489 + \\ + 0.566412 * NAO_{winter\ 3} \tag{5}$$

$$\mu_i = \mathrm{e}^{\left(-1.711558+0.003150*\mathrm{DBH}+0.024703*\mathrm{BAL}-0.025704*\mathrm{BA}- -0.727120*NAO_{winter\ 2}\right)} \tag{6}$$

ZIP full models

Models with variables representing crown dimensions, radial growth and growth efficiency showed an improvement between 0.62 and 4.45 % in AIC reduction over the basic model (Table S1 [suppl]). The variables identified as best from each group (crown dimensions, radial growth and growth efficiency) were tested in different combinations to identify a best model that potentially included one variable from each group (Table 4).

Table 2. Models for testing the effect of tree size, stand density, inter-tree competition, and climate on occurrence and intensity of cones in *Pinus pinaster.*

Hypothesis/Model	Response	Size	Density	Competition	Climatic variables
1a/Model 1	Occurrence	DBH	BA_6	BAL	NAOwinter0, NAOwinter1, NAOwinter2, NAOwinter3
	Intensity	DBH	BA_6	BAL	NAOwinter0, NAOwinter1, NAOwinter2, NAOwinter3
1b/Model 2	Occurrence	DBH	BA_6	BAL	NAOwinter3
	Intensity	DBH	BA_6	BAL	NAOwinter3
1c/Model 3	Occurrence	DBH	BA_6	BAL	NAOwinter2, NAOwinter3
	Intensity	DBH	BA_6	BAL	NAOwinter3
1d/Model 4	Occurrence	-	-	-	NAOwinter3
	Intensity	DBH	BA_6	BAL	NAOwinter3
1e/Model 5	Occurrence	-	-	-	NAOwinter3
	Intensity	DBH	BA_6	BAL	NAOwinter2

Table 3. Results of fitting ZIP models to cone occurrence and cone count in *Pinus pinaster*.

Hypothesis/Model	Response	Size	Density	Competition	Climate	AIC
1a/Model 1	Occurrence	DBH (ns)	BA_6 (ns)	BAL (ns)	$NAO_{winter}0$ (ns)	2752
					$NAO_{winter}1$ (ns)	
					$NAO_{winter}2$ (ns)	
					$NAO_{winter}3$(**)	
	Intensity	DBH (***)	BA_6 (***)	BAL (***)	$NAO_{winter}0$ (***)	
					$NAO_{winter}1$ (ns)	
					$NAO_{winter}2$ (ns)	
					$NAO_{winter}3$(***)	
1b/Model 2	Occurrence	DBH (ns)	BA_6 (ns)	BAL (ns)	$NAO_{winter}3$(**)	2882
	Intensity	DBH (***)	BA_6 (***)	BAL (***)	$NAO_{winter}3$(***)	
1c/Model 3	Occurrence	DBH (ns)	BA6 (ns)	BAL (ns)	$NAO_{winter}2$ (***)	3064
					$NAO_{winter}3$(***)	
	Intensity	DBH (***)	BA_6 (***)	BAL (***)	$NAO_{winter}3$(***)	
1c/Model 4	Occurrence	-	-	-	$NAO_{winter}3$(***)	2879
	Intensity	DBH	BA6	BAL(***)	$NAO_{winter}3$(***)	
1d/Model 5	Occurrence	-	-	-	$NAO_{winter}3$(***)	2743
	Intensity	DBH (***)	BA_6 (***)	BAL (***)	$NAO_{winter}2$ (***)	

