

Modelling *Pinus pinea* forest management to attain natural regeneration under present and future climatic scenarios

Rubén Manso, Timo Pukkala, Marta Pardos, Jari Miina, and Rafael Calama

Abstract: Natural regeneration-based silviculture has been increasingly regarded as a reliable option in sustainable forest management. However, successful natural regeneration is not always easy to achieve. Recently, new concerns have arisen because of changing future climate. To date, regeneration models have proved helpful in decision-making concerning natural regeneration. The implementation of such models into optimization routines is a promising approach in providing forest managers with accurate tools for forest planning. In the present study, we present a stochastic multistage regeneration model for *Pinus pinea* L. managed woodlands in Central Spain, where regeneration has been historically unsuccessful. The model is able to quantify recruitment under different silviculture alternatives and varying climatic scenarios, with further application to optimize management scheduling. The regeneration process in the species showed high between-year variation, with all subprocesses (seed production, dispersal, germination, predation, and seedling survival) having the potential to become bottlenecks. However, model simulations demonstrate that current intensive management is responsible for regeneration failure in the long term. Specifically, stand densities at rotation age are too low to guarantee adequate dispersal, the optimal density of seed-producing trees being around 150 stems·ha⁻¹. In addition, rotation length needs to be extended up to 120 years to benefit from the higher seed production of older trees. Stochastic optimization confirms these results. Regeneration does not appear to worsen under climate change conditions; the species exhibiting resilience worthy of broader consideration in Mediterranean silviculture.

Key words: multistage models, transition probability, stochastic spatial optimization, stochastic simulation, climatic change.

Résumé : La sylviculture fondée sur la régénération naturelle est de plus en plus considérée comme une option fiable pour l'aménagement forestier durable. Cependant, il n'est pas toujours facile de réussir à établir une régénération naturelle. Récemment, de nouvelles préoccupations ont été soulevées en raison des futurs changements climatiques. Jusqu'à présent, les modèles de régénération se sont avérés utiles pour la prise de décision concernant la régénération naturelle. L'application de ces modèles dans des routines d'optimisation est une approche prometteuse pour fournir aux aménagistes forestiers des outils précis pour la planification forestière. Dans la présente étude, nous présentons un modèle de régénération stochastique multistage pour les forêts aménagées de *Pinus pinea* L. du centre de l'Espagne où la régénération a historiquement été infructueuse. Le modèle est en mesure de quantifier le recrutement en fonction de différentes méthodes sylvicoles et de divers scénarios climatiques, en plus d'optimiser le calendrier d'aménagement. Le processus de régénération de cette espèce a montré une forte variation interannuelle et tous les sous-processus (production, dispersion, germination et prédation des graines ainsi que survie des semis) peuvent devenir des goulots d'étranglement. Cependant, les simulations du modèle montrent que l'aménagement intensif présentement appliqué est responsable de l'échec de la régénération à long terme. Spécifiquement, la densité des peuplements à l'âge d'exploitabilité est trop faible pour garantir une dispersion adéquate, la densité optimale des arbres semenciers étant d'environ 150 tiges ha⁻¹. De plus, la durée de la rotation doit être allongée jusqu'à 120 ans pour tirer profit de la plus forte production de semences des plus vieux arbres. L'optimisation stochastique confirme ces résultats. L'établissement de la régénération ne semble pas devenir plus difficile sous des conditions de changement climatique; l'espèce fait preuve d'une résilience qui mérite d'être mieux considérée par la sylviculture méditerranéenne. [Traduit par la Rédaction]

Mots-clés : modèles multistages, probabilité de transition, optimisation spatiale stochastique, simulation stochastique, changements climatiques.

Introduction

One of the main aims of sustainable forest management is to guarantee forest persistence over time (Nyland 2002). This general objective implies that managed stands need to be successfully regenerated. Depending on the local ecological conditions, forest type, and specific management objectives, regeneration can be

achieved either naturally (relying on the natural processes involved) or artificially (through plantations or direct seeding), after conducting regeneration fellings (Smith et al. 1996). In recent years, natural regeneration-based silviculture has increasingly attracted the attention of forest managers. Societal demands have tended towards less altered landscapes, in contrast to the forest

Received 7 May 2013. Accepted 15 November 2013.

R. Manso,* M. Pardos, and R. Calama. Departamento de Selvicultura y Gestión de Sistemas Forestales INIA-Forest Research Center. Ctra. La Coruña km 7.5, 28040 Madrid, Spain.

T. Pukkala. University of Eastern Finland, School of Forest Sciences, Yliopistokatu 7, Borealis Building, 80101 Joensuu, Finland.

J. Miina. Finnish Forest Research Institute (METLA), Jokiniemenkuja 1, FI-01301 Vantaa, Finland.

Corresponding author: Rubén Manso (e-mail: rimgforestal@hotmail.com).

*Present address: LERFoB (Laboratoire d'Etude des Ressources Forêt-Bois), Institute National de Recherche Agronomique, Centre INRA de Nancy, 54280 Champenoux, France.

areas derived from the use of artificial regeneration techniques (Pukkala and Kolström 1992). In addition, seeding and planting operations have nowadays become more and more unsustainable within an economic context of rationalization and optimization of silvicultural resources, especially in non-intensive systems (Gordo et al. 2012). Nonetheless, this approach requires a deeper knowledge of the ecological processes involved in each stage of regeneration, from seed production to seedling establishment (Pardos et al. 2005). This knowledge may be crucial under a scenario of climatic change, particularly in water-limited areas, such as the Mediterranean basin, where regeneration is expected to be even more challenging to achieve in the future (Valladares et al. 2005).

Decision-making related to natural regeneration is not an easy task for forest managers. Given the complexity of the aforementioned processes, the regeneration phase of forest management usually relies on forester experience. Therefore, it is of great interest to create efficient tools that allow us to anticipate the result of different silvicultural alternatives for natural regeneration. Furthermore, predictions on regeneration performance considering climatic change scenarios may prove supportive for forest planning under criteria of adaptive silviculture. Consequently, natural regeneration modelling has become increasingly popular. Natural regeneration in forest species has been modelled from two main perspectives: recruitment models (e.g., Erikäinen et al. 2007; Fortin and DeBlois 2007; Barbeito et al. 2011) and multistage models (e.g., Leak 1968; Ferguson et al. 1986; Pukkala and Kolström 1992; Ordóñez et al. 2006). Recruitment models require relatively little sample and modelling effort, but they are often too simplistic when the mechanisms involved in regeneration at the subprocess level (e.g., seed production, dispersal, etc.) require special attention (Price et al. 2001). Multistage regeneration models constitute an alternative approach to overcome these shortcomings. This approach considers regeneration as a multistage process consisting of underlying consecutive subprocesses that often can be identified as a series of successive survival thresholds for potential seedlings (Pukkala and Kolström 1992).

In addition to new improvements in modelling, decision-making in forestry has largely benefited from the development of optimization techniques. Although optimization has been widely used in forestry studies to maximize the output of different products and services (González-Olabarría et al. 2008; Pasalodos-Tato et al. 2010), to our knowledge the target has never been natural regeneration.

This background was taken into account when we undertook the modelling of natural regeneration by *Pinus pinea* L. in the Northern Plateau of Spain, a particularly complicated case of even-aged forest management experiencing frequent failures in natural regeneration. Natural regeneration in these forests is rarely successful when using the existing regeneration methods (Gordo et al. 2012), and this situation may worsen under future climate scenarios in Spain (De Castro et al. 2005). To date, several studies have focused on the modelling of the different stages of natural regeneration in *P. pinea*, namely seed production (Calama et al. 2011), seed dispersal (Manso et al. 2012c), germination (Manso et al. 2013), seed predation (Manso et al. 2012b), and seedling mortality (Manso et al. 2012a), concluding that all these subprocesses can potentially become a bottleneck for regeneration, particularly due to the low stand densities occurring during the regeneration period. However, the challenge remained to assemble this information into an integrated regeneration model for the species.

To accomplish this task, a multistage stochastic model was developed based on the aforementioned partial studies, which include climatic, environmental, and silvicultural variables. This model formulation is particularly useful as it makes it possible to predict regeneration under different climatic scenarios and varying silvicultural alternatives in both spatial and temporal dimen-

sions. In addition, the model was implemented in an optimization framework designed to identify the management schedule that maximizes the probability of uniform recruitment occurrence.

The main aim of this study was to evaluate the suitability of different silvicultural alternatives with regard to natural regeneration under different climatic scenarios in even-aged *P. pinea* stands in the Northern Plateau of Spain.

Material and methods

Study area

The study area is located in the Northern Plateau of Spain, north-central Iberian Peninsula, in the Mediterranean Region. It consists of an inland tableland of about 50 000 km² at 700 m a.s.l. Total precipitation ranges from 300 to 500 mm·year⁻¹, with a period of extreme drought from June to September (66 mm). Mean monthly temperatures range from 21.7 °C in July to 4.0 °C in January, given the altitude of the plateau. Soils are poor and highly sandy. *P. pinea* plays an essential ecological role in the study area, as it is one of the very few tree species able to thrive. There are over 50 000 ha of managed *P. pinea* forest on the Northern Plateau. Under the aforementioned conditions, *P. pinea* would naturally form mixed stands with *Pinus pinaster* Aiton. Currently, management has transformed the original landscape into pure stands of either *P. pinea* or *P. pinaster*. Concerning regeneration techniques, the shelterwood method is recommended (Romero 1886). However, prior intense thinning aimed at promoting single-tree cone production led to stand densities lower than 100 stems·ha⁻¹ at the beginning of the regeneration period. Consequently, the method actually applied is the seed-tree method (Gordo et al. 2012), and the initially low density of seed-bearing trees was further reduced in two harvesting operations (Montero et al. 2008). Inventories carried out by the Regional Forest Service show that 44% of the ground in regeneration blocks holds less than 200 seedlings·ha⁻¹, which is the threshold for conducting corrective direct seeding across the whole surface of the block (Gordo et al. 2012).

Regeneration model

The probability of regeneration occurrence in space and time can be seen as the product of transition probabilities corresponding to each of the sequential regeneration subprocesses. In the present study, seed dispersal, seed germination, post-dispersal seed predation, and seedling survival were considered as regeneration subprocesses with transition probabilities of Pd_{ij} , Pg_{ij} , Pp_{ij} , and Ps_{ij} , respectively, for location i in time j . In the case of dispersal, the probability of a seed reaching location i in time j needs to be summed over all trees k expected to disperse seeds to location i . The product of these probabilities multiplied by the number of seeds N_{kl} produced by tree k in year l represents the complete sequence of the regeneration process. Therefore, the generic expression for the number of established seedlings for location i in time $j = 1$ would be:

$$(1) \quad S_{i1} = \sum_k N_{kl} \cdot Pd_{ik} \cdot Pg_{i1} \cdot (1 - Pp_{i1}) \cdot Ps_{i1}$$

The generalized equation for any time j is:

$$(2) \quad S_{ij} = \left[S_{i,j-1} + \sum_k (N_{kl} \cdot Pd_{ijk} + N_{il,j-1}) \cdot Pg_{ij} \cdot (1 - Pp_{ij}) \right] \cdot Ps_{ij}$$

These transition probabilities were separately modelled as a set of explanatory variables, including climatic and silvicultural variables, which is convenient from a management standpoint. The submodels explaining the transition probabilities are briefly detailed below. Given the temporal precision of the submodels, a

monthly time step was set for the regeneration model. In the spatial dimension, the minimal size to evaluate the model was set to 1 m² in grids of 100 m × 100 m.

Seed production

The submodel for seed production provides annual predictions of seed production at the individual tree level. The original model was formulated as a zero-inflated lognormal linear mixed model, which allowed us to account for *P. pinea* masting habit. Thus, the model predicts whether cones are going to be produced at all (cone occurrence), and in case they are, predictions on the expected weight of cones are generated (cone abundance). The weight of cones for a given tree was transformed into our variable of interest N_{kl} (seeds·(year·tree)⁻¹) using a dimensional correction. Covariates accounting for cone occurrence and cone weight are of four types: tree variables (diameter at breast height, *dbh*, and the ratio between the *dbh* of the target tree and the stand mean squared diameter, *d/dg*), stand variables (logarithm of stand density), site variables (Site Index and Natural Unit, denoting homogeneous ecological stratification of the landscape), and climatic variables (spring and fall precipitation three years before dispersal, summer precipitation two years before dispersal, spring precipitation the year before dispersal, and number of days with frost the year before dispersal). Large *dbh* and advantageous hierarchical position (high *d/dg*) promotes seed production. Stands that are too dense diminish the seed crop per tree, as a result of lower radiation levels reaching the crown and competition for limiting water resources. Fertile locations denoted by the Site Index and the Natural Unit favour cone yield. The aforementioned climatic variables affect the key periods of cone formation. In general, water availability and reduction of days with frost in the corresponding periods increase the weight of cones per tree. The variables involved in the model define the different factors limiting seed production at the stand level, including (i) stand densities that are too low or too high, which could lead either to seed limitation or to a reduction in the cone production per tree, respectively (Calama et al. 2008, 2011) and (ii) intense dry conditions and extreme frost events during the critical periods of cone formation, which give rise to *P. pinea* masting habit (Mutke et al. 2005; Calama et al. 2011). Furthermore, tree age over 120–140 years diminishes seed production (Calama et al. 2011).

The multistage model does not consider seeds remaining from previous years in calculations, due to the likely seed viability loss (Agrimi and Ciancio 1993). Therefore, N_{kl} strictly denotes seeds produced in the year *l*.

Dispersal

In this submodel, Pd_{ik} is defined through a dispersal kernel, a decreasing function of the distance to parent trees (Ribbens et al. 1994). Potential animal-dispersed seeds are not considered, as their fraction has proved negligible (Manso et al. 2012b). Providing year *l* is a mast year, low values of Pd_{ik} are due to relative long distances between a given location and the closest parent trees. Therefore, low Pd_{ik} may occur when stand densities are below a certain threshold and (or) when there exists a highly aggregated pattern of adult trees' spatial distribution. Low stand densities or highly clumped trees may result in a dispersal limitation, due to the very short dispersal distance characteristic of *P. pinea*: less than 1% of seeds are expected to drop beyond two crown radii (Barbeito et al. 2008; Manso et al. 2012c).

In the submodel accounting for the temporal pattern of seed release in *P. pinea*, a suitable thermal threshold for cones opening is set (mean monthly temperature >16 °C). When this threshold is reached, the model produces monthly predictions on the proportion of released seeds with respect to those still remaining in the cones in the previous month. This proportion is a linear function of the square root of total monthly precipitation (Manso et al. 2012c), with rainfall events promoting seed release.

Germination

Germination modelling in *P. pinea* was approached through a proportional-hazards mixed model. Covariates controlling germination were climatic (thermal) and stand-related (overstorey influence) factors. Thermal variables included (i) maximal daily temperature, which promotes germination in an interval from 12 to 16 °C, 14 °C being optimal and (ii) the days elapsed from the last frost event; the closer to a day with frost, the less likely that a seed germinates. An additive autoregressive term was included in the model to deal with daily correlation in the instantaneous germination rate, implying that emergence can still occur for several days although conditions become unfavourable. From this submodel it can be inferred that in the temporal dimension, germination is favoured by occurrence of adequate, although rare, thermal conditions, which mainly take place in autumn and spring, and is limited by frost events, only absent in summer. As a result, the optimal period for germination is limited to a few days in late fall and spring. Moreover, occasional dispersal to sufficiently large overstorey gaps may significantly lead Pg_{ij} to decrease, as shading promotes germination (Manso et al. 2013). Water-availability variables, including soil water-holding capacity, daily precipitation, and relative air humidity, proved nonsignificant in this submodel. This fact does not necessarily mean that they are irrelevant; it only implies that the importance of these covariates, under these conditions, is reduced in contrast to the influence of thermal variables. The notable homogeneity of soil characteristics throughout the study area implies that water-holding capacity is almost invariable. High drainage coefficients render precipitation effects temporary. Finally, the high collinearity between air temperature and relative humidity (controlling water loss through evapotranspiration) could be responsible for this lack of significance.

Predation

The seed predation submodel used in the current study produces monthly predictions of predation probability Pp_{ij} for *P. pinea* seeds through a zero-inflated binomial linear mixed model. The covariates accounting for seed predation described the main environmental trophic characteristics that control predator population: ecosystem primary productivity and *P. pinea* masting habit. Primary productivity was addressed through the monthly physiological drought and the precipitation of the three months prior to predation occurrence. *P. pinea* masting habit was represented by the expected monthly seed production. On the one hand, current drought occurrence and absence of precipitation in previous months negatively affect predator populations, increasing seed survival (Díaz et al. 2010). On the other hand, seed exploitation is also partially mitigated by masting pulses, as per the theory of predator satiation (Salisbury 1942; Janzen 1974). According to this model, the safe period for seeds is restricted to summer months, coinciding with dispersal in the species. Therefore, seed predation becomes a conditional bottleneck: whenever fall germination fails, most dispersed seeds will be destroyed due to total winter exploitation. Only predation by rodents is considered, as seed losses caused by birds can be assumed to be negligible (Manso et al. 2012b).

Seedling survival

To consider mortality of emerged seedlings in the regeneration process, the daily probability P_{sj} of a seedling surviving is predicted through a proportional-hazards regression model. In this model, mortality is strictly dependent on seedling age. The model predicts high mortality rates of seedlings during the first year after emergence, the number of surviving plants remaining almost constant afterwards. This curve basically reflects the strong impact of summer drought on first-year seedlings and the increasing resistance to water stress of the remaining individuals (Calama et al. 2013). As a result of this pattern, only a few individuals from

abundant cohorts that resulted from favourable conditions in all previous phases (fruit production, dispersal, germination, and predation) are likely to persist, which strongly limits recruitment in the species.

The present survival model does not include any variables related to overstory density, and a seedling growth model is not available yet. As a consequence, the multistage model cannot provide predictions of long-term seedling development and seedling response to shade release. Instead, model simulations actually test establishment performance, with an estimation of drought-related mortality.

Given the multiplicative structure of the multistage model, regeneration failure can be triggered by the existence of a bottleneck in any of the sequential subprocesses considered. As the explanatory variables included in the corresponding submodels account for both stand structure and climatic features, bottlenecks must be due to (i) the spatial arrangement and age of mother trees or (ii) the occurrence of adverse climatic conditions. A summary of the covariates included in all models as well as their influence in the corresponding subprocess is shown in Table 1. Details on submodel formulation and parameterization and associated literature citations are provided as Supplementary material.¹⁾

Stochastic simulation

To evaluate the effect of management on recruitment, the described model was used to simulate natural regeneration for different silvicultural alternatives. Specifically, the influence on regeneration of varying stand stocking levels and rotation lengths existing at the beginning of the regeneration period was tested over a 10 year period. To achieve realistic results on final recruitment, mortality was allowed to occur for an additional 10 year period, according to predictions from the weather-independent survival submodel. Moreover, provided that a majority of the subprocesses are climate-mediated, these simulations were conducted both under the current climatic conditions and also under projected scenarios for central Spain in the last third of the 21st century. The A2 emissions scenario, which is the most unfavourable in terms of precipitation reduction and temperature increment (De Castro et al. 2005), was used. This allowed us to test the effect of climatic change on natural regeneration to its full extent. As a starting point, 12 100 m × 100 m fixed plots, where tree location was the result of a Poisson process, were simulated. These plots did not change either across the stochastic simulations of regeneration performance nor across the climatic scenarios considered. Plot features were designed to emulate the typical stand conditions of the end of the rotation within the range of application of all submodels. A buffer strip of 12 m was also taken into account. Single tree development was simulated using the growth module of the software PINEA2 (Calama et al. 2007) projecting up to an age of 80, 100, and 120 years starting from an initial common 20 years old even-aged *P. pinea* stand with 500 stems·ha⁻¹ and site index of 15 m (dominant height at 100 years). Besides rotation length age, simulated plots differed in the thinning schedule applied, which led to stand densities at rotation age of 50, 100, 150, and 200 stems·ha⁻¹, resulting in 12 age × density combinations. Hereafter, stand density refers to the density of mature, seed-bearing trees.