Three of the combined models improved the performance of the basic model by including at least crown length (CL) as an additional explanatory variable in the basic model (Table 4). The best combined model (Basic+ CL + EFI_LAI_{s_t} in Table 4) included the two of the three variables that had the largest marginal effect on cone count when considered as the only variable added to the base model, *i.e.*, CL, Growth_0 and EFI_LAI_{s_0} (Table S1 [suppl]). AIC was reduced over 4.7% by this full model (Table 4). We conclude that cone occurrence and intensity were driven by climate (NAO_{winter} in the bud formation and flowering year), tree size (DBH), tree competition (BAL), tree density (BA_6), and crown length (CL) and growth efficiency (EFI_LAI_{s_1}), as indicated in below in eqs. [7] and [8]:

$$logit\,\theta = log\left(\frac{\theta}{1-\theta}\right) = -1.820881 + \\ + 0.56433 * NAO_{winter3} \tag{7}$$

$$\mu_i = \mathrm{e}^{\left(3.465026+0.003822*\mathrm{DBH}+0.015848*\mathrm{BAL}-0.043809*\mathrm{BA}- \\ -0.678152*NAO_{winter\,2}-0.026992*CL+0.319085*EFI\_LAI_{s\_1}\right)} \tag{8}$$

Discussion

To study tradeoffs between growth and reproduction in *P. pinaster*, a general ZIP model was fitted to estimate both occurrence and intensity of cone production in a mature stand only this species. The most influential variables were retained in the final model, including some growth-related variables. Specifically, the final model included variables related to the climate two and three years before cone maturation, tree size and crown attributes, local stand density (competition level), and growth efficiency. As in other similar studies (*e.g.*, Calama *et al.*, 2011), we studied the impact of weather up to one year before cone development was initiated. In *P. pinaster* two years are required to fully develop cones, so we considered the effects of weather three years prior to cone maturation. This model is more parsimonious that other previously reported for other Mediterranean pines. Calama *et al.* (2011), for example, used 41 different variables to estimate *Pinus pinea* L. cone production. However, Calama *et al.* (2011) used a much larger dataset with ten years of cone harvesting. Longer cone harvest period confers an important advantage because cone set varies dramatically across years. However, differences in reproductive effect measured by

Table 4. Models combining marginal effects of crown dimensions, radial growth, and growth efficiency for predicting cone intensity.

Model	AIC value	% AIC improvement of full model over basic model	W_i
Basic + CL+ Growth_t + EFI_LAI_{s_t}	2617	4.59	14.0244
Basic + CL + Growtht_t	2616	4.63	23.1224
Basic + CL + EFI_LAI_{s_t}	**2614**	**4.70**	62.8532
Basic + Growtht + EFI_LAI_{s_t}	2670	2.66	0.0000

W_i (Akaike weight) provides a relative weight of evidence for each model and can be interpreted as the probability of model *i* is the best model for the observed data set (Johnson & Omland, 2004).

cone harvesting records and visual cone counts should also be considered.

Different numerical simulations have been conducted to explore the impact of the predictor variables (winter weather during the bud formation and flowering years, tree size, stand density, competition from above, and growth efficiency) on cone occurrence and intensity of cone yield. Although a trade-off between cone yield and growth was not found, trends for tree size and stand density agreed with current scientific knowledge on cone production. Interestingly, in contrast with Calama *et al.* (2011), occurrence and intensity of fruiting are governed by different variables and just one factor (weather) was included in both parts of the model.

Variables affecting cone occurrence and intensity of cone production

Cone occurrence

When $\text{NAO}_{\text{winter}}$ is relatively high, the winter is drier in the Iberian Peninsula. The logistic model for cone occurrence showed that a year with relatively high $\text{NAO}_{\text{winter}}$ will lead three years later to a year with at least some cone production. In general, dry winters stimulate the development of reproductive buds in *P. pinaster*. This result is consistent with known relationships between environmental conditions and the life cycle of pine species. Mutke *et al.* (2005) found that rainfall during the fourth and the third years before cone maturation are key variables in cone production in *P. pinea*, a species that takes three years to produce mature cones (one year more than in *P. pinaster*).

Intensity of cone production

Four variables affected intensity of fruiting in our model: winter weather of the flowering year, tree size, stand density and competition.