The numerous sources of uncertainty arising from the subprocesses involved in regeneration often render deterministic models insufficient for management purposes. Contrastingly, stochastic models have been reported to be more informative for management, avoiding various prediction biases (Miina and Heinonen 2008). Thus, the regeneration process was stochastically simulated at each of the 12 plots, using scenarios (Rockafellar

and Wets 1987; Valsta 1992) by means of the software RODAL 5.0 (Pukkala 2003–2012). Each scenario consisted of a joint realization of the stochastic processes involved in the model over the planning horizon. Simulation under many scenarios provided a weighted outcome to be used to generate a regeneration probability map for the plot. Therefore, for each of our 12 initial plots, 500 simulations (corresponding to one scenario each) were computed at a 1 m² scale. As a result, 500 boolean regeneration maps were generated where 1 m² quadrats with at least one predicted established seedling were assigned the value of one. Otherwise, a zero value was given. We adopted the threshold of at least 1 seedling·m⁻², because it is a demanding criterion that allows us to test differences in regeneration at the cell level. Note that too low a threshold would lead to regeneration probabilities close to one throughout the 12 plots regardless of the conditions of each simulation (i.e., high number of simulations where the value of one is assigned to most cells).

Finally, the average value over the 500 maps for each quadrat was calculated, producing a regeneration map where the cell value ranged from zero to one, representing the probability of holding at least one seedling at the end of the regeneration period. Additionally, the average probability μ across all 1 m² quadrats and the standard deviation σ of the probability among all quadrats were calculated.

The stochastic scenarios were simulated using the necessary submodels according to the following procedures.

- (i) Climate data: for current climate, data series from seven meteorological stations throughout the study area were used, resulting in a total of 138 annual series of daily climatic records. To produce the data corresponding to predictions for future climate, current climate data were modified according to the specifications given in De Castro et al. (2005; see Table 6.2 therein). In each simulation, 14 annual records were randomly chosen to create a climatic scenario: 4 of them characterized pre-regeneration weather conditions determining seed crops of the first years, whereas the remaining 10 annual series were utilized in all submodels where climate is involved.
- (ii) Cone production submodel: for each chosen annual record, the probability to bear cones was predicted for every tree in the plot. A tree was assumed to produce cones when the predicted probability was higher than a random number generated from a uniform distribution $U(0,1)$. Then, the cone yield of each productive tree was estimated and a random number drawn from the model error distribution, assumed to be normal, with mean zero and model error variance. This random realization was subsequently added to the prediction.
- (iii) Dispersal submodel: for each randomly sampled annual record, cones were assumed open when the monthly mean temperature reached 16 °C. Starting in the month fulfilling this thermal condition, seeds are released and distributed spatially and temporally according to the predictions of the dispersal models. In the spatial dimension, a random realization of a Poisson distribution was added to the number of seeds expected to reach each quadrat. The only parameter of the Poisson distribution coincides with the expected number of seeds.
- (iv) Germination submodel: for every annual record, the probability of dispersed seeds to germinate was predicted at a monthly scale. Stochastic components were included in two ways. First, a realization of the random year effect of the germination model was added to the germination baseline in every evaluated year. Second, the predicted probability of a seed to germinate in a specific interval was compared with a random realization of the uniform

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2013-0179>.

Table 1. Description of the models, submodels, and their respective components used in simulations.

Model	Submodel	Level	Covariates	Effect	Random effect	Time lag
Cone production	occurrence	stand	log(N ^a)	—	plot	year
		tree	d ^b /dg ^c	+		
		site	SI ^d	+		
		temporal (climate)	NU ^e	categorical		
		pp ^f (may to jun 3 ybd)	+			
		pp (oct to nov 3 ybd)	+			
	abundance	stand	log(N)	—	—	—
		tree	D	+		
		site	d/dg	+		
		temporal (climate)	SI	+		
		pp (may to jun 3 ybd)	NU	categorical		
		pp (oct to nov 3 ybd)	+			
Dispersal (spatial)	—	stand	distance to trees	—	—	—
	—	tree	seed production	+	—	—
Dispersal (temp)	—	temporal (climate)	Pp	+	—	month
	—	thermal cut-off	+	—	—	—
Germination	—	stand	IPOT ^h	+	year	day
	—	temporal (climate)	max temperature	Optimal		
	—	time from last frost	+			
Predation	non-occurrence	temporal (climate)	autorregressive term	+	year	month
		drought	—			
	abundance	stand	cumulative pp 3 mbp	+		
		temporal (climate)	seed production	+		
Seedling survival	—	temporal (climate)	drought	+	—	day
	—	—	cumulative pp 3 mbp	—		
—	—	time	+	—	—	—

^aN: stand density.^bd: dbh.^cdg: mean squared dbh.^dSI: site index.^eNU: natural unit.^fpp: precipitation (ybd: years before dispersal; mbp: months before predation).^gfrost: number of days with severe frost.^hIPOT: influence potential (competition index).**Table 2.** Changes in mean temperature (°C) and total precipitation (%) under the A2 climatic scenario in the Central Iberian Peninsula projected for the last third of the 21 st century.

	Dec. to Feb.	Mar. to May	Jun. to Aug.	Sep. to Nov.
Temperature	+3.7	+4.6	+5.9	+4.9
Precipitation	-21.6	-40.8	-48.7	-26.2

distribution $U(0,1)$. Germination was assumed to occur when the predicted probability was larger than the generated random number.

- (v) Predation submodel: dispersed and nongerminated seeds are vulnerable to predation. For a specific meteorological annual record, the predation model predicted first the monthly probability of having total predation in a 1 m² quadrat. This probability was compared with a random number sampled from the uniform distribution, and total predation was assumed if the predicted probability was higher than the random realization. Conditional to quadrat-level survival, the probability of each seed to survive for that month was predicted and randomized through the same procedure, given its binomial nature. An additional source of stochasticity was the random year effect on both processes within the model. As the estimated covariance of both random components is nonnull, randomization cannot be carried out directly using uncorrelated random number generation. Therefore, a Cholesky decomposition of the variance-covariance matrix of the year effects was

calculated and then multiplied by a 2×1 matrix whose rows represented uncorrelated random realizations from two normal distributions of mean zero and variances equalling one (sensu Ripley 1987). The two values of the resulting matrix were used as correlated year effects in both parts of the model.

- (vi) Seedling survival submodel: the number of seedlings from different monthly cohorts was reduced uniformly across quadrats over time according to the climate-independent predictions from the survival submodel. No randomization was carried out in this model.

Stochastic optimization

Besides evaluating the impact of silvicultural treatments applied through the cycle on regeneration via simulations, scheduling of regeneration felling can be optimized to maximize the regeneration result.

Initial stand

A 250 stems·ha⁻¹ stand 1 ha in size with a bimodal diameter distribution was simulated. The diameter distribution resulted from the mixture of two normal distributions of mean 20 and 40 cm and standard deviation 3 and 7 cm, respectively. Two-thirds of the diameters were sampled from the first distribution, whereas the rest were randomly selected from the second one. Lower diameters were assigned to those trees standing in denser positions. The coordinates of 80 trees were generated by a Poisson process. Subsequent tree locations were identically simulated, but

the position was only retained when the distance to the closest tree was less than a random realization of a Weibull distribution (shape parameter = scale parameter = 1), leading to an aggregated distribution of trees. Such an initial complex stand provides a convenient framework for the optimization routine to make decisions as a function of tree size and location.

Objective function

A function was defined to represent the features of interest for managers concerning natural regeneration. Regeneration was expected to be successful when it was abundant and evenly distributed. These two features were summarized by the following objective function (OF):

$$(3) \quad OF = \mu + (1 - \sigma)$$

with μ and σ being defined in the Regeneration model section above. In the most favourable case of all quadrats holding an empirical probability of 1, OF equals 2, which is its maximum value. When linearly including μ in the OF, we are assuming that maximization of the probability of achieving at least 1 seedling·m⁻² is optimal. This assumption matches the criterion adopted by managers, given the current difficulties for regeneration and the low probability of seedling overstocking (Gordo et al. 2012). Generally, higher values of μ imply better average conditions for regeneration in the stand, whereas lower values of σ indicate a more even distribution of seedling throughout the considered space.

Decision variables

A management schedule is defined by a set of controllable variables, called decision variables. Optimization of decision variables leads to an optimum management schedule that, in the case of this study, maximizes the probability of abundant and uniform natural regeneration. The chosen decision variables determined the felling intensity during the regeneration period, and the sequence in which trees are removed in fellings. The sequence depended on the size and spatial distributions of trees. Decision variables were chosen to take into account the main stand conditions affecting regeneration. The tree-selection algorithm developed by Pukkala et al. (1998) and modified for optimization purposes by Pukkala and Miina (1998) was adopted. When using the original algorithm, tree *dbh* and tree height are used to define the harvesting order, the less competitive trees being cut first. The aforementioned modification includes two parameters b_1 and b_2 representing continuous variables. They are inserted in the algorithm as powers of tree *dbh* and tree height, respectively, providing a higher degree of flexibility in felling tree selection. For instance, when both b_1 and b_2 are large, small trees tend to be removed from dense locations, whereas small b_1 and b_2 values indicate that large trees are to be logged if they overtop small trees. These parameters are also optimized along with the other decision variables, which in turn makes it possible to accommodate the optimal spatial organisation of tree diameter with regard to regeneration. The number of fellings (N_{fell}) was not optimized, but a feasible schedule was set consisting of two operations taking place in the first and fifth year of the regeneration period, respectively ($N_{\text{fell}} = 2$). In summary, decision variables implemented in the present optimization problem were felling intensity (in percentage of removed trees) and parameters b_1 and b_2 , which yields $N_{\text{fell}} + 2$ decision variables.

Optimization method

The optimization algorithm utilized in this problem was the direct search method of Hooke and Jeeves (1961). This method does not require the use of derivatives and therefore is appropriate for nonsmooth and nondifferentiable objective functions. It consists of two differentiated steps: exploratory search and pat-

tern search. From a user-defined starting base point, the exploratory search alternately looks for the best solution in the direction of the coordinate axes by altering one decision variable at a time. This procedure basically provides a direction defined by the original base point and the best solution found by exploratory search. Then, pattern search moves the base point along this new direction and the process is repeated again. The step size is reduced when the search does not find a better solution in the next move. Convergence is assumed to occur when step size is lower than a certain proportion (0.001 in this study) of the initial step size for all decision variables. Each search-move implies a call to the simulator, which evaluates the value of the objective function with the information provided by the optimizer based on 500 scenarios. To test the effect of using different starting points, optimization was initialized from two different base points, defined by two sets of decision variables. The first of them corresponds to light cuttings from below (intensity of fellings of 10% and 20%, respectively; $b_1 = 1$ and $b_2 = 2$). The second starting point was set to be representative of intensive high cuttings (intensity of fellings of 70% and 50%; $b_1 = -1$ and $b_2 = -2$). The two different initializations lead to two separate optimizations. The optimizations were assessed through the software RODAL 5.0.

Results

Stochastic simulations

Effect of stand structure

The mean probability of holding at least one seedling·m⁻² (μ) after a 10 year period increased with both stand density and rotation age (Figs. 1 and 2a). The increment in μ was lower as the tested stand densities became larger, with a tendency to level off when stand density was higher than 150 stems·ha⁻¹. This pattern was similar for all rotation ages, the effect of which was basically to intensify the effect of stand density in the same proportion for all situations. The mean values of μ over the 3 rotation lengths, were 0.50 for overstory densities of 50 stems·ha⁻¹, 0.74 for 100 stems·ha⁻¹, 0.82 for 150 stems·ha⁻¹, and 0.85 for 200 stems·ha⁻¹.

F1-F2

Concerning the degree of aggregation of the established seedlings, measured by the standard deviation of the probability of holding at least one seedling·m⁻² at quadrat level (σ), there was a trend for aggregation to decline as stand density increased. σ values started to level off at densities as high as 150 stems·ha⁻¹. The mean values of σ across rotation ages were 0.23 for 50 stems·ha⁻¹, 0.11 for 100 stems·ha⁻¹, 0.06 for 150 stems·ha⁻¹, and 0.06 for 200 stems·ha⁻¹. However, no clear pattern arose in regard to all rotation age.

Effect of climate

Simulations under the A2 climatic scenario revealed that climate change would presumably influence natural regeneration of *P. pinea*. The effect of future climate is mainly evidenced by higher μ values than those predicted for the current climate. This increment occurs with decreasing densities and increasing ages when considering rotations of 80 and 100 years. Under a future climate, densities over 50 stems·ha⁻¹ showed reductions in μ (Table 3; Figs. 2b and 3). Overall, μ reached its maximum A2 climate scenario values of 0.74 and 0.82 with 80 and 100 year rotation lengths, respectively. Levelling off was appreciable at stand densities as low as 100 stems·ha⁻¹, and μ even tended to decrease beyond 150 stems·ha⁻¹. On the contrary, for the longest rotation of 120 years, μ exceeded 0.90 at the highest stocking. In contrast, σ values underwent little change under the A2 climatic scenario, compared to the current climate.

T3

F3

Regeneration optimization

The optimization algorithm converged for the first initial point, representing light cuttings from below, when the objective function was OF = 1.6608 ($\mu = 0.8250$, $\sigma = 0.1642$). This maximum of the

Fig. 1. Maps of the simulated probabilities of achieving at least one established seedling per 1 m² in 100 m × 100 m plots at the end of the regeneration period for varying stand densities and rotations under current climatic conditions. Dark colours (dark shades in the print version) indicate higher probability whereas light colours (shades) denote lower probability. Circle positions represent tree locations, and circle size is proportional to a tree's *dbh*. μ and σ are, respectively, the mean and standard deviation of the probability among 1 m² quadrats. $OF = \mu + (1 - \sigma)$.

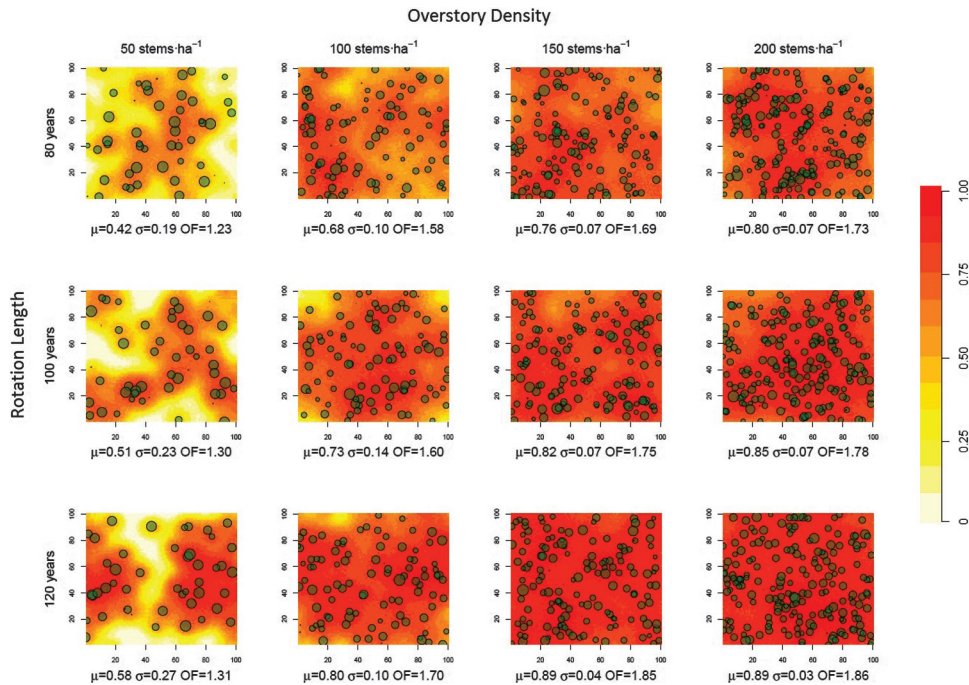
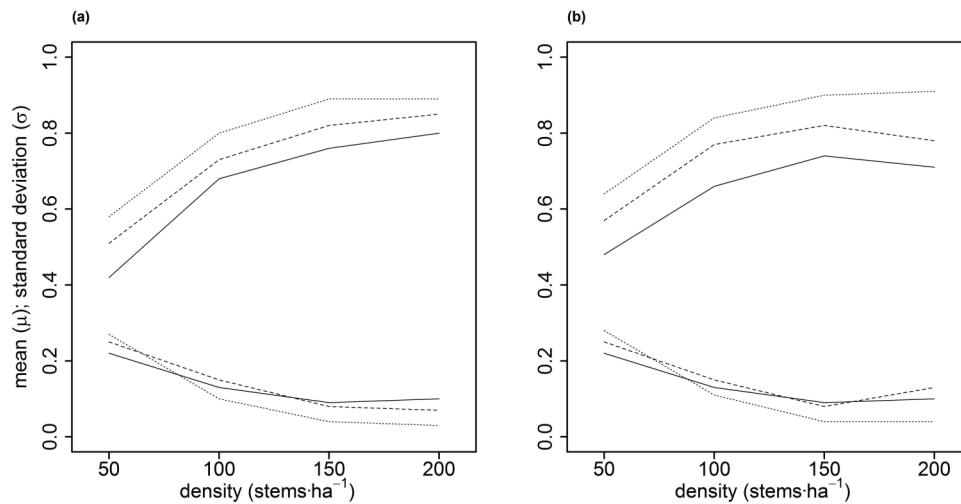


Fig. 2. Mean (μ , higher lines) and standard deviation (σ , lower lines) probability of establishment for varying stand densities and rotation lengths (dotted line, 120 years; dashed line, 100 years; solid line, 80 years) under (a) current and (b) potential future (A2 scenario) conditions.