Wet winters (indicated by lower $\text{NA}_{\text{Owinter}}$) during the flowering year (2) lead to higher cone yields. These results suggest that the necessary conditions for high cone counts include a relatively dry winter followed by a relatively wet winter. Dry winters ensure the occurrence of cones by favoring development of cone primordia, and a subsequent wet winter ensures a high cone count by enhancing primordia survival, flowering and pollination success (Fig. 1a).

Trees with larger diameter are predicted to produce a larger number of cones than smaller trees (Fig. 1b). This result has been previously documented in other species such as *Pinus ponderosa* (Krannitz & Duralia, 2004) and *Pseudotsuga menziesii* (El-Kassaby & Barclay, 1992), and is probably explained in part by the generally greater vigor of larger trees in even-aged stands. Higher tree vigor has also been shown to produce a higher number of recruits in next generation (González-Martínez *et al.*, 2006). As thinning promotes diameter growth, an increase in cone production is expected as a longer-term benefit of thinning (Krannitz & Duralia, 2004).

As stand density declines the number of cones produced by a given tree increases (Fig. 1c). This result is consistent with previous observations of increased cone production after thinning (Verkaik & Espelta, 2006; Ruano *et al.*, 2013), and can probably be explained in part by the greater resources available for each tree in less dense stands, allowing more carbon to be allocated to reproductive efforts.

Trees that are experiencing higher levels of competition were predicted to produce higher average cone counts than more dominant trees (Fig. 1d). This result seems to contradict the previously described effect of stand density, by suggesting that trees under more competitive stress from above may be induced to invest more resources in reproductive effort. Some previous studies suggest the opposite (Fowells & Schubert, 1956; Larson & Schubert, 1970), so in *P.*