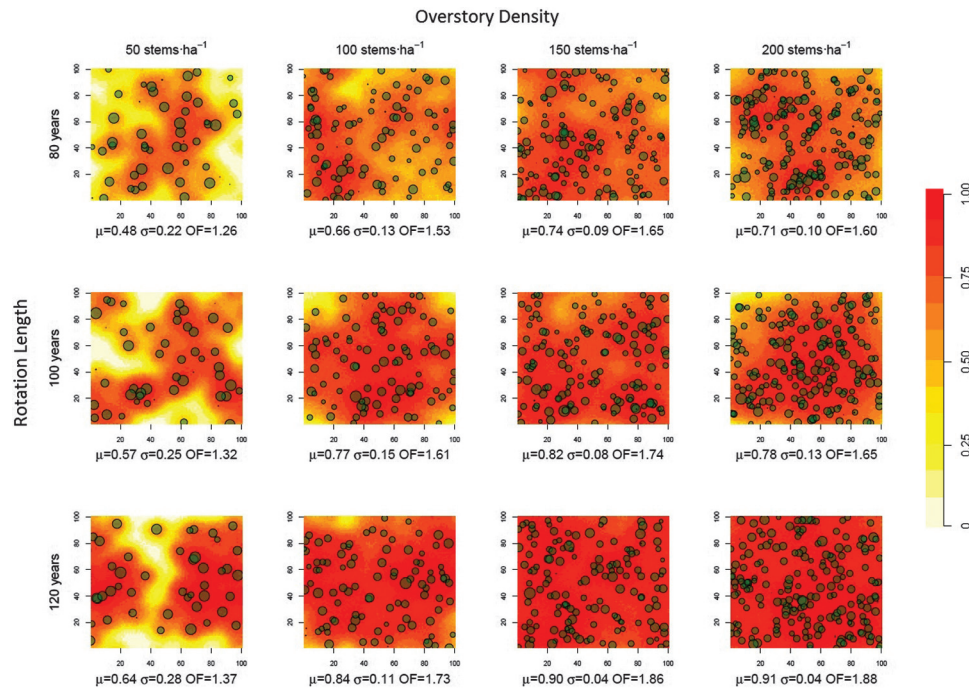
objective function corresponds to optimized decision variables denoting fellings intensities of 30.16% and 18.75%, for the first and second fellings, respectively, and $b_1 = 1$ and $b_2 = 4$, implying that small trees are to be removed from dense places. Concerning the second starting point, two intensive high cuttings, the maximized value of the objective function was $OF = 1.6298$ ($\mu = 0.7998$, $\sigma = 0.1700$), which implied intensity fellings of 20.00% and 12.50%, respectively, and $b_1 = 1$ and $b_2 = 0.75$, as the optimal solution. In both cases the optimal scheme for achieving natural regeneration included a slight reduction of the initial stand density and an even less intensive second felling, both of them removing thinner trees located in the densest areas (Figs. 4 and 5). The progress of the objective function and the decision variables over the iterative

Table 3. Variation in predicted mean probability of establishment between A2 climate and current climate relative to the current mean ($(\mu_{A2} - \mu_{Current})/\mu_{Current}$) for different stand densities and rotation lengths.

Rotation length (year)	Overstory density (stems ha ⁻¹)			
	50	100	150	200
80	0.145	-0.033	-0.029	-0.113
100	0.124	0.052	-0.003	-0.079
120	0.112	0.056	0.015	0.027

Note: Negative values represent decreasing future probabilities and positive values denote increasing future probabilities.

Fig. 3. Maps of the simulated probabilities of achieving at least one established seedling per 1 m² in 100 m × 100 m plots at the end of the regeneration period for varying stand densities and rotations under projected climatic conditions in the A2 scenario. Circle positions represent tree locations and circle size is proportional to a tree's *dbh*. Dark colours (dark shades in print version) indicate higher probability whereas light colours (shades) denote lower probability. μ and σ are, respectively, the mean and standard deviation of the probability among 1 m² quadrats. OF = $\mu + (1 - \sigma)$.



process is shown in Fig. 6. The provided light-management initial solution was found to be a close-to-optimal solution, as the objective function did not substantially improve through the optimization. Only the intensity of the first felling and the b_2 parameter changed to some extent from the starting point, rapidly stabilizing after the first moves of the direct search. In contrast, when started from the intensive-management solution, the algorithm iterated up to 20 times before the objective function levelled off, the initial values of decision variables being noticeably modified.

Discussion

We have presented the development and results of a stochastic multistage model for natural regeneration in *P. pinea*. This model specification (i) renders the estimation of the transition probabilities highly flexible across a continuous range of relevant ecological inputs and (ii) enables simulations of seedling establishment under different climatic scenarios and management alternatives. In addition, the further implementation of an optimization algorithm based on the model represents a novel tool for decision making in managed *P. pinea* stands.

Stochastic simulations and stochastic optimization

Model simulations suggested that stand densities below 150 stems·ha⁻¹ at the beginning of the regeneration period may be suboptimal for attaining an adequate number of emerged seedlings in a 10 year period (i.e., attaining high μ values), mainly due to dispersal limitations and seed shortage. Similarly, stocking levels above the aforementioned value do not appear to improve μ , revealing the effect of declining cone production at high stand densities (Calama et al. 2011). In contrast, spatial variability of regeneration (σ) varied less among different stockings (the higher density of mature trees, the lower σ ; Figs. 3a and 3b). In the light of these results, μ seems to be strongly dependent on factors driving seed production and dispersal, whereas σ is related to the spatial arrangement of parent trees. This fact is also observed when con-

sidering the effect of rotation length, which only affects μ ; shorter rotations (i.e., 80 years) would reduce μ due to seed limitation because younger trees are less productive (Calama et al. 2011).

The best results for natural regeneration during a 10 year period are attained for the longest rotation tested (120 years; $\mu = 0.89$, $\sigma = 0.04$) when stand density was 150 stems·ha⁻¹. In spite of not being directly comparable because of the different survey standards, this result is clearly better than records from manager inventories under the current felling schedules, in which seedling density was below 200 seedlings·ha⁻¹ ($\mu = 0.02$) in 44% of the surveyed area, and only in 10% it was over 1600 seedlings·ha⁻¹ ($\mu = 0.16$), as mentioned in Gordo et al. (2012).

The results from the optimizations carried out in the first and fifth year of the regeneration period under a specific showed that the optimal stand density with regard to natural regeneration is 150 stems·ha⁻¹. This fact confirms the findings of the above-mentioned simulations. Specifically, the optimization initialized with the first set of parameters (representing light cuttings from below) led to optimized fellings that reduced the initial stand density (250 stems·ha⁻¹) by 39% (leaving 152 stems·ha⁻¹). Similarly, the second optimization (representing intensive high cuttings) yielded a stand density reduction of 32.5% (leaving 162 stems·ha⁻¹). Nevertheless, it needs to be noted that the optimization routines run considering two fixed harvesting operations, and that the simulations were carried out under a limited number of management alternatives.

From a spatial perspective, final b_1 and b_2 values indicate that fellings should remove small trees from dense areas in both cases. Seed production and dispersal subprocesses mainly drive this behaviour. On the one hand, smaller trees are potentially less productive and account for a decrease in the productivity per tree at the stand level (Calama et al. 2011); hence, they are to be cut rapidly. On the other hand, trees located in open areas should remain (Figs. 4 and 5), even if their seed production is low, given the short dispersal distances of the species (Manso et al. 2012c), as

Fig. 4. Optimized order of tree logging for the optimization initialized from close-to-optimal initial values. In (a), circle sizes and colours represent the logging order (larger and darker circles are to be cut first); in (b) and (c), circle sizes are proportional to a tree's *dbh*, and darker circles stand for the logged trees in the first and second harvest operation, respectively.

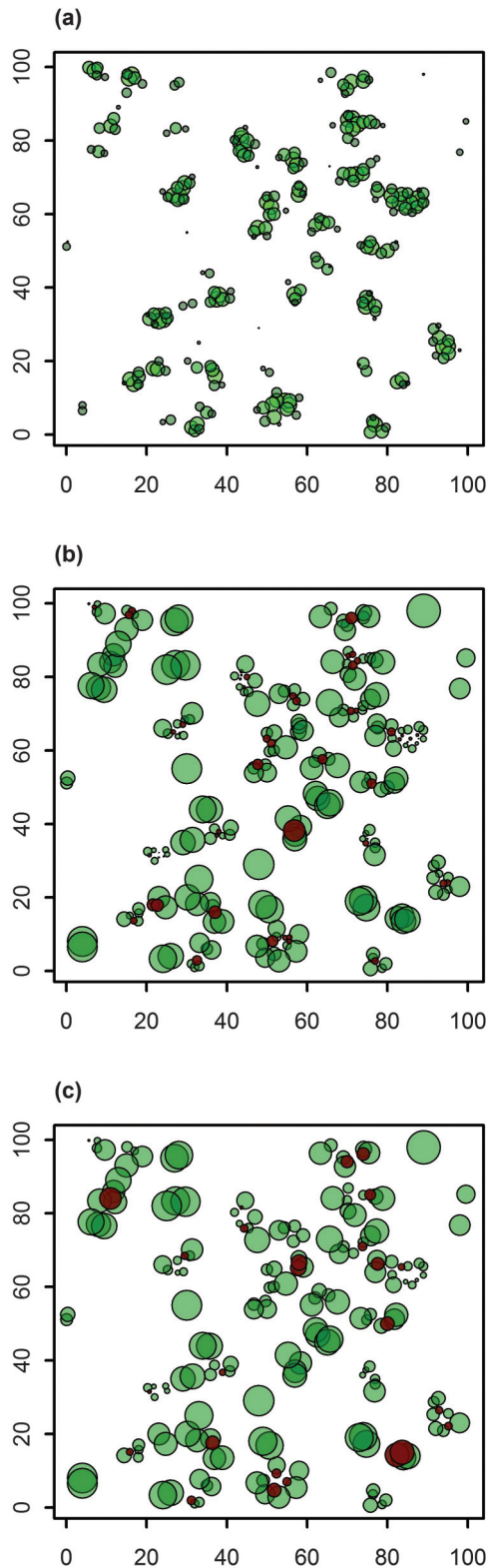


Fig. 5. Optimized order of tree logging for the optimization initialized from sub-optimal initial values. In (a), circle sizes and colours represent the logging order (larger circles and darker are to be cut first); in (b) and (c), circle sizes are proportional to a tree's *dbh* and darker circles stand for the logged trees in the first and second harvest operation, respectively.

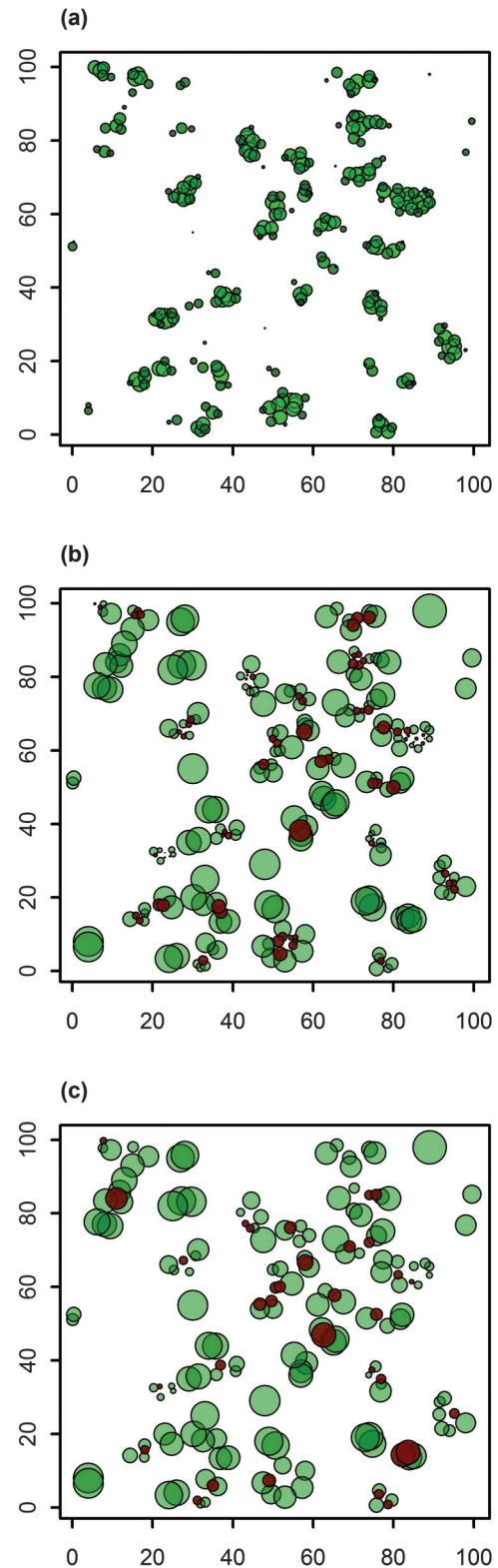
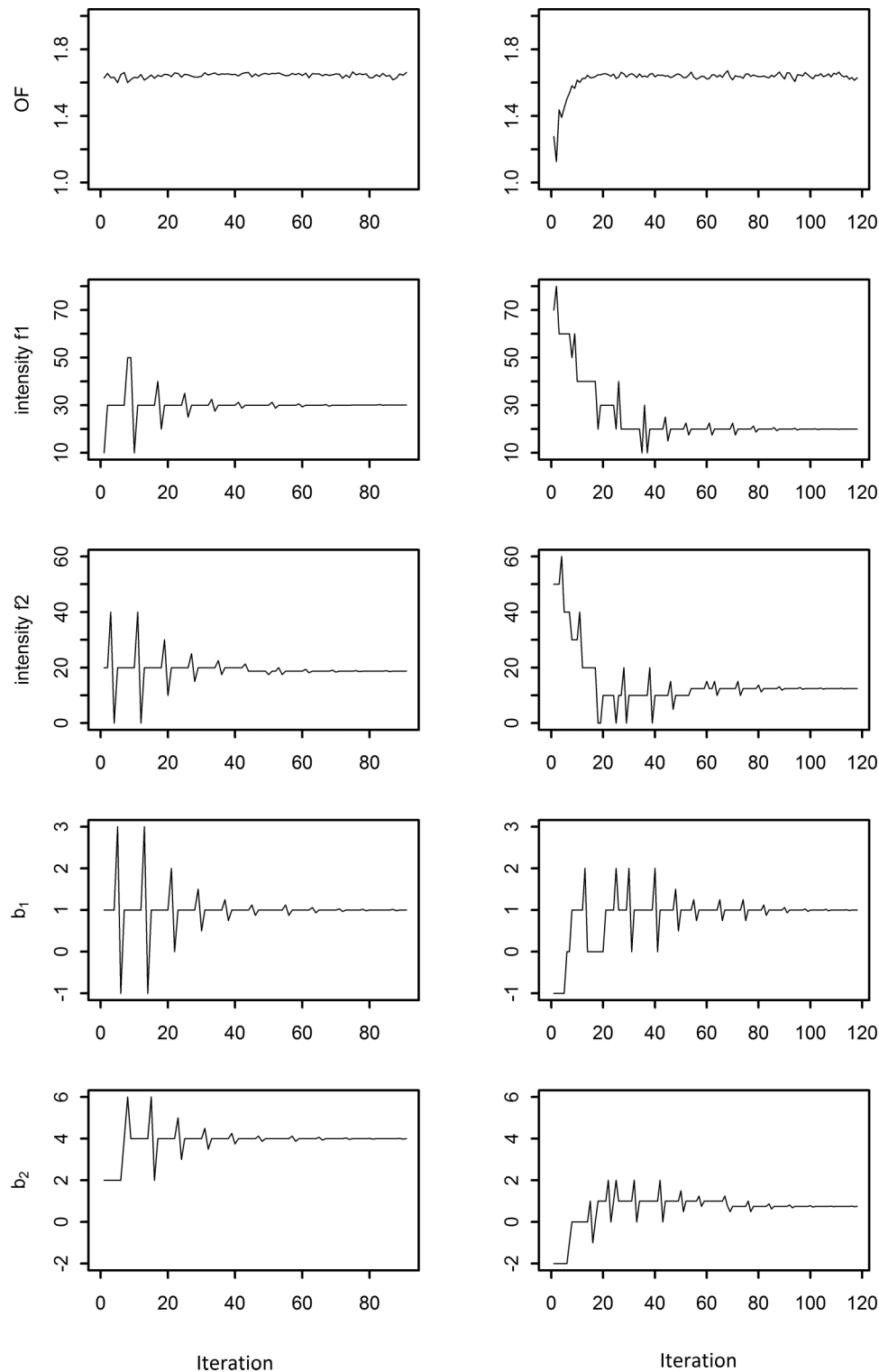


Fig. 6. Evolution of the utility function (OF) and decision variables (felling intensities and parameters, b_1 and b_2) through iterations in the optimization initialized from close-to-optimal (left) and the optimization initialized from sub-optimal values of decision variables (right).



the final seedling distribution should be as uniform as possible. In contrast, under economic optimization for timber production, the optimal values of b_1 and b_2 usually lead to the removal of large trees first (Pukkala and Miina 1998).

The two optimizations initialized from different starting points led to final management schedules that were qualitatively equivalent, although not exactly the same. This is because the algo-

rithm used does not necessarily converge to the global optimum (Miina 1998). There are two particularities in this study that potentially can hamper the determination of an absolute maximum. On the one hand, the remarkable degree of stochasticity involved in the regeneration process implies that every call to the simulator may result in highly varying values of the objective function, even for identical values of the decision variables. This drawback

was counteracted by using a high number of simulations (500) in each call. On the other hand, estimated transition probabilities are generally positively related to stand density. Therefore, several combinations of felling intensity may lead to nearly identical values for the objective function, so long as the cuttings are light enough to just cancel out the unfavourable effect of over-dense stands in seed production. In other words, instead of a single optimal solution, there may be a range of possible solutions leading to a final stand density around 150 stems·ha⁻¹. The same applies for b_1 and b_2 parameters; given that few subprocesses are controlled by spatial covariates, only the positive effect of age (*dbh*) on seed production and the clustered distribution of dispersal can inform the parameter values.

The objective function used in the present optimization problem combines two features of interest for regeneration: the mean (μ) and the standard deviation (σ) of the probability of regeneration for a given plot at 1 m² precision. Although these two variables are obviously correlated, neither can be neglected. Whereas very high values of μ will lead unequivocally for σ to be null, lower μ values are possible under different spatial distributions of seedlings (varying σ), some being more adequate than others. Nevertheless, caution must be taken when using this objective function below realistic stand densities and spatial arrangements. The relationship between μ and σ is not monotonic for the full domain of the two variables, but was found to be always decreasing within the range used in the present study (μ over 0.35).

Implications for management

The current management of *P. pinea* in the study area focuses primarily on pine seed production for the purposes of harvesting edible seeds. Consequently, stands reach the regeneration period with very low densities ranging from 80 to 125 stems·ha⁻¹ at age 80–100 years. According to Montero et al. (2008), the shelterwood method is then applied to regenerate the stands, consisting of two intensive fellings (50% reduction of the remaining trees) to be carried out between the first and the 10th year of the regeneration period (preparatory felling and seeding felling) and a final felling that extracts the few stems still standing in the 20th year. This scheme strongly contrasts with the results of this paper for an adequate management scheduling.

In fact, given that stand density at the beginning of the regeneration period is normally below 150 stems·ha⁻¹, no preparatory or even secondary fellings should be conducted. Afterwards, the initial stand density should be maintained as long as needed, until the occurrence of successful establishment events. Actually, earlier forest managers in the region at the end of the 19th century were already aware of this circumstance (Romero 1886). Despite the good results achieved in terms of number of recruits, problems were detected concerning the viability of these saplings in the 1960s. These problems were attributed to an excess of shade, promoting an artificial regeneration-based silviculture model, including strip clearcuttings (Gordo 1999). Indeed, seedlings need to be released from overstorey shade at some point, which implies that a longer maintenance of relatively high stocking levels would not necessarily be better for natural regeneration (Smith et al. 1996). However, the medium shade-tolerant behaviour exhibited by *P. pinea* (Awada et al. 2003) suggests that seedlings can tolerate relatively high stand densities for at least a few years, these stocking levels favouring the establishment of new recruits. Subsequently, parent trees should be progressively removed to release those cohorts as their light requirements increase (Smith et al. 1996). The present multistage model does not include a seedling survival submodel that takes into account the shading effect on long-term established seedlings. Similarly, a seedling growth submodel to consider the effect of shade release is not currently available. Further improvements in this respect will make it possible to optimize also the progressive removal of the remaining trees, as their role as a constraining factor for regeneration be-

comes more important than their beneficial effects as a seed source (Manso et al. 2013) and shelter (Calama et al. 2012).