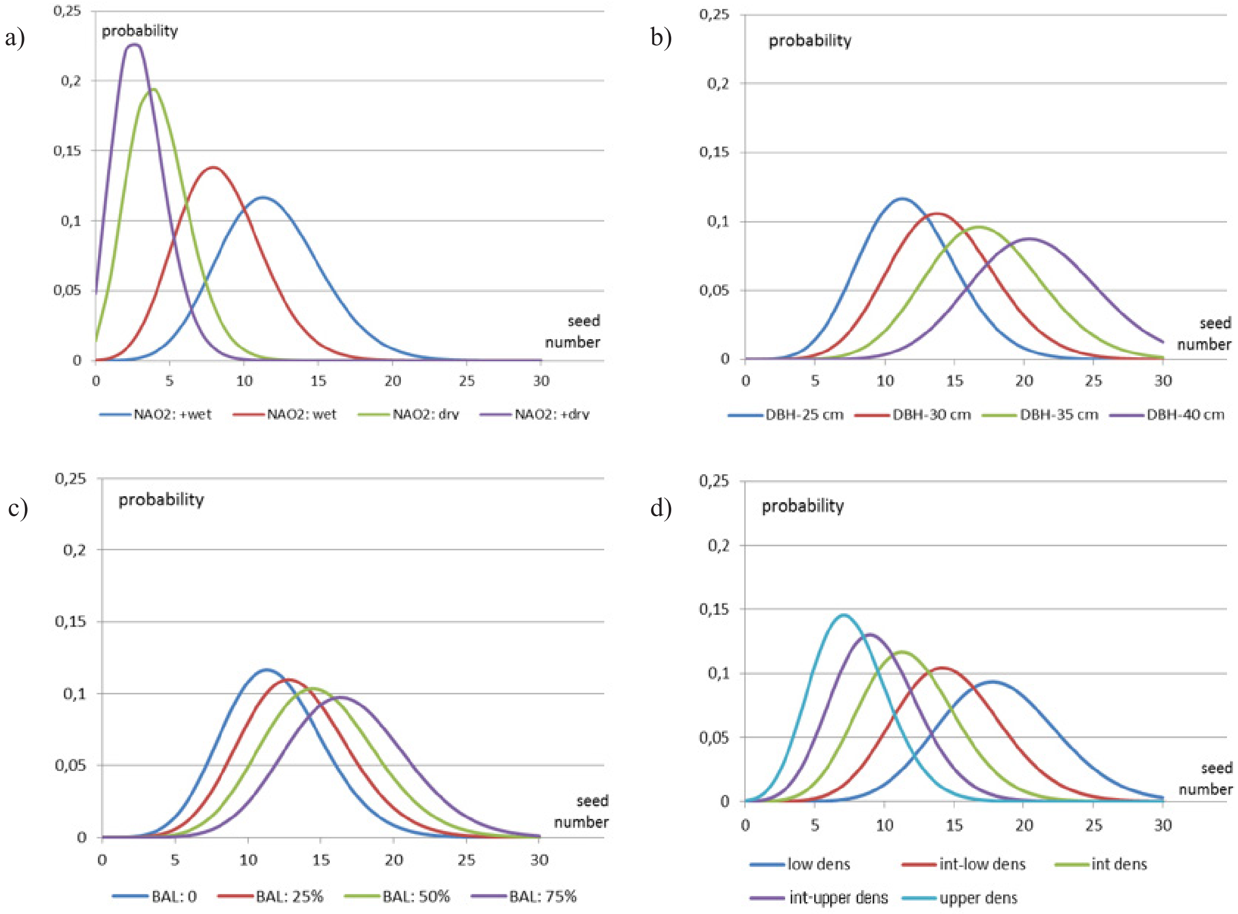

Figure 1. Response of cone count frequency distribution to increasing NAO_{winter} during flowering year (t-2). (a): DBH=250 mm, BAL= 0 m^2/ha, BA_6= 30 m^2/ha, CL= 50 dm and EFI_LAIs =0.1 mm/m^2. NAO2 = -1, -0.5, 0.5 and 1 (negative: wet while positive: dry). (b): BAL= 0, BA_6= 30, CL= 50 and EFI_LAIs =0.1, NAO2 = -1, DBH= 250, 300, 350 and 400 mm. (c) DBH=250, BAL= 0, NAO_2 = -1, CL= 50 and EFI_LAIs =0.1, BA_6 = 25, 30, 35 and 40. (d): DBH= 250, BA_6= 30, CL= 50 and Efficiency =0.1, NAO_2 = -1, BAL= 0, 7.5, 15, 22.5. BA_6 (Basal area based on the 6 nearest trees); BAL (Basal area in larger trees); CL (crown length); EFI_LAI (Growth efficiency based on Leaf Area Index); NAO (Northern Atlantic Oscillation)

pinaster we similarly expected that dominant trees would produce the largest number of cones. The positive effect of BAL must be considered with caution, however, because *P. pinaster* stands in Central Spain are typically of very low density and tree vertical differentiation is weak, perhaps resulting in similar cone production for trees in different social classes (Fig. 1d). Furthermore, large trees (note dominant effect of tree diameter) may benefit from some surrounding tall trees if, for example, a larger proportion of cone primordia survive frost events with some protective cover.

Growth/Reproduction tradeoffs

No tradeoffs were detected between vegetative growth and cone production. However, a reduction of vegetative growth when cone production is high has been repeatedly found in different pine species (Linhart & Mitton, 1985; Krannitz & Duralia, 2004; Climent *et al.*, 2008). In some cases, these tradeoffs have been proposed to have a genetic basis (Schmidtling, 1981; Linhart & Mitton, 1985). In natural stands of *P. pinaster* (this study), trees with higher growth efficiency also produced higher cone counts on average (Fig. 2), but the frequency distribution of cone counts was also wider than for trees with lower growth efficiency. In a study of *Pinus contorta*, Dick *et al.* (1990) found that presence of male cones reduced tree photosynthetic potential while presence of female cones did not. Tradeoffs between secondary growth and defense (Sampedro *et al.*, 2011) and secondary growth and cone production (Climent *et al.* 2008) have been previously reported for Mediterranean pines evaluated under controlled conditions. Sampedro *et al.* (2011) found negative tradeoffs between growth and defensive investment in a greenhouse experiment with *P. pinaster* seedlings from different provenances. However, these latter tradeoffs emerged only under phosphorus limiting conditions. Climent *et al.* (2008) found that cone production in a *Pinus halepensis* seed orchard was