Concerning rotation length, the currently used rotations are also often below the optimal (120 years). It is not uncommon that regeneration in managed forests is perceived as unsuccessful because rotation lengths are too short (Tiscar-Oliver 2007; Kerr et al. 2008). In these cases, if parent trees were allowed to remain longer (increasing the length of the regeneration period as well as seed production per tree), the probability of establishment will increase, overcoming the effect of the various factors responsible for the reduction in the transition probabilities or even the system's collapse due to a bottleneck in one or several subprocesses. Moreover, even for optimal rotation lengths, the enormous stochasticity of the process and (or) shorter rotation lengths may lead to repeated failures over a longer time interval, and therefore flexibility will be needed to delay the planned cuttings after favourable regeneration events. Similarly for those locations of very low site quality, longer periods might be required. A high degree of stochasticity in unfavourable conditions for regeneration was also found for Mediterranean *Pinus nigra* by Tiscar-Oliver (2007), who also concluded that more flexible timing of fellings (discontinuous fellings) were required to guarantee successful recruitment. As a consequence, if the regeneration period needs to be extended over 20 years in *P. pinea*, a semi-even-aged stand structure would typically be expected. Interestingly, this management schedule has been marginally attempted in our study area for *P. pinea*, achieving reasonably good results (Finat et al. 2000).

From a spatial perspective, our results coincide with current silviculture practices. The present cone production-oriented management regime highlights the importance of maintaining large trees as evenly distributed as possible (Montero et al. 2008). The proposed optimized silvicultural scheme maximizes seedling density. Given that the probability of densities over 1 seedling·m⁻² in the simulations is only over 0.95 in 13% of the cases for the optimal schedule, an excess of seedlings is not expected. Should that happen, subsequent thinning operations can reduce sapling densities, the treatment being much more affordable than those of soil preparation, direct seeding, and the related early thinnings.

Application of the multistage model using simulated climatic data for the A2 scenario did not reveal worse natural regeneration performance. On the contrary, the mean probability of establishment increased in most tested circumstances. These findings can be explained in the light of the specific impact of changing climate in the different climate-mediated subprocesses. The first of them, seed production, is notably sensitive to precipitation reduction and consequently fewer mast events and less abundant crops are expected. However, this negative effect is counter-balanced by expectation of a longer annual predation-free period linked to rainfall decrease (Manso et al. 2012b). Consequently, predation may be a less severe limiting factor, as seeds would be available to germinate during a wider period. Germination, however, is only thermally mediated; on the one hand it is not negatively affected by rainfall variations and on the other hand, it is likely to be favoured by a decrease in the incidence of frost. Consequently, suitable conditions for germination would be more probable, and they would last longer. Unfortunately, the survival model does not explicitly include any climatic variable, so the impact of increasing summer drought on seedling survival is unknown. Therefore, we only can state that sensible management of seed production (extending rotation length) and dispersal (maintaining adequate stocking) can mitigate the impact of climate change, at least on seedling establishment of *P. pinea*. In any event, these recommendations also apply to the current climate; emphasis should be given to rotation length and scheduling flexibility. These measures are compatible with the general recommendations for adaptive silviculture in Mediterranean forests in a context of climatic change (Lindner et al. 2008). Whereas future conditions will promote increasing growth in boreal and moun-

tainous forests and therefore shortening of rotation lengths may be a suitable adaptive measure (Kellomäki et al. 1997; García-Gonzalo et al. 2007), the negative impact of drought on growth in the Mediterranean suggests the opposite silvicultural strategy. Moreover, when silviculture aims at natural regeneration, shortened rotations are generally regarded as inadequate (Lindner et al. 2008). Nevertheless, the conclusions from our study must be considered prudently. First, although precipitation reduction appears to be a beneficial factor for natural regeneration, water shortage may also result in negative effects on tree growth (Lindner et al. 2008). These circumstances indirectly affect regeneration through seed production, modulating the effect of rotation length on natural regeneration. Second, predator-prey relationships, represented in this case by the pressure exerted by rodents on *P. pinea* seeds, consist of complex interactions (Kratina et al. 2009), and therefore predictions based on current behaviour cannot simply be extrapolated. Third, the effect of more intense drought on seedling survival is unknown, although seedling performance is likely to worsen (Valladares et al. 2005; Calama et al. 2012). Finally, future climate conditions used in this study are the result of model projections, and therefore they are subject to some degree of uncertainty (De Castro et al. 2005). In this respect, an advantage of the proposed stochastic model is that it can accommodate all feasible scenarios, likewise providing multiple solutions for different problems. This is known as flexible adaptive planning, and it has been stated to be an optimal alternative among forest planning strategies (von Gadow 2000).

Overall, natural regeneration of *P. pinea* in the Northern Plateau of Spain appears to be a reachable target, as long as management is adequate. In addition, the acceptable behaviour exhibited by the species concerning natural regeneration in a context of climate change, together with its capacity to adapt to demanding environments, makes *P. pinea* a potentially resilient species of remarkable interest throughout areas in the Inner Iberian Peninsula that are susceptible to aridification.

Acknowledgements

We are grateful to all researchers, technicians, forest managers, and students involved in *P. pinea*-related INIA projects during the last 20 years. Their selfless time devoted to the study of the species has made this work possible. Specifically, we wish to thank the Forest Service of the Junta de Castilla y León for permission and support to carry out the field experiments and particularly to Francisco Javier Gordo. Also, we would like to express our gratitude to Gregorio Montero and Sven Mutke, who are behind most former and present *P. pinea* researching initiatives in Spain and to Guillermo Madrigal, Enrique Garriga, Santiago de Blas, and Mar Conde for helping with data collection and experiment maintenance. Finally, we acknowledge the helpful comments and edits of two anonymous reviewers and the journal's Associate Editor. This specific research was supported by projects AGL2010-15521, S2009-AMB1668, and RTA2007-00044.

References

Agrimi, M., and Ciancio, O. 1993. Le pin pignon (*Pinus pinea* L.). *Silva Mediterranea*. Comité des questions forestières méditerranéennes. FAO.

Awada, T., Radoglou, K., Fotelli, M.N., and Constantinidou, H.I.A. 2003. Ecology of seedlings of three Mediterranean pine species in contrasting light regimes. *Tree Physiol.* 23(1): 33–41. doi:10.1093/treephys/23.1.33. PMID:12511302.

Barbeito, I., Pardos, M., Calama, R., and Cañellas, I. 2008. Effect of stand structure on Stone pine (*Pinus pinea* L.) regeneration dynamics. *Forestry*, 81(5): 617–629. doi:10.1093/forestry/cpn037.

Barbeito, I., LeMay, V., Calama, R., and Canellas, I. 2011. Regeneration of Mediterranean *Pinus sylvestris* under two alternative shelterwood systems within a multiscale framework. *Can. J. For. Res.* 41(2): 341–351. doi:10.1139/X10-214.

Calama, R., Sanchez-Gonzalez, M., and Montero, G. 2007. Integrated management models for Mediterranean multifunctional forests: the case of stone pine (*Pinus pinea* L.). *EFI Proceedings*.

Calama, R., Gordo, F.J., Mutke, S., and Montero, G. 2008. An empirical ecological-type model for predicting stone pine (*Pinus pinea* L.) cone production in the

Northern Plateau (Spain). *For. Ecol. Manage.* 255(3–4): 660–673. doi:10.1016/j.foreco.2007.09.079.

Calama, R., Mutke, S., Tomé, J., Gordo, J., Montero, G., and Tomé, M. 2011. Modelling spatial and temporal variability in a zero-inflated variable: The case of stone pine (*Pinus pinea* L.) cone production. *Ecol. Model.* 222(3): 606–618. doi:10.1016/j.ecolmodel.2010.09.020.

Calama, R., Madrigal, G., Manso, R., Garriga, E., Gordo, F.J., and Pardos, M. 2012. Germinación, emergencia y supervivencia de regenerado en *Pinus pinea* L. In *La regeneración natural de los pinares en los arenales de la Meseta Castellana*. Edited by J. Gordo, R. Calama, M. Pardos, F. Bravo, and G. Montero. Instituto Universitario de Investigación en Gestión Forestal Sostenible (Universidad de Valladolid-INIA), Valladolid.

Calama, R., Puértolas, J., Madrigal, G., Manso, R., and Pardos, M. 2013. Modelización fisiológica de la supervivencia del regenerado de *P. pinea* L: efecto de los factores ambientales. In *6º Congreso Forestal Español*. Edited by Sociedad Española de Ciencias Forestales, Vitoria, Spain.

De Castro, M., Martín-Vide, J., and Alonso, S. 2005. The climate of Spain: past, present and scenarios for the 21st century. Ministerio de Medio Ambiente.

Díaz, M., Torre, I., and Arribalaga, A. 2010. Relative roles of density and rainfall on the short-term regulation of Mediterranean wood mouse *Apodemus sylvaticus* populations. *Acta Theriol.* 55(3): 251–260. doi:10.4098/j.at.0001-7051.046.2009.

Eerikainen, K., Miina, J., and Valkonen, S. 2007. Models for the regeneration establishment and the development of established seedlings in uneven-aged, Norway spruce dominated forest stands of southern Finland. *For. Ecol. Manage.* 242(2–3): 444–461. doi:10.1016/j.foreco.2007.01.078.

Ferguson, D.E., Stage, A.R., and Boyd, R.J. 1986. Predicting regeneration in the grand fir-cedar-hemlock ecosystem of the Northern Rocky Mountains. *For. Sci. Monogr.* 26.

Finat, L., Campana, V., and Seseña, A. 2000. La ordenación por entresaca en las masas de piñonero de la provincia de Valladolid. In *I Simposio del pino piñonero (Pinus pinea L.)*. Edited by Junta de Castilla y León, Valladolid. pp. 147–157.

Fortin, M., and DeBlois, J. 2007. Modeling tree recruitment with zero-inflated models: The example of hardwood stands in southern Quebec, Canada. *For. Sci.* 53(4): 529–539.

García-Gonzalo, J., Peltola, H., Briceño-Elizondo, E., and Kellomäki, S. 2007. Effects of climate change and management on timber yield in boreal forests, with economic implications: A case study. *Ecol. Model.* 209: 220–234. doi:10.1016/j.ecolmodel.2007.06.021.

González-Olabarria, J.R., Palahí, M., Pukkala, T., and Trasobares, A. 2008. Optimising the management of *Pinus nigra* Arn. stands under endogenous risk of fire in Catalonia. *Investigacion Agraria-Sistemas y Recursos Forestales*, 17(1): 10–17.

Gordo, F. 1999. Ordenación y silvicultura de *Pinus pinea* L. en la provincia de Valladolid. In *Ciencias y técnicas forestales. 150 años de aportaciones de los ingenieros de montes* Edited by Fundación Conde del Valle de Salazar, Madrid. p. 638.

Gordo, F.J., Rojo, L.I., Calama, R., Mutke, S., Martín, R., and García, M. 2012. Silvicultura de regeneración natural de *Pinus pinea* L. en montes públicos de la provincia de Valladolid. In *La regeneración natural de los pinares en los arenales de la Meseta Castellana*. Edited by J. Gordo, R. Calama, M. Pardos, F. Bravo, and G. Montero. Instituto Universitario de Investigación en Gestión Forestal Sostenible (Universidad de Valladolid-INIA), Valladolid. p. 254.

Hooke, R., and Jeeves, T.A. 1961. "Direct search" solution of numerical and statistical problems. *J. Assoc. Comput. Mach* 8: 212–229. doi:10.1145/321062.321069.

Janzen, D.H. 1974. Tropical blackwater rivers, animal and mast fruiting by the Dipteroocarpaceae. *Biotropica*, 4: 69–103. doi:10.2307/2989823.

Kellomäki, S., Karjalainen, T., and Väisänen, H. 1997. More timber from boreal forests under changing climate? *For. Ecol. Manage.* 94: 195–208. doi:10.1016/S0378-1127(96)03975-8.

Kerr, G., Gosling, P., Morgan, G., Stokes, V., Cunningham, V., and Parratt, M. 2008. Seed production and seedling survival in a 50-year-old stand of Corsican pine (*Pinus nigra* subsp. *laricio*) in southern Britain. *Forestry*, 81(4): 525–541. doi:10.1093/forestry/cpn026.

Kratina, P., Vos, M., Bateman, A., and Anholt, B.R. 2009. Functional responses modified by predator density. *Oecologia*, 159(2): 425–433. doi:10.1007/s00442-008-1225-5. PMID:19034528.

Leak, W.D. 1968. Birch regeneration: a stochastic model. *U.S. Forest Service Research NE-85*.

Lindner, M., García-Gonzalo, J., Kolström, M., Green, T., Reguera, R., Maroschek, M., Seidl, R., Lexer, M.J., Netherer, S., Schopf, A., Kremer, A., Delzon, S., Barbati, A., Marchetti, M., and Corona, P. 2008. Impacts of climate change on European forests and options for adaptation. *EFI, BOKU, INRA, IAFS, Joensuu*.

Manso, R., Calama, R., Madrigal, G., Conde, M., Gordo, F.J., and Pardos, M. 2012a. Supervivencia del regenerado en *Pinus pinea* L. en la Meseta Norte. Previsiones en un contexto de cambio climático. In *V Reunión del Grupo de Trabajo de Silvicultura de la Sociedad Española de las Ciencias Forestales (SECF) "Regeneración natural y cambio global"*. Edited by R. Ruiz-Peinado, J. Reque, and R. Serrada. Sociedad Española de Ciencias Forestales, Madrid.

Manso, R., Calama, R., Madrigal, G., Garriga, E., De Blas, S., Gordo, F.J., and Pardos, M. 2012b. Dispersión primaria, dispersión secundaria y predación post-dispersión en *Pinus pinea* L. In *La regeneración natural de los pinares en*

- los arenales de la Meseta Castellana. Edited by J. Gordo, R. Calama, M. Pardos, F. Bravo, and G. Montero. Instituto Universitario de Investigación en Gestión Forestal Sostenible (Universidad de Valladolid-INIA), Valladolid. p. 254.
- Manso, R., Pardos, M., Keyes, C.R., and Calama, R. 2012c. Modelling the spatio-temporal pattern of primary dispersal in stone pine (*Pinus pinea* L.) stands in the Northern Plateau (Spain). *Ecol. Model.* **226**: 11–21. doi:10.1016/j.ecolmodel.2011.11.028.
- Manso, R., Fortin, M., Calama, R., and Pardos, M. 2013. Modelling seed germination in forest tree species through survival analysis. The *Pinus pinea* L. case study. *For. Ecol. Manage.* **289**: 9–21.
- Miina, J. 1998. Preparation of management models using simulation and optimization. In *Tree seedling production and management of plantation forests*. Edited by T. Pukkala, and K. Eerikäinen. University of Joensuu. Faculty of Forestry, Joensuu. pp. 165–180.
- Miina, J., and Heinonen, J. 2008. Stochastic simulation of forest regeneration establishment using a multilevel multivariate model. *For. Sci.* **54**(2): 206–219.
- Montero, G., Calama, R., and Ruiz Peinado, R. 2008. Selvicultura de *Pinus pinea* L. In *Compendio de Selvicultura de Especies*. Edited by G. Montero, R. Serrada, and J. Reque. INIA - Fundación Conde del Valle de Salazar, Madrid. pp. 431–470.
- Mutke, S., Gordo, J., and Gil, L. 2005. Variability of Mediterranean Stone pine cone production: Yield loss as response to climate change. *Agr. For. Meteorol.* **132**(3–4): 263–272. doi:10.1016/j.agrformet.2005.08.002.
- Nyland, R. (Editor). 2002. *Silviculture: Concepts and Applications*. 2nd ed. The McGraw-Hill Companies, New York.
- Ordóñez, J.L., Molowny-Horas, R., and Retana, J. 2006. A model of the recruitment of *Pinus nigra* from unburned edges after large wildfires. *Ecol. Model.* **197**(3–4): 405–417. doi:10.1016/j.ecolmodel.2006.03.027.
- Pardos, M., Ruiz del Castillo, J., Cañellas, I., and Montero, G. 2005. Ecophysiology of natural regeneration of forest stands in Spain. *Investigación Agraria: Sistemas y Recursos Forestales*, **14**(3): 434–445.
- Pasalodos-Tato, M., Pukkala, T., and Rojo Alboreca, A. 2010. Optimal management of *Pinus pinaster* in Galicia (Spain) under risk of fire. *Int. J. Wildl. Fire* **19**(7): 937–948. doi:10.1071/WF08150.
- Price, D.T., Zimmermann, N.E., van der Meer, P.J., Lexer, M.J., Leadley, P., Jorritsma, I.T.M., Schaber, J., Clark, D.F., Lasch, P., McNulty, S., Wu, J.G., and Smith, B. 2001. Regeneration in gap models: Priority issues for studying forest responses to climate change. *Clim. Change*, **51**(3–4): 475–508. doi:10.1023/A:1012579107129.
- Pukkala, T. 2003–2012. RODAL 5.0: Simulation-optimisation system for the management of any-aged stands in Spain.
- Pukkala, T., and Kolström, T. 1992. A stochastic spatial regeneration model for *Pinus sylvestris*. *Scan. J. For. Res.* **7**: 377–385. doi:10.1080/02827589209382730.
- Pukkala, T., and Miina, J. 1998. Tree-selection algorithms for optimizing thinning using a distance-dependent growth model. *Can. J. For. Res.* **28**(5): 693–702. doi:10.1139/x98-038.
- Pukkala, T., Miina, J., Kurttila, M., and Kolström, T. 1998. A spatial yield model for optimizing the thinning regime of mixed stands of *Pinus sylvestris* and *Picea abies*. *Scan. J. For. Res.* **13**(1): 31–42. doi:10.1080/02827589809382959.
- Ribbens, E., Silander, J.A., and Pacala, S.W. 1994. Seedling recruitment in forests - calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**(6): 1794–1806. doi:10.2307/1939638.
- Ripley, B.D. (Editor). 1987. *Stochastic Simulation*. Wiley, New York.
- Rockafellar, R.T., and Wets, R.J.B. 1987. Scenario and policy aggregation in optimization under uncertainty. IASA Working Paper WP-87-119. Laxenburg, Austria.
- Romero, F. 1886. El pino piñonero en la provincia de Valladolid. Imprenta y Librería Nacional y Extranjera de los Hijos de Rodríguez, Libreros de la Universidad y del Instituto, Valladolid.
- Salisbury, E.J. 1942. *The reproductive capacity of plants*. Bell, London.
- Smith, D., Larson, B., Kelty, J., and Ashton, P. 1996. *The practice of silviculture: applied forest ecology*. 9th ed. John Wiley & Sons, Inc., Hoboken.
- Tiscar-Oliver, P.A. 2007. Dinámica de regeneración de *Pinus nigra* subsp. *salzmannii* al sur de su área de distribución: etapas, procesos y factores implicados. *Investigación Agraria-Sistemas y Recursos Forestales*, **16**(2): 124–135.
- Valladares, F., Peñuelas, J., and de Luis, E. 2005. Impacts on terrestrial ecosystems. In *A preliminary assessment of the impacts in Spain due to the effects of climate change*. ECCE Project-Final report. Ministerio de Medio Ambiente, Madrid.
- von Gadow, K. 2000. Evaluating risk in forest planning models. *Silva Fenn.* **34**: 181–191.