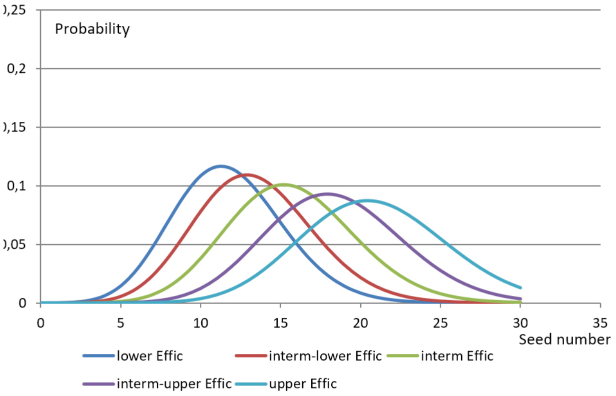

Figure 2. Response of cone count frequency distribution to tree growth efficienc.

incompatible with high vegetative growth while Almqvist *et al.* (2001) found no statistically significant correlation between cone production and height growth in *Picea abies*. Stands of *P. pinaster* in Central Spain are located on sandy soils of various depths and are characterized by high heterogeneity in available water and nutrients. Therefore, sites with good conditions for growth may also foster reproduction, while in more homogenous conditions (as those of greenhouse or common garden experiments), tradeoffs between growth and reproduction could emerge or simply be more detectable under the more uniform conditions.

In a detailed fruiting study in natural populations of *Quercus lobata* in southern California, Sánchez-Humanes *et al.* (2011) found that the cost of seed production differed at different levels of organization within the tree (tree canopy, individual branch and shoot within branch). Likewise the cost of seed production also varied among trees with different average seed production level. Only trees with consistently low seed production potential supported the trade-off theory, and only at the branch level. Their results suggest that any tradeoffs in reproductive allocation in natural populations would be detected at lower levels within trees, such as leaves or branches rather that at the level of the entire tree (Lovett-Doust & Lovett-Doust, 1988; Obeso, 1997). Our results for *P. pinaster* in a natural stand in Central Spain agreed with a lack of tradeoffs at the tree level, as also reported by Knops *et al.* (2007).

As an alternative possible microsite effects in extreme Mediterranean landscapes (see above), lack of apparent growth/reproduction tradeoffs in *P. pinaster* may be controlled by more general climatic factors. Cone production and growth interact with climate and this fact could have hidden tradeoffs in our study, as growth and cone development were driven by the same variables describing climate (Despland & Hoyles, 1997). Winter NAO is negatively related with radial tree growth over the Iberian Peninsula. However, Bogino & Bravo (2008) found that the growth variance explained by atmospheric indices at a finer scale among *P. pinaster* forests within the Iberian Peninsula was low (8.95 to 37.46%).

Conclusions and perspectives

Climate, stand density and tree conditions (size and vigor, competition and growth efficiency) influence significantly both cone occurrence and intensity of fruiting as shown by a ZIP model. As the climate variables included in the model (based on NAO) are general and easily obtained, the proposed model has practical applicability to predicting *Pinus pinaster* cone production in the Iberian Peninsula. Our results are limited because we used just one monitoring site during three years, so specific studies are needed at local scales and in other geographical ranges of the species before the method can be applied at operational level. Judging from this model, no strong tradeoffs occurred between growth and reproduction in *P. pinaster* from Central Spain, so that phenotypic selection of those trees that have larger cone production as seed parents should not forfeit future stand growth in this region. However, trade-offs with other uses of photosynthates such as for defensive chemicals or structures (studied by Moreira *et al.*, 2015 or Di Matteo & Voltas, 2016) should be also considered. Our model also points to silvicultural actions (*e.g.* changes in stand density) that could increase cone production in natural forests of the species, which may prove useful in the face of impending environmental threats such as climate change

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